GENETIC STUDIES OF SPRING AND WINTER HABIT
OF GROWTH IN BARLEY*

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Contents

I. INTRODUCTION

Physiology and genetics of ear emergence in cereals are the subjects of practical as well as scientific interest for agronomists and plant-breeders. Since the discovery of photoperiodic responses of crop plants and the vernalization of winter cereals, multitude of physiologic studies of this kind have been accumulated, and these gave us a deeper insight into these phenomena. Due attentions have also been paid for the genetics of earliness and the spring vs. winter habit of growth in cereals. Nevertheless, these informations are still insufficient for thorough understanding of the physiologic mechanisms of ear emergence and especially to explain these phenomena in term of genetics.

As is pointed out by Bell (1939), the date of ear emergence in the open

field is certainly more in the nature of physiological complexes which require resolution into their components. Again these characters are strongly affected by and intricately bound up with environments. It is often met with that different genotypes ear simultaneously under a certain set of growing condition, because the environment has failed to differentiate between them. On the other hand, some similar varieties behave quite differently under different growing condition.

In spite of these circumstances, we are obliged to judge the physiological and genetical peculiarities of varieties or their hybrid plants on the basis of such simple criteria as success or failure in earing, relative earliness of ear emergence or of flower-bud initiation, or some morphological features like number of leaves on main stem, etc. However, they are mere temporary aspects of development which have resulted from the complicated interactions of various internal and external factors during the whole period of the plant life. We should, therefore, be extremely careful in designing experiments and especially in interpreting the implication of the experimental data.

With a hope to associate the physiology of ear emergence in barley and wheat with their genetic behaviors, and thereby to contribute to the breeding of early varieties, genetic and physiologic studies have been conducted for these ten years. Efforts have especially been concentrated on the genetics of spring vs. winter habit of growth, which has been regarded as one of the important internal factors responsible for the ear emergence and the ecology of barley and wheat. In this series of experiments the following considerations have been given throughout :

(1) To gather in advance as much knowledge as possible about the physiologic characteristics of the materials to be crossed. Studies were made of the responses of the materials to different conditions of light and temperature, which may be helpful in understanding their inherent features, unless otherwise, undetectable.

(2) To grow hybrids and their parents under the long photoperiodic condition at moderately high temperature. This is because a spring variety has been known to ready for earing under such a condition, while a winter one is markedly retarded or prevented to ear. Moreover, exposure to low temperature, especially at its young stage or to short photoperiod, makes the difference between the spring and winter types obscure.

(3) To establish, as much as possible, the linkage relations of the physiological characters with some visible characters that are indifferent of the environment, which may make the results confident.

A series of experiments using as many as 90 or more crosses including barley varieties of different geographic origin have revealed that spring vs. winter habit of growth in barley is inherited in rather simple manner. At least three kinds of major genes, two dominant and one recessive, have been found to be each responsible for the initiation of spring habit, and in so far

as the materials used are concerned, the spring varieties may be classified into the following five groups, which are composed of various combination of these three genes; namely, a varietal group or a variety having (1) a single recessive spring gene, $shsh$, (2) a single dominant one, Sh_2Sh_2, (3) one dominant and one recessive genes, $shshSh_2Sh_2$, (4) all of three genes altogether, $shshSh_2Sh_2Sh_3Sh_3$, (5) two dominant spring genes, $Sh_2Sh_2Sh_3Sh_3$. Linkage of two out of three spring genes has also been established. Moreover, some efforts made for the elucidation of genetic mechanism that governs varietal difference in so-called grade of spring or winter habit of growth have given a result suggesting that a series of multiple alleles are responsible for it. In the following are presented these results.

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II. REVIEW OF LITERATURE

Inheritance of spring vs. winter habit of growth in barley has been worked out by considerable number of investigators. Majority of them, dealing with the hybrids between spring and winter varieties, observed that this character pair was inherited in rather simple manner. The spring habit was dominant over winter in general. Tschermak (1910), Takahashi, N. (1924) and Schiemann (1925) reported monofactorial difference between spring and winter habit. Lutkov (1937) also confirmed that a winter-habit mutant obtained by X-ray treatment behaved simple recessive to the original spring type. There are also some investigations which have showed the spring type being governed by two or more dominant genes. According to Smith (1951), Hehn (1948) found growth habit to be determined by two factor pairs in some crosses and by three in others. Two of the factors were completely dominant for spring habit, the third being incompletely dominant. Grevennikov (1935) in his experiments with a number of crosses, obtained different segregation ratios of spring and winter types, suggesting two, three and four gene pair differences existing between the parents. He concluded that there might be as many as five or six genes for this character.

In two crosses between spring varieties, Gaines (1917) found that the winter plants segregated in a ratio of 3 : 13 in the F_2 generation. The result was accounted by assuming one dominant winter gene, W, and one inhibitor, I. Li (1932) obtained a result that "Wechsel" or alternate type was inherited as simple recessive to winter type, and explained the result on a similar factorial basis, namely, Wi for winter and WI for alternate habit. Another example of dominance of winter habit over spring one was afforded

by Tokhtuyev (1940). He found also that six other crosses gave a preponde-
rance of the spring types.

There are also several observations where a number of winter-type plants
have segregated among the hybrid progenies between two spring varieties
(Neatby 1929, Vavilov and Kouznetsov 1923, and Kuckuck 1930, 1933).
Neatby (1926, 1929) informed that three different recessive genes had to exist
for the expression of winter habit, and these genes were cumulative in their
effects on earliness within the spring types. A similar explanation was given
by Kuckuck (1933) for the appearance of "winter"-type segregates which
showed the rosette habit of growth. He stated in this paper that lateness,
the winter habit and winter hardiness in barley are so closely correlated that
they cannot be regarded as distinct phenomena, although other authors used
the term "winter" as synonymous with "late". Huber (1932) explained his
genetic data on the assumption that spring varieties had three dominant
genes to hasten the earing and that the winter varieties had one dominant
gene. Hoffmann (1944) studied the F_2 segregation in the crosses of all
possible combinations between typical spring, typical winter and alternate
varieties. These experiments were conducted under a controlled condition of
light and temperature. He concluded from the results that spring-, winter-
and alternate-types were determined by an allelic series, S, s and s', respec-
tively.

Association of spring vs. winter habit or earliness with some qualitive
characters has been suggested by several workers, but most of them failed to
calculate the linkage value. Middleton and Chapman (1941) and Middleton
and McMillen (1944) suggested the existence of linkage between growth habit
and smooth-awnedness. Neatby (1929) found one of the genes for earliness
to be correlated with the genes for row number and density of ear and culm
length. Huber (1932) drew an inference that the gene for pubescence on
basal leaf-sheaths might be linked with one of the four genes for winter
habit because winter types usually had pubescent sheaths, while most of the
spring types were glabrous.

It is felt that there are considerable discrepancies between the results
above stated. Based on the genetic studies of ear emergence in barley, Bell
(1939) emphasized that the genetic analysis should be made in conjunction
with a physiological analysis and with a proper consideration and under-
standing of the effect of environment.

There are a number of genetic studies on the earliness in barley besides
those above mentioned. It is possibly supposed that some of them, especially
those which treated the hybrids sown in the spring might have dealt in
reality with the genes for spring vs. winter habit of growth, but no com-
ment is made here on them.

Meanwhile, it has been shown by Enomoto (1929) that there exists
among varieties of wheat and barley a rather continuous gradation regarding

spring and winter habit of growth from typical spring habit to extremely winter habit. This physiological difference was called by him as the difference in the grade of spring (or winter) habit of growth. He has shown that a variety with the highest grade of spring habit can head out even if it is sown so late as in late spring or in early summer, but the lower the grade of spring habit of a variety is, the earlier it must be sown in spring in order to head out normally. Ecological importance of the grade of spring habit for winter cereals sown in autumn has been emphasized by a number of Japanese plant breeders. For wheat Wada and Akihama (1934 a, b) and Kakizaki and Suzuki (1937), and for barley Yamamoto (1939), Yamamoto and Ohara (1943) and Takahashi (1943) attacked this problem. No information as to the genetic mechanism of this nature has ever been published, however.

III. MATERIALS AND METHODS

As the materials for this study 68 varieties of barley collected from different countries or regions of the world were used. Crossings were made between various spring or intermediate varieties and typical winter varieties. Sometimes triple crosses between these F_1 and an alternate strain, Mensury C and also some other type of triple crosses were raised. Number of crosses tested amounted to more than ninety. Before the genetic experiment, behaviors of most of these parental varieties were investigated under 24 and 12 hours' illumination in a glass house. Moreover, the critical or the latest sowing time in spring by which time the variety was possible to ear were investigated by sowing seeds of each variety at 10 days interval from late February to late June. Judged from relative earliness under continuous light and the critical sowing date of each variety, the "grade of spring habit of growth" or the grade for pre-chilling requirement for removing winter habit was determined. It is because, Enomoto (1929) has defined that a variety with the highest degree of spring habit is the latest as to the critical sowing date, and the lower the grade of spring habit of a variety is the earlier the critical sowing date becomes. And, the definition implies that there must be a correlation between the relative earliness under continuous illumination and the grade of spring growth habit. The grade of spring habit thus determined was designated by the figures I to VI, wherein I indicated the highly spring type, VI the highly winter type, and II~V the intergrades between these two extremities. In table 1 are shown the name of varieties used in this series of experiments, their origin, and some physiological and morphological characteristics. For readers' convenience genic constitution of the respective varieties ascertained by the experiments mentioned below is also listed in the table.

The F_2 and F_3 hybrids and their parental varieties, together with the F_1 hybrids in some cases, were usually sown in nursery bed or in wooden flats

Table 1. Characteristics of the materials.

Name of variety	Origin	Grade of spring habit	Growth habit genes involved	Sheath hairs	The other characteristics peculiar to the variety
Colsess I	U.S.A.	I	$shSh_2Sh_3$	none	hooded, s-rachilla
Clipford	Europe	I	$shSh_2$	none	two-rowed, s-rachilla
Golden Melon-K.*	Japan	I	$shSh_2$	none	two-rowed
Golden Melon-N.*	Japan	I	$shSh_2^{II}$	none	two-rowed
Hadostreng	Germany	I	$shSh_2Sh_3$	none	two-rowed
Harbin	Manchuria	I	$shSh_2$	none	
H. E. 3649	Pakistan	I	$shSh_2$	none	two-rowed, smooth awn, elongated outer glume
Ihsien	North China	I	$shSh_2^{II}$	none	
Indian barley	Formosa	I	Sh_2	hairy	
Iwate Mensury C*	Japan	I (alt.)	sh	none	s-rachilla
Kanjyu	North Korea	(I)**	$shSh_2$	none	
Kinai No. 5*	Japan	I	$shSh_2$	none	two-rowed
Kindoku	Germany	I	$shSh_2$	none	two-rowed
Lutai	North China	(I)	$shSh_2^{II}$	none	
Native No. 1	Formosa	I	Sh_2	hairy	
Natsudaikon-mugi	North Korea	I	$shSh_2$	none	
Nigrinudum	U.S.A.	I	$shSh_2Sh_3$	none	two-rowed, s-rachilla, naked
Olli	Finland	I	$shSh_2Sh_3$	none	s-rachilla
Russian No. 54	Russia	I	$shSh_2$	none	s-rachilla, smooth awn
Russian No. 74	Russia	I	$shSh_2$	none	
Saigen	North Korea	(I)	sh	none	
Saghalien	Saghalien	I	$shSh_2$	none	
Sapporo Rokkaku*	Japan	I	$shSh_2$	none	s-rachilla
Shokubi-mugi	North Korea	I	$shSh_2$	none	laterals awnless
Spring barley No. 2	North Korea	(I)	$shSh_2$	none	
Svanhals	Sweden	(I)	$shSh_2^{II}$	none	two-rowed
Taiki*	Japan	(I)	$shSh_2$	none	s-rachilla
Tainan No. 1	Formosa	I	Sh_2	none	
Tammi	Finland	I	$shSh_2Sh_3$	none	s-rachilla
Vaga	Sweden	I	$shSh_2Sh_3$	none	s-rachilla
Vankhuri	Finland	I	$shSh_2$	none	two-rowed
Vladivostok	Manchuria	I	$shSh_2$	none	
Winter Chevalier*	Japan	I (alt.)	sh	none	two-rowed, s-rachilla
A 222	India	(II)	Sh_2^{II}	none	laterals awnless, naked
Akashinriki	Japan	II	Sh_2^{II}	none	naked, uzu type
Baitori No. 11	Japan	II	Sh_2^{II}	hairy	uzu type
Brachytic	U.S.A.	II	$Sh_2^{II}Sh_3$	none	naked, brachytic type
Coast III	U.S.A.	II	Sh_2^{II}	hairy	
French No. 1	France	(II)	Sh_2^{II}	none	naked

Name of variety	Origin	Grade of spring habit	Growth habit genes involved	Sheath hairs	The other characteristics peculiar to the variety
H. agriocrithon C. I. 6496	Tibet	II	Sh_2^{II}	none	brittle rachis
Hōjō	South Korea	(II)	Sh_2^{II}	hairy	
Hozoroi	Japan	II	Sh_2^{II}	hairy	
Hsinwuko-1	Central China	II	Sh_2^{II}	none	naked
Kuromugi No. 148	Japan	II	Sh_2^{II}	hairy	uzu type
Liguleless	Japan	II	Sh_2^{IJ}	hairy	liguleless
Marumi No. 16	Japan	II	Sh_2^{II}	none	naked
Mushihchang-1	Central China	II	Sh_2^{II}	none	naked
Nudideficiens	U. S. A.	(II)	Sh_2^{II}	none	two-rowed, naked
Ohgara	Japan	II	Sh_2^{II}	hairy	
Paisha-Tayeh-5	Central China	II	Sh_2^{II}	none	naked
Sumiremochi	Japan	II	Sh_2^{II}	hairy	naked, glutinous, purple
Chinko No. 83	Japan	III	Sh_2^{III}	none	naked, uzu type
Shirochinko	Japan	III	Sh_2^{III}	none	naked, uzu type
Dairokkaku No. 1	Japan	IV	Sh_2^{IV}	hairy	
Hayakiso No. 2	Japan	IV	sh_2	hairy	laterals awnless
Kobinkatagi	Japan	IV	sh_2	none	naked, uzu type
Paisha-Tayeh-1	Central China	(IV)	sh_2	none	awnless
Riku-u No. 1	Japan	IV	sh_2	none	naked, short awn
Sakigake	Japan	IV	Sh_2^{IV}	hairy	s-rachilla, uzu type
Sekitori	Japan	IV	Sh_2^{IV}	hairy	uzu type
Sekitori Sai No. 1	Japan	IV	Sh_2^{IV}	hairy	uzu type
Wasehadaka (Kochi)	Japan	IV	sh_2	none	naked
Hanbozu	Japan	V	sh_2	hairy	laterals awnless
Iwate Mensury A₁*	Japan	V	sh_2	hairy	
Shimabara	Japan	V	Sh_2^{V}	hairy	naked, uzu type
Shinkyō	South Korea	(V)	sh_2	hairy	
Iwate Omugi No. 1	Japan	VI	Sh_2^{VI}	hairy	
Kesajiro*	Japan	VI	Sh_2^{VI}	hairy	

* Variety not indigenous to Japan.

** The grade of spring habit in parenthesis was determined only by the relative earliness under 24 hours of illumination in a glass house.

filled with fertile soil. For the economy of space, seeds were generally spaced 3.5 cm by 3.5 cm for growing in a flat (Fig. 1). According to our experience, a flat with a dimention of $60 \times 40 \times 15$ cm permitted to grow safely 170 plants without any impediment or technical difficulty. Wider space was, however, given to those which were expected to secure a large amount of seeds for the test of the following generations. Growing of the plants were made in general in a glass house, which was sometimes heated, if necessary, during

Fig. 1. Seedlings of some F_2 and F_3 hybrids grown in the wooden flats.

Fig. 2. Experimental materials under illumination in a glass house.

very cold winter months. In cases when it became too hot for barley plants, plants grown in the flats were moved to outdoor. As soon as the plumules began to appear, they were illuminated every day from before sunset to after sunrise with 100 watt incandescent lamps suspended about 60 to 100 cm above the plants (Fig. 2). The seeds were sown mainly in the fall, between late September and early November. Spring sowing, generally in late February or early March was practised for the tests of F_3 progenies obtained during the winter and of a part of the F_2 or the triple crosses.

Diurnal temperature at 10 o'clock, and the maximum and minimum temperature as well, in the glass house and outdoors were recorded throughout the periods of all these experiments. To show the typical variation of room temperature from autumn to spring, data of 1953/1954 was selected and shown in Fig. 3. As seen in Fig. 3, the temperature at 10 o'clock was
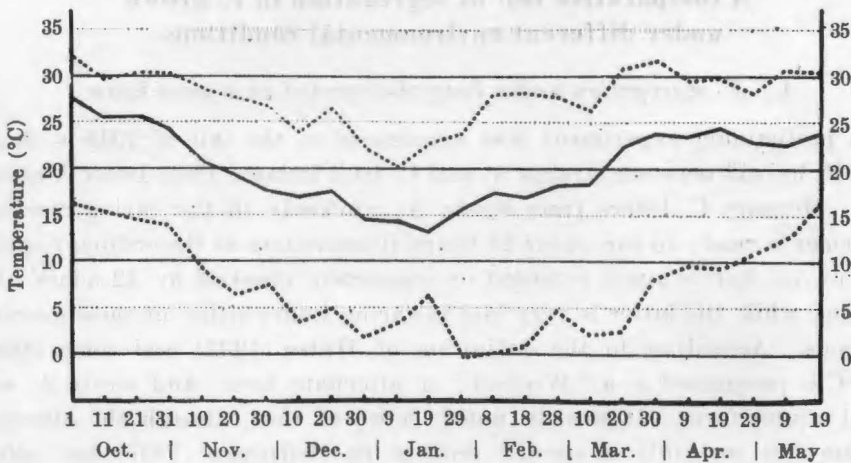

Fig. 3. Average room temperature of every ten days from October 1, 1953 to May 20, 1954 in the glass house. Full line indicates temperature at 10 o'clock in the morning and dotted lines the maximum and minimum ones.

maintained between 25° and 15°C, but the minimum temperature sometimes fell lower than 5°C at night in the winter months, which might have been effective to an extent in removing the winter habit and converting winter forms into spring ones. It is noted, however, that even in the coldest season barley could ear only with a slight retardation.

Although it is general that the date of ear emergence is used as the criterion of the relative earliness of the plants or varieties, the date when the uppermost leaf-blade (flag-leaf) on the main stem appeared from the leaf-sheath below was substituted for the date of earing in this series of experiments. This is because a part of the plants often by accident failed to show their ears out of the last leaf-sheaths and unabled us to record it. Plants were grown under good care as possible, and daily records were taken for the time of the flag-leaf emergence of each plant, together with the day

to ear in some cases. Total number of leaves on the main stem of each plant was read also at the stage of their full growth.

Interaction of the spring vs. winter habit with the following morphological character pairs were investigated in a number of F_2 and F_3 hybrid progenies involving them: hairy vs. non-hairy sheath ($Hshs$); non-six-row vs. six-row (Vv) and normal vs. elongated outer glume (Ee) in linkage group I; covered vs. naked grain (Nn) and lax vs. dense ear (Ll) in group III; long- vs. short-haired rachilla (Ss) and rough vs. smooth awn (Rr) in group V; and normal vs. uzu or semi-brachytic growth ($Uzuz$) in group VI.

IV. EXPERIMENTAL RESULTS

1. Monogenic recessive inheritance of the spring habit —
A comparative test of segregation in F_2 grown
under different environmental conditions

A. F_2 segregation under long photoperiod in a glass house

A preliminary experiment was commenced in the fall of 1946 with the use of F_2 hybrid between strains A_1 and C, both isolated from Iwate Mensury No. 2. Mensury C differs from strain A_1 markedly in the earing reaction; the former is ready to ear under 24 hours' illumination as the ordinary spring varieties do, but is much retarded or completely checked by 12 hours' illumination, while the latter is very late in earing under either of these growing conditions. According to the definition of Huber (1932) and some others, strain C is recognized as a "Wechsel" or alternate form, and strain A_1 as a typical winter form. It must be noted, however that, though the alternate type may be certainly a specific ecotype as Hoffmann (1937) and others pointed out, this is no more than a form of spring habit characterized by its higher sensibility than the ordinary spring type to a slightly shortened photoperiod.

About 150 F_2 seeds from the cross above mentioned and 20 seeds each of the parents were sown on October 2 in a glass house and grown under 24 hours' illumination throughout the whole period of the experiment.

In this experiment, which is denoted briefly as Exp. I-F_2, it was confirmed that the F_2 plants segregated into two distinct classes, the early and the late; 35 plants produced their flag-leaves during the period from 1 to 11 of November and completed to ear between 10 and 21 of the same month. The remaining 116 plants, however, continued vegetative growth until February 8 of the following year when one of them showed its flag-leaf, and most of them eared at last between early March and early April. The parental strains behaved quite the same as these two classes of the hybrid; strain C eared between 4 and 13 of November, while strain A_1, a winter type, remained uneared until March the next year.

This experiment indicated that the segregation of the early and the late types was undoubtedly clear-cut, when the hybrid was grown under continuous illumination in a glass house. As seen in the first line of table 2, the observed number of the early and the late plants fitted well to the calculated on the basis of a 1 : 3 ratio, with the dominance of the late type.

Table 2. Segregation of the early (spring habit) and the late (winter habit) in the F_2 generation of a cross, strain $A_1 \times C$ of Iwate Mensury No. 2.

Experiments	Early (Spring)	Late (Winter)	Total	χ^2*	P
I-F_2	35	116	151	0.2711	0.7—0.5
II-F_2	55	220	275	3.6668	0.1—0.05
III-F_2	80	222	302	0.3576	0.7—0.5
IV-F_2	57	229	286	3.9214	<0.05

* Compared with the calculated 1 : 3 ratio.
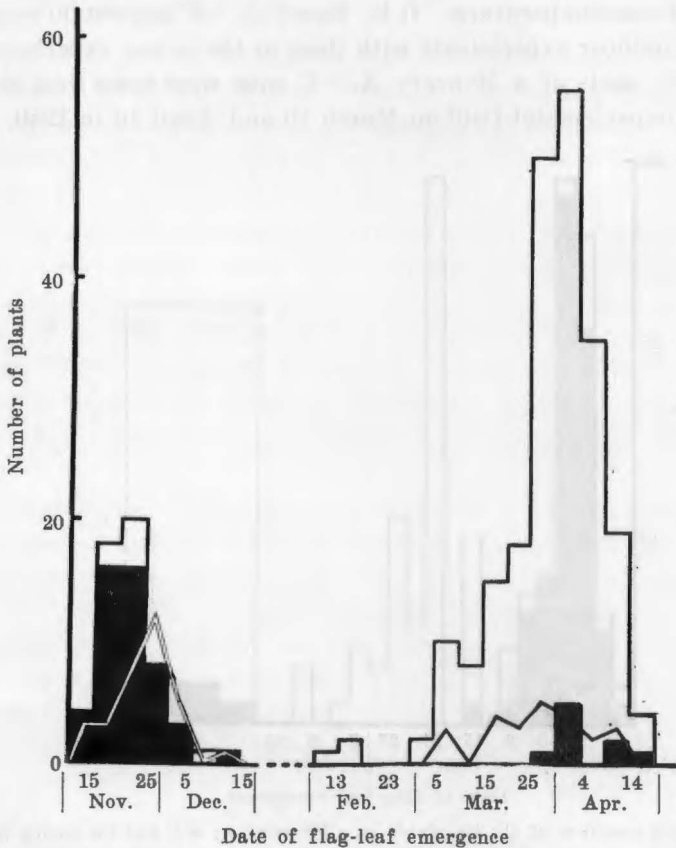

Date of flag-leaf emergence

Fig. 4. Date of flag-leaf emergence of the F_2 plants from a cross between Mensury A_1 and C, and of the parental strains, grown under continuous illumination in a glass house (Exp. II-F_2). F_2 plants with and without sheath-hairs are shown by white and blacken histogram, and C and A_1 strains by white and black lines, respectively.

A quite similar experiment was repeated again in 1949/50 with some more F_2 plants from the same cross (Exp. II-F_2). The seeds were sown on October 10. In Fig. 4 is shown the date of flag-leaf emergence of the F_2 plants and those of parental strains, A_1 and C. The segregation of the early and the late types is given in the second line of table 2. It is apparent from these that the result of Exp. II-F_2 is exactly the same as that of Exp. I-F_2. In this experiment, number of leaves on the main stem of each plant was investigated also, which result revealed that the early plants, and the strain C as well, had 6 to 8 leaves, while the late ones and the strain A_1 had 18 to 21 leaves each. This also indicates clearly the physiologic difference between the early and the late being remarkable.

B.   Behavior of F_2 plants when sown in the spring in the open field

Almost all of the results hitherto reported by many other workers are those which have been obtained from the outdoor experiments without any control of light and temperature. It is, therefore, of interest to compare the results of such outdoor experiments with those of the indoor experiments. For this purpose, F_2 seeds of a Mensury $A_1 \times C$ cross were sown 8 cm apart each in rows of the experimental field on March 10 and April 10 in 1950.

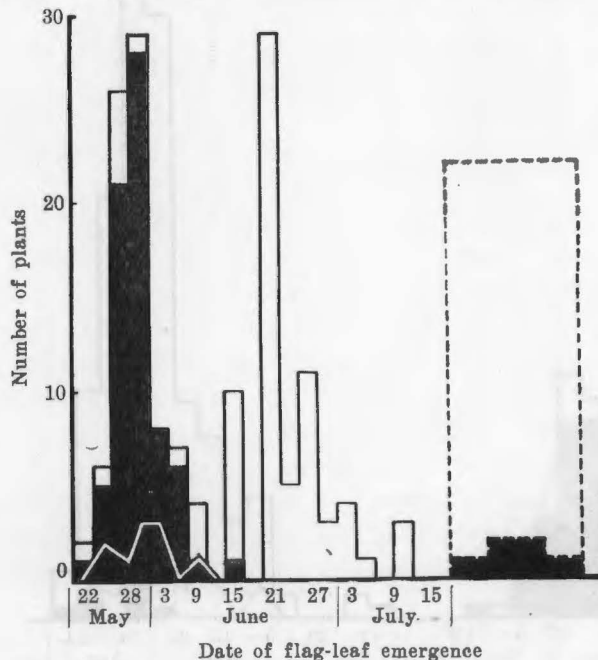Fig. 5.   Earing reaction of the F_2 plants in a Mensury $A_1 \times C$ and the spring parent, Mensury C, which were sown outdoors on March 10 (Exp. III) F_2 plants with and without sheath-hairs are represented by white and black histogram.   Number of F_2 plants that have failed to ear is shown by histogram surrounded by broken line.   A white line shows the date of flag-leaf emergence of Mensury C.

Fig. 5 indicates the date of flag-leaf emergence of the F_2 sown on March 10 (Exp. III-F_2), which is obviously different from Fig. 4 showing the result of the indoor experiment (Exp. II-F_2). In this outdoor experiment were found hybrid plants that succeeded to ear and those failed to ear in almost equal number. Consequently, it is difficult to explain the result on the basis of monogenic segregation, if the classification of spring and winter types by such a striking difference as success or failure of ear emergence, which is the commonest criterion used for this purpose. But, as seen in Fig. 5, the eared plants may also safely be subdivided into two classes, the early and the late, at 11 of June where just corresponds to the botton of the bimodal frequency curve as to the date of ear emergence. It is noted also that strain C finished earing before that day, while strain A_1 remained at the vegetative stage, with one exception. Judged from this result, together with those of F_3 and the linkage test shown later, it seemed to be adequate to classify the plants that eared before June 11 as the spring type and the remainders, including those failed to ear as the winter type. The result was found to fit well to a 1:3 segregation ratio, which was shown in the third column of table 2.

The result of the Exp. IV-F_2, the seeds of which were sown on April 10, differed again considerably from those of II-F_2 and III-F_2; about one fifth of the F_2 eared between June 15 and July 22, and strain C also eared in late June. The remaining F_2 and strain A_1 died without ear formation, however. As shown in the last column of table 2, the segregation of eared and uneared was difficult to fit the expected ratio on account of a slight shortage of eared ones.

C.   Results of F_3 test

The results of above F_2 tests were further examined by F_3 tests. Progenies derived from a part of F_2 populations of Exp. I, II and III were grown under continuous illumination in a glass house. Twenty to 30 plants of each progeny were raised. It was known from these tests that all the early F_2 plants, including 17 for Exp. I and 55 for Exp. II, bred true without exception. On the other hand, 46 late plants from I-F_2 and 96 from II-F_2 proved to include two different genotypes: the homozygously late and the heterozygous, each of the latter strains segregating in an almost 1 early and 3 late ratio. Actual number of these different genotypes involved in the late classes from Exp. I and II are shown in table 3. The results afforded a good fit to a 1:2 ratio just as was expected from the F_2 data above mentioned.

Table 3.   Number of various genotypes of the late plants involved in the F_2 population of a $A_1 \times C$ cross as determined by F_3 progeny test.

Experiments	F_2 Genotypes		Total	χ^2*	P
	Homo. late	Hetero.			
I-F_3	17	29	46	0.2718	0.7—0.5
II-F_3	28	68	96	0.7500	0.5—0.3

* Compared with the expected 1:2 ratio.

The data of Exp. III-F_3 will be presented and discussed later.

Above results clearly show that the early is inherited as singly recessive to the late under 24 hours' illumination in a glass house, although the spring sowing in the open field results in more or less modified segregation ratios. As stated before, a spring-type plant is known to ear early under continuous illumination, while a winter-type plant is much retarded. Therefore, we may be safe to conclude that those plants eared early under long photoperiod in a glass house can be regarded as having spring habit and those much retarded as winter one. Herewith, a gene symbol *sh* is given for the spring habit involved in the strain C of Mensury No. 2. A symbol with a subscription, namely, sh_m, will also be used in the following, if necessary for distinguishing it from other similar ones.

D. Linkage relation of the gene sh for the spring habit

Since strain A_1 of Mensury No. 2 is characterized by long-haired rachilla and hairy sheath, and strain C by short-haired rachilla and non-hairy sheath, the interactions of the growth habit with these two morphological character pairs were studied. As has already been known, the gene for the rachilla hairs, *Ss*, is located in linkage group V, and that for the sheath hair is governed by a single gene, *Hshs*, the linkage group of which is still unknown.

Relation to rachilla hairs: Interrelation between spring vs. winter habit and rachilla hair character pairs was investigated in F_2 of Exp. II as well as the early segregants of III-F_2. The results are given in table 4. It is apparent from this that these character pairs are inherited independently.

Table 4. Independent inheritance of *Shsh* for spring vs. winter habit and *Ss* for long- vs. short-haired rachilla.

Experiments	Long-haired		Short-haired		Total	χ^2	P
	Winter	Spring	Winter	Spring			
II-F_2	160	43	52	12	267	2.8545	0.5—0.4
III-F_2	—	60	—	22	82	0.1464	0.8—0.7

Relation to hairs on leaf-sheaths: A close study was made on the interaction between growth habit and sheath hairs. Figure 4, wherein the date of flag-leaf emergence and presence or absence of sheath hairs of each plant in Exp. II-F_2 are shown, indicates existence of a close linkage in coupling phase between these character pairs being apparent, because of the excess of parental types. Number of different types involved in the populations of II-F_2 and III-F_2 as well as in the doubly heterozygous strains of II-F_3 are shown in table 5. The recombination percentages calculated after Immer's product method were 6.5% in II-F_2 and 6.3% in II-F_3 heterozygotes. The observed data afforded a good fit to the calculated segregation for the respective recombination values.

Table 5. Interrelation of *Shsh* for winter vs. spring habit and *Hshs* for hairy vs. non-hairy leaf-sheath in II-F$_2$, III-F$_2$, IV-F$_2$ and the doubly heterozygous strains derived from II-F$_2$ in a Mensury A$_1$ × C cross.

Items		Winter type		Spring type		Total	χ^2	P
		Hairy	Hairless	Hairy	Hairless			
II-F$_2$	Obsvd. number	211	9	7	48	275		
	Calc. as 9:3:3:1	154.69	51.56	51.56	17.19	275	149.36	small
	Calc. as 6.5% of recomb.	197.60	8.65	8.65	60.10	275	3.67	0.5—0.3
II-F$_3$	Obsvd. number	965	40	41	286	1332		
	Calc. as 9:3:3:1	749.25	249.75	249.75	83.25	1332	906.59	small
	Calc. as 6.3% of recomb.	958.36	40.64	40.64	292.36	1332	0.20	0.98—0.95
III-F$_2$	Obsvd. number	212	10	9	71	302		
	Calc. as 9:3:3:1	169.87	56.63	56.63	18.87	302	232.84	small
	Calc. as 6.3% of recomb.	217.3	9.2	9.2	66.3	302	0.54	0.95—0.90
IV-F$_2$	Obsvd. number	192	41	13	44	290		
	Corrected for *Hshs* segregation	203.7	35.0	13.8	37.5	290		
	Calc. as 6.4% of recomb.	208.52	8.98	8.98	63.52	290		

The linkage relation was further confirmed by the F$_3$ test. The observed number of different genotypes involved in the doubly dominant class of II-F$_2$ was as shown in table 6. The data fitted well to the calculated number for 8.1% between *sh* and *hs*, but not for a 1:2:2:4 ratio for independent assortment.

Table 6. Number of different genotypes in the doubly dominant class of II-F$_2$ (Mensury A$_1$ × C) as determined by F$_3$ progeny test.

Items	Number of F$_2$ genotypes				Total	χ^2	P
	AABB	AABb	AaBB	AaBb*			
Obsvd. number	26	2	8	60	96		
Calc. as 1:2:2:4	10.67	21.33	21.33	42.67	96	54.91	small
Calc. as 8.1% of recomb.	28.503	5.024	5.024	57.448	96	3.92	0.3—0.2

* Aa stands for *Shsh* and Bb for *Hshs*.

Linkage of *sh* and *hs* thus established seems to be useful for the interpretation of the F$_2$ data of the outdoor experiments. In Fig. 5 had been shown the interrelation of earing date and the condition of sheath hairs in the population of Exp. III which were sown outdoors on March 10. It is apparent in this that majority of the plants eared before June 11 are of non-hairy sheath, while those eared thereafter and also those failed to ear are of hairy sheaths. This suggests that the former group is of spring habit and the latter of winter habit. A test made under continuous illumination with the use of some of the F$_3$ progenies proved this supposition being true. The F$_2$ data arranged on this basis was presented in table 5, which fitted well to the calculated for 6.3% of recombination between *sh* and *hs*. It is perhaps right to conceive that when sown on March 10, 68 out of 222 individuals were, in spite of their winter habit, possible to ear.

As pointed out previously, there was a slight shortage of eared plants in the Exp. IV-F_2, on the contrary. The observed number of the four pheno-types distinguished by the earing reaction and sheath hair was compared with the calculated on the basis of 6.4% of recombination between both character pairs (last column of table 5). The result reaveals that the non-hairy plants are included about 30 more than the expected in the winter type, while it is about 20 less in the spring type. It is therefore possible to infer from this that 20 or more plants of intrinsically spring habit might have failed to ear owing to having been sown too late in the spring.

Here, it seems to be adequate to combine various data to secure a recom-bination value between $Shsh$ and $Hshs$ which best satisfies all of them. The weighted average value of recombination was calculated after the method suggested by Robertson *et al.* (1944). It was 6.4 $\pm$ 0.56%.

E. *Behaviors of the crosses with various winter varieties*

It is also interesting to know the genetic constitution of various winter varieties. To approach in part to this problem, a spring variety, Mensury C, was crossed to a number of winter varieties differing in the grade of winter habit of growth, and the behaviors of the F_2's of these crosses were studied under 24 hours' illumination in a glass house.

The results are summarized in table 7. It is apparent in the table that all

**Table 7. Interrelation of spring vs. winter habit of growth with hairy vs.
non-hairy character in several crosses between Mensury C and winter
varieties differing in the grade of winter habit of growth.**

Mensury C crossed with	Winter type			Spring type			Grand total	χ^2	P
	Hairy	Hairless	(Total)	Hairy	Hairless	(Total)			
Sekitori (IV)	177	61	(238)	7	71	(80)	318	0.000*	large
Sakigake (IV)	147	33	(180)	6	46	(52)	232	0.827*	0.5—0.3
Dairokkaku(IV)	210	38	(243)	10	66	(76)	324	0.412*	0.7—0.5
Kesajiro (VI)	192	66	(258)	12	58	(70)	328	2.342*	0.2—0.1
Shimabara (V)	229	8	(237)	13	71	(84)	237		
Calc. No.	230.81	9.94		9.94	70.31		237	1.342**	0.8—0.7
Iwate Omugi 1 (VI)	225	15	(240)	6	80	(86)	326		
Calc. No.	234.4	10.1		10.1	71.4		326	5.454**	0.2—0.1

* Compared with the calculated on a 3 winter : 1 spring ratio.

** Compared with the calculated on the basis of *hs* and *sh* linked with 6.4% of recombination.

the crosses segregated in a 1 spring : 3 winter ratio.

The materials were arranged in advance so as to test the linkage of the spring gene with that for the sheath-hair character pair, but unfortunately the segregation of the latter character pair was not occurred regularly, and resulted in the shortage of plants with hairy sheaths, which was perhaps due to the incomplete penetrance of *Hs* gene. Nevertheless, a definite indication of linkage existing between two character pairs was observed in all of the

crosses. Namely, most of the spring-type plants in these F_2 were hairless in their sheaths, while the plants with hairy sheaths were mostly involved in the winter type of each cross, on the other. It may therefore be safe to conclude that these winter varieties, though different considerably as to the grade of winter habit, possess at least one pair of winter gene allelic to the spring gene, sh_m, in Mensury C. The results also suggest us that any one of these winter varieties seems to have no genetic element for expressing spring habit of growth.

F. Genetic analyses of two other crosses with the spring varieties, Winter Chevalier and Saigen

Since Winter Chevalier, a typical alternate-habit form from Hokkaido, Japan and Saigen, a native variety of North Korea, have been known to be the same in genic constitution for growth habit as Mensury C, the results of studies of the crosses involving them are stated herein. For the sake of brevity, in table 8 are shown only interrelation of spring vs. winter habit and

Table 8. Interrelation of growth habit and sheath-hair character pairs in the crosses involving spring varieties, Winter Chevalier and Saigen.

Items	Winter type		Spring type		Total	χ^2	P
	Hairy	Hairless	Hairy	Hairless			
F_2 of Winter Chevalier × Shimabara							
Obsvd. number	143	7	8	43	201		
Calc. as $9:3:3:1$ ratio	113.05	37.69	37.69	12.57	201	129.98	small
Calc. 6.4% of recombination	144.52	6.23	6.23	44.02	201	0.63	0.9—0.8
F_1 (Saigen × Shinkyo) × Mensury C							
Obsvd. number	21	2	0	17	40		
Calc. as $1:1:1:1$ ratio	10	10	10	10	40	33.40	small
$sh_m = sh_s$, linked with hs 6.4% of recombination	18.69	1.28	1.28	18.69	40	2.12	0.7—0.5

hairy vs. non-hairy sheath in a simple cross between Winter Chevalier and Shimabara, and also in a triple cross, F_1 (Saigen × Shinkyo) × Mensury C, wherein Shimabara and Shinkyo are both typical winter varieties.

It is obvious from the table that the former cross has segregated the spring-and winter-type plants in a $1:3$ ratio, and at the same time that the gene for growth habit is linked with that for sheath hairs with approximately 6.4% of recombination. This suggests that Winter Chevalier may be the same in genic constitution for growth habit as Mensury C.

The latter cross, on the other hand, has been planned to know the allelic relation of sh_m in Mensury C with a spring gene, if any, involved in Saigen directly from the segregation. The genetic basis of this study is that, if $sh_m = sh_s$, it is expected that the spring type and the winter one will segregate in a $1:1$ ratio, while no spring plant will be found if $sh_m \neq sh_s$. Furthermore, in the former case will also be verified a close linkage between

aforementioned two character pairs. As seen in table 8, the actual data obtained is certainly such that Saigen has a recessive spring gene, *shsh*, which is perhaps identical with $sh_m sh_m$ involved in Mensury C.

The results stated above may be summarized as follows :

1. A typical alternate-habit strain isolated from Iwate Mensury No. 2 has a single recessive gene pair, *shsh*, for spring habit of growth.

2. Various winter varieties, though different as to the grade of winter habit, possess each at least one pair of winter gene *ShSh*, and they seem to have no genetic element for expressing spring growth habit.

3. The gene pair, *Shsh*, for winter vs. spring habit is linked with *Hshs* for sheath-hair character pair with 6.4% of recombination.

4. The experiments made under 24 hours' illumination in a glass house seem to give always consistent and reliable data as regards the inheritance of spring vs. winter habit of growth, whereas those performed outdoors in spring may sometimes lead us to erroneous conclusions.

5. Two spring varieties, Winter Chevalier (Hokkaido) and Saigen (North Korea) has each the same genic constitution as to growth habit as Mensury C.

2. A varietal group with one dominant and one recessive gene pairs for spring habit of growth

A. *Genic analyses of two spring varieties, Natsudaikon-mugi and Kinai No. 5*

Among various spring varieties which were subjected to our genetic analyses, 21 varieties were recognized to involve each one dominant and one recessive spring gene pairs altogether. The genetic behaviors of the hybrids with these spring varieties are described in this section. For convenience, results of the crosses with two spring varieties, Natsudaikon-mugi from North Korea and Kinai No. 5 of hybrid origin will be explained at first in detail, though the others have shown no particular difference in their genetic behaviors.

Both Natsudaikon-mugi and Kinai No. 5 are of the highest degree in the spring habit (grade I). They ear equally very early under 24 hours of illumination, although differential behavior is recognized under more or less shortened photoperiod.

F_2 seeds of a cross between Shimabara, a winter variety of grade V, and Natsudaikon-mugi were sown on October 1, 1950 in the nursery bed in a glass house and reared under continuous illumination. In Fig. 6 are graphically shown the date of flag-leaf emergence of F_2 plants of this cross and their parents. It is perceived in this figure that the early and the late types in F_2 are easily distinguished, because the earing periods of both types are clearly separated by the intervenient 100 or more days of uneared period. Moreover,

coincidence in earing period is recognized between Natsudaikon-mugi and the early-F_2 types in one hand, and between Shimabara and the late ones on the other. They showed also a marked difference in the number of leaves on the main stems; the early-F_2 plants and Natsudaikon-mugi have only 7 to 9 leaves, while the late plants and Shimabara have as much as 18 to 22 leaves. It seems, therefore, as true, that there is a possible genic difference between the early and the late types in F_2 with respect to the spring vs. winter habit of growth. Similar results were obtained in the F_2 of two other crosses, namely, Hanbōzu × Natsudaikon-mugi and Hayakiso No. 2 × Kinai No. 5.
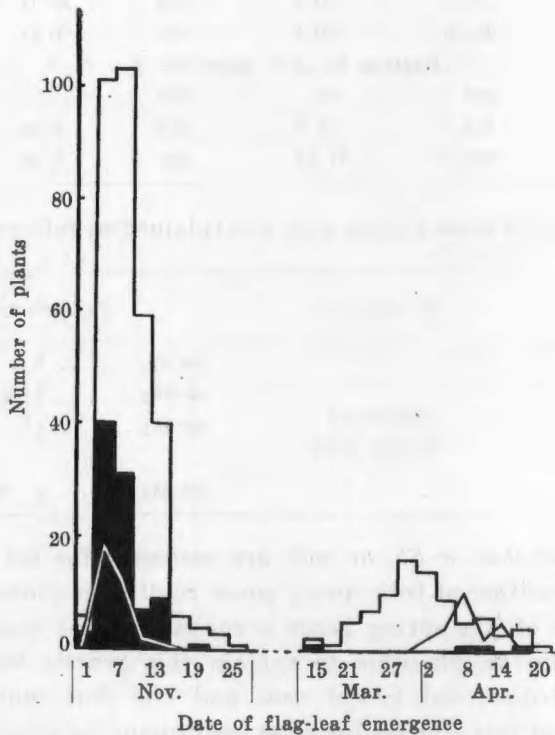

Fig. 6. Frequency distribution as regards the date of flag-leaf emergence in F_2 of a Shimabara × Natsudaikon-mugi and of their parents, grown under continuous illumination. Histogram in black shows the F_2 plants without sheath hair, and that in white the F_2 plants with hairy sheaths. White and black lines show the spring and winter parents, respectively.

Table 9 shows the observed number of the early and the late plants in these three crosses, along with two kinds of calculated numbers each to be compared with them. It is evident from the table that these observed numbers fit well to the calculated for the segregation of the early and the late types in a 13 : 3 ratio, but not to a 3 : 1 ratio. It is certain, therefore, that each of these crosses involves two pairs of genes responsible for spring vs. winter habit. Assumed now the two genes for spring habit sh and Sh_2, respectively,

Table 9. Segregation of early (spring) and late (winter) types in F_2 of the crosses of Natsudaikon-mugi and Kinai No. 5 with some winter varieties.

Items	Early (Spring)	Late (Winter)	Total	χ^2	P
Shimabara × *Natsudaikon-mugi*					
Observed No.	323	84	407		
Calc. as 3:1	305.25	101.75	407	4.128	0.05—0.02
Calc. as 13:3	330.69	76.31	407	0.715	0.5 —0.4
Hanbōzu × *Natsudaikon-mugi*					
Observed No.	267	55	322		
Calc. as 3:1	241.5	80.5	322	10.77	<0.01
Calc. as 13:3	261.6	60.4	322	0.41	0.7—0.5
Hayakiso No. 2 × *Kinai No. 5*					
Observed No.	289	69	358		
Calc. as 3:1	268.5	89.5	358	6.26	0.02—0.01
Calc. as 13:3	290.87	67.13	358	0.05	0.9 —0.8

the genetic behavior of these crosses may be explained as follows:

Genotypes of parents	F_1 genotype	F_2 phenotypes	
Spring variety *shshSh₂Sh₂*		$Sh\ Sh_2 \ldots\ldots9$	
	ShshSh₂sh₂ (Spring type)	$sh\ Sh_2 \ldots\ldots3$	Spring type
		$sh\ sh_2 \ldots\ldots1$	
Winter variety *ShShsh₂sh₂*		$Sh\ sh_2 \ldots\ldots3$	Winter type

Namely, either *shsh* or Sh_2 or both are necessary for the expression of spring habit, and neither of both spring genes results in winter habit. This implies that each of the spring genes is epistatic to the non-allelic winter genes. It may also be plausible to explain this genetic behavior on the assumption of one dominant winter gene and one dominant inhibitor of the winter gene, but this appears for us as inadequate for some reasons.

For the confirmation of the F_2 results, about one third of the spring plants and almost all of the winter ones from the F_2 of a Shimabara × Natsudaikon-mugi cross were carried through the F_3 generation. For the cross with Kinai No. 5, 44 F_3 strains derived from the winter forms in F_2 were also raised. The detailed results will be presented later, and suffice it to mention here that about two thirds of the winter plants in F_2 have proved to be heterozygous for spring vs. winter habit, which clearly indicates that a recessive spring gene has been involved in these crosses.

B. Linkage of the recessive spring gene with the gene for hairless sheath character

It was our deep interest to determine whether the recessive spring genes

involved in these two spring varieties were also allelic to or identical with that found in Mensury C. Since both of the spring parents under consideration are non-hairy in leaf-sheaths, while the winter parents mated with the former are both hairy, it was convenient for us to pursue further these relations.

In Fig. 6 was already shown the interrelation of hairy vs. hairless sheath character pair and the date of flag-leaf emergence of the F_2 plants in a Shimabara × Natsudaikon-mugi cross. It is apparent in that figure that majority of the non-hairy plants (shown by histogram in black) are of the spring habit, while the winter plants have almost exclusively hairy sheaths. Such an excess of parental types indicates the existence of a close linkage between the gene pair $Hshs$ for sheath hair character and either of the growth habit gene pairs, $Shsh$ or Sh_2sh_2. As seen in table 10 a and b, the observed numbers do not fit to the calculated for independent assortment of both character pairs. To our regret, however, it is hard to determine from these

Table 10. Linkage of either of the spring gene pairs and $Hshs$ for sheath-hair character pair in (a) Shimabara × Natsudaikon-mugi, (b) Hayakiso No. 2 × Kinai No. 5, and (c) F_1 (Hayakiso × Kinai) × Kobinkatagi.

Items		Spring type		Winter type		Total	χ^2	P
		Hairy	Hairless	Hairy	Hairless			
	Observed number	232	91	80	4	407		
(a)	Calc. as independent.	248.00	82.67	57.23	19.08	407	22.85	small
	Calc. as sh—hs 8% or Sh_2—hs 22%	232.85	97.85	72.40	3.90	407	1.28	0.8—0.7
	Observed number	187	102	68	1	358		
(b)	Calc. as independent.	218.15	72.72	50.35	16.78	358	49.91	small
	Calc. as sh—hs 6.4% or Sh_2—hs 20%	204.15	86.73	64.35	2.77	358	4.18	0.2—0.1
	Observed number	20	32	31	21	104		
(c)	Calc. Sh_2—hs 20%	9.6	41.6	41.6	9.6	104	24.58	small
	Calc. Sh_2—hs independ.	26	26	26	26	104	4.69	0.2—0.1

F_2 data which of the spring genes is actually linked with the sheath-hair gene. Because, two kinds of recombination values are possibly calculated, which are ca. 22% between Sh_2 and hs in repulsion phase and 8.0% between sh and hs in coupling phase, and the calculated numbers on both bases are in a good agreement with the observed ones.

The difficulty was, however, easily conquered by the following triple hybrid test. Since F_1 hybrid between Hayakiso No. 2 and Kinai No. 5 was already known to be heterozygous for the three genes, sh, Sh_2 and hs, the F_1 plants were again crossed with Kobinkatagi, a winter variety with glabrous sheath. It was naturally expected in this hybrid segregation that, if Sh_2 and hs was linked with 20% of recombination, the original parental types would be about four times more than the recombinate types, while equal numbers of

parental and recombinate types would appear in the case of no linkage be-
tween the two pairs of genes under consideration. The actual data shown in
table 10c has proved the latter being true. Therefore, it is possible to
conceive that the spring gene linked with $Hshs$ for sheath-hair character is
not Sh_2, but the recessive gene, sh.

The tests with the F_3 strains from both crosses have made the matter
more clearly. In tables 11 and 12 are indicated the interrelation between the

**Table 11. Number of different genotypes in F_2 individuals of spring
habit derived from a Shimabara × Natsudaikon-mugi cross as
determined by F_3 progeny test.**

Items	Spring homo.			Heterozygous			Total	χ^2	P
	$HsHs$	$Hsks$	$hshs$	$HsHs$	$Hsks$	$hsks$			
Observed number	11	16	26	20	37	1	111		
Calc. Sh_2—hs (20%)	9.78	25.86	24.12	8.80	33.64	8.80	111	25.56	small
Calc. sh—hs (8%)	8.70	20.85	30.22	16.96	31.65	2.62	111	4.78	0.5—0.4

**Table 12. Interrelation between growth habit and sheath-hair characters
in the F_3 strains derived from the F_2 winter types in two crosses,
Shimabara × Natsudaikon-mugi and Hayakiso No. 2 × Kinai No. 5.**

Items	No. of F_3 strains with genotypes of						Total	χ^2	P
	Winter homo.			Heterozygous					
	$HsHs$	$Hsks$	$hshs$	$HsHs$	$Hshs$	$hshs$			
	Shimabara × Natsudaikon-mugi								
Obsvd. number	26	4	0	3	44	3	80		
Calc. Sh_2—hs (22%)	16.23	9.15	1.29	32.44	18.31	2.58	80	72.30	small
Calc. sh—hs (8%)	22.57	3.93	1.07	3.93	45.47	3.93	80	1.18	0.95—0.90
	Hayakiso No. 2 × kinai No. 5								
Obsvd. number	11	1	—*	3	29	—*	44		
Calc. Sh_2—hs (20%)	9.78	4.89		19.55	9.78		44	55.03	small
Calc. sh—hs (8%)	13.44	1.84		1.84	26.88		44	1.72	0.7—0.5

* Non-hairy winter plants were excluded.

growth habit and the sheath-hair character pairs in F_3 of both crosses. It is
apparent in these tables that the gene hs for non-hairy sheath is linked with
a recessive spring gene sh_n (in Natsudaikon-mugi) and also sh_k (in Kinai No.
5) with about 8% of recombination, but is certainly independent of the domi-
nant spring genes involved in both spring parents.

It is remembered in this connection that the recessive spring gene sh_m in
the strain C of Mensury No. 2 is linked with hs with the recombination value
of 6.4%. Such a close approximation of the value with those found here leads
us to a supposition that all of these recessive spring genes, sh_m, sh_k and sh_n
may be identical or at least allelic. The relation was studied by the triple
cross method as stated before. Since the genotypic constitution of F_1 hybrid
between Hayakiso No. 2 and Kinai No. 5 wask nown to be $ShshSh_2sh_2Hshs$,

and that of Mensury C $shshsh_2sh_2hshs$, the hybrid between the F_1 and Mensury C will be expected to segregate the spring and winter types in a $3:1$ ratio if the recessive spring gene, sh_k, in Kinai No. 5 is identical with sh_m in Mensury C, but, if not so and the genes are on different loci, the segregation will occur in a 1 spring : 1 winter ratio. At the same time, it is expected that majority of the hairless-sheath plants are chiefly of spring type owing to the close linkage of sh_m with hs in the former case, while in the latter case the sheath-hair character is inherited independently of the growth habit.

Therofore, crossing was made between F_1 (Hayakiso No. 2 × Kinai No. 5) and Mensury C, and the hybrid plants were raised under continuous illumination in a glass house. Segregation of spring vs. winter habit and hairy vs. non-hairy sheath character pairs in this cross was as shown in table 13. It is apparent from the table that the observed number fits well to

Table 13. A test for allelic relation of recessive genes, sh_k and sh_m, in
a triple cross, F_1 (Hayakiso No. 2 × Kinai No. 5) × Mensury C.

Items	Spring types		Winter types		Total	χ^2	P
	Hairy	Hairless	Hairy	Hairless			
Observed number	26	41	23	2	92		
Calc. as $sh_k \neq sh_m$	23	23	23	23	92	25.53	small
Calc. as $sh_k = sh_m$	21.53	47.47	21.53	1.47	92	2.04	0.7—0.5

the calculated on the basis of $sh_k = sh_m$ which is linked with hs with 6.4% of recombination. Therefore, the recessive spring gene involved in Kinai No. 5 is regarded as identical or at least allelic to that in Mensury C, or simply, $sh_m = sh_k$.

C. Genic analyses of nineteen other spring varieties

The crosses dealt with here include the following 19 spring varieties of different geographic origin.
Europe ; Clipford, Vankhuri, Svanhals and Kindoku
Russia : Russian No. 54 and No. 74, and Saghalien
India : H. E. 3649 (Lyallpur) collected by Freisleben
Manchuria and North China : Harbin, Vladivostok, Lutai and Ihsien
North Korea ; Shokubi-mugi, Kanjyu and Spring barley No. 2
Japan : Sapporo Rokkaku (=Erhardt Frederickson), Taiki, and two types
       of Golden Melon from Nagasaki and Kagoshima Prefecture.

As shown in table 1, all these spring varieties are of the first grade in spring habit, and characterized by glabrous leaf-sheath. Crossings were made between these spring varieties and anyone of such winter varieties as Shimabara (S), Hayakiso No. 2 (H), Dairokkaku (D), Paisha-Tayeh No. 1 or tonsum (T), or Mensury A_1 (MA). Out of these 22 F_1 hybrids thus obtained, 17 were crossed again with Mensury C (MC). The seeds of these F_2 and/or

triple crosses, along with their parents were sown in the fall or spring. The
methods of growing, recording and cares of the hybrid plants were almost
alike to those stated before.

All cross combinations had been determined so as to be included in each
cross at least two character pairs, spring vs. winter habit and hairy vs. non-
hairy sheath. Segregation of these character pairs in the F_2 generation of

**Table 14 A. Interrelation between spring vs. winter habit and hairy vs.
hairless sheath character pairs in the F_2 generation of a number of
crosses between spring and winter varieties.**

Crosses	Spring type		Winter type		Total	χ^{2*}	P
	Hairy	Hairless	Hairy	Hairless			
1. Sapporo Rokkaku × MA	127		31		158	0.05	0.9—0.8
2. Sapporo Rokkaku × D	328		85		413	0.91	0.5—0.3
3. Kanjyu(N. Korea) × T	236		62		298	0.83	0.5—0.3
4. Clipford × S	97	37	34	4	172	0.15	0.7—0.5
5. Vankhuri × H	165	69	57	5	296	3.67	0.5—0.3

* Compared with a 13 : 3 segregation ratio of spring and winter types with 6.4% of recombi-
nation with $Hshs$ and $Shsh$.

**Table 14 B. Interrelation between spring vs. winter habit and hairy vs.
hairless sheath character pairs in a number of triple crosses.**

Crosses*	Spring type		Winter type		Total	χ^{2**}	P
	Hairy	Hairless	Hairy	Hairless			
6. Sapporo Rokkaku × D × MC	21	63	32	2	118	4.76	0.2—0.1
7. Saghalien × S × MC	21	28	18	1	68	1.48	0.7—0.5
8. Vladivostok × H × MC	10	28	12	2	52	3.03	0.5—0.3
9. Shokubi-mugi × H × MC	15	39	18	1	73	1.46	0.7—0.5
10. Golden Melon (Nagasaki) × H × MC	18	31	18	0	67	1.48	0.7—0.5
11. Golden Melon (Kagoshima) × S × MC	41	59	26	3	129	2.50	0.5—0.3
12. H. E. 3649 × S × MC	55	72	39	4	170	4.02	0.3—0.2
13. Russian 54 × H × MC	18	27	16	0	61	1.60	0.7—0.5
14. Russian 74 × H × MC	21	32	10	5	68	16.25	<0.01
15. Kindoku × H × MC	42	57	27	2	128	2.54	0.5—0.3
16. Svanhals × H × MC	20	40	21	0	81	1.65	0.7—0.5
17. Clipford × S × MC	35	58	23	5	121	6.07	0.2—0.1
18. Taiki × S × MC	21	40	19	0	80	1.33	0.8—0.7
19. Spring barley No. 2 × S × MC	16	26	15	0	57	1.25	0.8—0.7
20. Harbin × H × MC	19	35	21	2	77	1.22	0.8—0.7
21. Lutai × H × MC	24	39	18	0	81	1.63	0.7—0.5
22. Ihsien × H × MC	35	45	23	1	104	2.84	0.5—0.3

* D = Dairokkaku ; MA = Mensury A_1 ; T = *Tonsum* or Paisha-Tayeh No. 1;
S = Shimabara ; H = Hayakiso No. 2 ; MC = Mensury C.

** Compared with the calculated for a 3 spring : 1 winter ratio wherein sh and hs linked with
6.4% of recombination.

the five simple crosses are shown in table 14 A. It was noted, however, that 3 crosses gave apparently smaller a number of hairy plants in F_2 than was expected, and unabled us to see the interrelation between these two character pairs. This might be due to the insufficient penetrance of the hairy gene, Hs.

It is obvious in the table that the segregation of spring and winter types agree well to the calculated for a 13 : 3 ratio, but not to those for a 3 : 1 ratio. This indicates that these crosses involve each one dominant and one recessive spring genes. Moreover, the results of the crosses with Clipford and Vankhuri revealed the recessive spring gene being linked with the hairy sheath character with 6.4% of recombination, since the agreement to the calculated on this basis was good in both crosses.

In table 14 B are shown the results of the 17 other triple crosses. As stated before, the purpose of such a triple cross was to determine the genotypic constitution of these spring varieties and at the same time to testify the interrelation of the recessive spring genes involved in the varieties to be tested with that of Mensury C. The result was that the spring and the winter types in each of these crosses segregated in a 3 : 1 ratio, but not in a 1 : 1 or a 7 : 1 ratios, which indicated two spring genes being involved in these crosses. Moreover, spring types with glabrous sheath were in excess, while winter types consisted chiefly of those with hairy sheath. It may be safe, therefore, to assume that each of the spring varieties tested was possessed of a recessive spring gene identical with sh_m involved in Mensury C, together with one dominant spring gene. The fit to the expected number on this basis is good in all but one crosses, which proves the above assumption being true. In the cross with Russian No. 74 the fit was recognized as poor ($X_2 = 16.25$), but this variety may nevertheless belong to this group. Because, the spring and the winter types segregated in a 3 : 1 ratio, and the four phenotypes observed are hard to be regarded as equal in number, which is expected for the case of two dominants, instead of one dominant and one recessive, genes being involved.

It may also be of interest to note that, whereas the frequency distribution curve in respect to the earing date was in most of these crosses such a typical bi-modal one as illustrated for the cross with Natsudaikon-mugi for an instance in Fig. 6, crosses involving three spring varieties, Svanhals, Lutai and Ihsien, showed a tri-, instead of bi-modal, curves, and hence early, medium early and late types are clearly distinguished among their segregates. Moreover, the early plants were for the most part hairless in their sheaths, while the medium early plants were wholly consisted of hairy ones. Such a peculiar segregation is certainly worth while considering, so that these results will later again be mentioned and discussed in some details.

D. Interrelation between the dominant spring genes involved in different spring varieties

Another problem whether the dominant spring genes which have proved to be involved in various spring varieties tested above are the same one or not was studied by means of the "triple cross method". The theoretical basis of this method is as follows; Now suppose that both of the dominant spring genes in Natsudaikon-mugi and Kinai No. 5, for example, are identical, no winter plant will be expected to segregate among the triple hybrid plants between the F_I (Natsudaikon-mugi × Kinai No. 5) and a certain winter variety. If, however, the dominant spring genes, Sh_n and Sh_k are different, the F_I genotype between them will be $Sh_n sh_n Sh_k sh_k shsh$, and hence the hybrid plants between the F_1 and a winter variety will segregate spring and winter types in a $3:1$ ratio. Therefore, a test made with such a cross will tell which of the above two is truly the case. According to Warwick's table (1932), only twenty hybrid plants suffices for this purpose.

Such an experiment as stated above was performed with the use of 72 triple hybrid plants. In this cross Hayakiso No. 2 was used as the winter parent. It was recognized in this experiment that all of the hybrid plants eared almost as early as the spring parents within 53 days after sowing, while the winter parent was so late that its first plant among them eared 46 days after the last hybrid plant eared. It seems, therefore, to be right to conclude the dominant spring genes involved in Natsudaikon-mugi and Kinai No. 5 are identical.

As to six other spring varieties randomly taken, similar tests as mentioned above were undertaken. Namely, earing reaction of the six different triple crosses involving Natsudaikon-mugi and Hayakiso No. 2 and anyone of the spring varieties, H. E. 3649, Golden Melon from Nagasaki, Shokubi-mugi, Vankhuri and Svanhals were investigated under long photoperiodic condition in a glass house. It was found in this series of experiments that all these hybrid plants eared almost simultaneously with the spring parents, while the winter parent was belated about 80 days or more from the hybrid plants. These are indicative of the spring dominant gene in each of these spring varieties being identical with or at least allelic to Sh_n in Natsudaikon-mugi. Therefore, these dominant spring gene pair in them are all symbolized as $Sh_2 Sh_2$.

E. Linkage of the dominant spring gene Sh₂

Establishment of linkage relation of the dominant spring gene, Sh_2, with certain visible character pairs in a known linkage group is certainly of practical and scientific interest. Difficulties were, however, encountered in selecting cross combinations appropriate to such linkage tests, and data obtained from the following four crosses only are presented here.

(1) Shimabara × Natsudaikon-mugi

  (2)   Natsudaikon-mugi × Sakigake
  (3)   F₁ (Vladivostok × Sakigake) × Sakigake   :
  (4)   H. E. 3649 × Shimabara

      As is known from table 1, these crosses involve the following character
pairs, along with the spring vs. winter habit of growth: non-six-rowed vs.
six-rowed and normal vs. elongated outer glume (group I), covered vs. naked
kernel and lax vs. dense ear (group III), long-vs. short-haired rachilla and
rough vs. smooth awn (group V) and normal vs. uzu growth habit (group VI),
where the linkage group to which respective characters are presumed to
belong is shown in parenthesis. Segregation of these character pairs were
investigated in the second generation of the first three simple crosses and in
the first generation of the back-cross.

      In table 15 are shown the interaction of spring vs. winter habit with
anyone of these visible character pairs. The result reveals that spring vs.

Table 15. Interrelation between spring vs. winter habit of growth and
some visible character pairs in several crosses.

Character pairs A vs. a	Items	Spring type		Winter type		Total	χ^2	P
		A	a	A	a			
Shimabara × Natsudaikon-mugi								
Covered vs. naked	Observed number	241	61	75	15	392		
	Corrected number	224.22	78.66	69.78	19.34	392		
	Calc. as independent*	238.88	79.63	55.13	18.38	392	4.85	0.2—0.1
Lax vs. dense	Observed number	247	66	58	22	393		
	Calc. as independent*	239.48	79,83	55.27	18.42	393	3.46	0.5—0,3
Normal vs. uzu	Observed number	245	78	61	22	406		
	Calc. as independent*	247.41	82.47	57.09	19.03	406	1.00	0.9—0.8
Natsudaikon-mugi × Sakigake								
Long vs. short-haired rachilla	Observed number	304	58	71		433		
	Calc. as independent*	263.86	87.95	81.19		433	17.58	<0.01
	Calc. as $Sh_2—S$ 20%	295.52	56.29	81.19		433	1.57	0.5—0.3
	of recombination							
F_1 (*Vladivostok × Sakigake*) × *Sakigake*								
Long vs. short-haired rachilla	Observed number	41	26	29	47	143		
	Calc. as 1:1:1:1 ratio	35.75	35.75	35.75	35.75	143	8.25	0.05—0.02
	Calc. as $Sh_2—S$ 38.5%	44.27	27.23	27.23	44.27	143	0.58	0.95—0.9
	of recombinbtion							
Normal vs. uzu	Observed number	34	33	44	32	143		
	Calc. as 1:1:1:1 ratio	35.75	35.75	35.75	35.75	143	2.59	0,5—0.3
H. E. 3649 × Shimabara								
Non-six-row vs. six-row	Observed number	272	91	76	24	463		
	Calc. as independent*	282.14	94.05	65.11	21.70	463	2.53	0.5—0.3
Normal vs. elong. glume	Observed number	274	89	77	23	463		
	Calc. as independent*	282.14	94.05	65.11	21.70	463	2.76	0.5—0.3
Rough vs. smooth awn	Observed number	247	116	98	2	463		
	Calc. as independent*	282.14	94.05	65.11	21.70	463	v. large	small
	Calc. as $Sh_2—r$ 14%	262.05	114.05	85.11	1.70	462.9	2.90	0.5—0.3
	of recombination							
Normal vs. uzu	Observed number	285	78	76	24	463		
	Calc. as independent*	282.14	94.05	65.11	21.70	463	4.83	0.2—0.1

  * Compared with the segregation ratio of 39 : 13 : 9 : 3.

winter habit is inherited independently of non-six-rowed vs. six-rowed (Vv), normal vs. elongated outer glume (Ee), covered vs. naked grain (Nn), lax vs. dense ear (Ll) and normal vs. uzu (Uuz), and hence the growth habit genes seem not to be located in the linkage groups I, III and VI. But, rough vs. smooth awn (Rr) and long- vs. short-haired rachilla (Ss) presumably in linkage group V proved not to be inherited independently of the growth habit genes. Since the spring parents, Natsudaikon-mugi and Vladivostok, are both characterized by long-haired rachilla and H. E. 3649 by smooth-awn, while the winter varieties, Sakigake and Shimabara, both mated with either of former spring varieties, possess the contrasting characters, it is apparent that the parental types are in excess in the segregating generation of these crosses, which fact suggests existence of linkage between growth habit and rachilla-hair and also barbed awn character pairs. It is believed, herewith, that the spring gene linked with these visible character pairs may be the dominant one, but not the recessive one, inasmuch as some genetic studies have already revealed that the gene for sheath-hair and the recessive spring gene, sh, too, are both independent of the rachilla-hair character. As to a Natsudaikon-mugi × Sakigake cross, discrimination of two possible types to be involved in the winter class was impossible, because the F_2 seeds from the cross were sown too late in winter and most of the winter plants failed to ear. Nevertheless, existence of linkage of these character pairs in coupling is doubtless from the data. The recombination value calculated on this basis was about 20%. F_1 between Vladivostok and Sakigake, which was back-crossed by Sakigake, a doubly recessive form, gave a similar, and more trustworthy result, in which the recombination value between the dominant spring gene and rachilla-hair character was found to be 38.5%. To our regret, no evidence for the identity of the dominant spring genes involved in Natsudaikon-mugi and Vladivostok is available at present, but they may be the same one, and certainly different at least from Sh_3 shown later. The recombination value between Sh_2 and r in repulsion phase was also calculated from the F_2 data of the cross with H. E. 3649. It was 14%. And, the observed data in these crosses proved to afford good fit to the calculated on these bases. It is almost certain therefore that the dominant spring gene Sh_2 is located on Vth chromosome in barley. Location of the gene in Vth chromosome, of course, necessitates a three point test, and such a test is now under way.

Middleton and Chapman (1941) and Middleton and McMillen (1944) have already suggested the linkage of growth habit with the smooth-awned character pair. It seems probable, therefore, that these authors might have dealt with the same gene as that herein reported. There are also analogous results reported by some other investgators: Freistedt (1935) suggested the smooth-awnedness and susceptibility to winter injury being in linkage, and Wexelsen (1934) and Frey (1954) indicated association of the smooth-awnedness with

earliness. According to Wexelsen, the gene for earliness may be between r and s genes. It is regreted, however, that the interrelation of the gene for winter hardiness or that for earliness thus found by these authors with the gene for growth habit remains quite obscure.

The results obtained in this series of experiments may be summed as follows:

(1) There is a group of spring varieties where each possesses one recessive and one dominant gene pairs, $shsh$ and Sh_2Sh_2 altogether, each of which is responsible for the expression of spring habit.

(2) The recessive spring gene involved in the varieties tested seemed to be identical with sh in Mensury C, linked with the gene, $Hshs$, for sheath-hair character with about 6—7% of recombination.

(3) It was also shown that all of the dominant spring genes in the varieties which have been subjected to the "triple cross" examination are the same one as that involved in Natsudaikon-mugi. A gene symbol, Sh_2, was given to them. The gene Sh_2 was found to be in linkage group V.

3. Spring varieties involving three spring gene pairs

A. Genic analysis of a cross with Tammi

The third group of spring barleys is that which involves a combination of two dominant and one recessive spring gene pairs. Below is first presented the result of a study of a Hayakiso No. 2 × Tammi cross.

The male parent, Tammi, originated from Finland, is among the earliest varieties in our growing condition and is characterized by the highest grade in spring habit (grade I). Like Kinai No. 5 retardation of earing under shortened photoperiod down to 12 hours a day is so slight that this variety may be conceived as almost neutral to day length. The leaf-sheaths are glabrous and the rachilla covered with short hairs. Another parent, Hayakiso No. 2, is a Japanese endemic form of moderate winter habit, ranking IV grade of our criterion, and is capable to ear considerably early when sown outdoors in the fall. Extraordinary thick hairs on the leaf-sheath is a characteristic peculiar to this variety. Its rachilla is long-haired.

The seeds of the F_2 and their parents were sown on October 1 in the nursery bed in a glass house, and raised under 24 hours' illumination. In Figure 7 are graphically shown the date of heading and presence or absence of the leaf-sheath hairs of the F_2 plants and their parents. It is apparent in this that the classification of early or spring type and the late or winter type among F_2 plants is clear-cut, because the former type, and the spring parent as well, has eared almost simultaneously before November 22, while the latter type and the winter parent after February 11 of the following year.

With regards the number of leaves on the main stem a marked difference

was also recognized between the spring and the winter types: the early F_2 plants and the spring parent had only 7 to 9 leaves, while the late segregates and the winter parent had as many as 17 to 21 leaves. It is noted also that the spring-type plants are involved by far larger in number than the winter-type plants. This suggests at least two dominant spring genes being involved in this cross. Moreover, an indication of a linkage between the gene for sheath-hair and the growth habit genes is exhibited in this. Table 16 shows
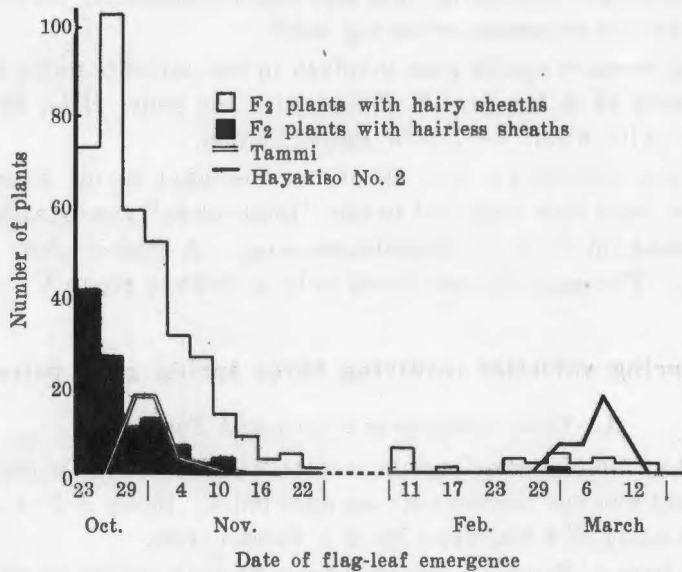

Fig. 7. Earing reaction of the F_2 plants segregated from a cross between Hayakiso No. 2 (winter type with hairy sheaths) and Tammi (spring type with non-hairy sheaths). Seeds were sown on October 1.

Table 16. Interrelation between spring vs. winter habit and hairy vs. non-hairy sheath character pairs in F_2 of a Hayakiso No. 2 × Tammi cross.

Items	Spring types Hairy	Hairless	Winter types Hairy	Hairless	Total	χ^2	P
Obsvd. No.	304	108	25	1	438		
Calc. (1)*	307.97	102.66	20.53	6.84	438	6.29	0.1—0.05
Calc. (2)	302.19	108.44	26.31	1.06	438	0.08	>0.99
Calc. (3)	313.10	104.37	15.40	5.13	438	9.70	<0.01
Calc. (4)	308.82	108.65	19.68	0.85	438	1.54	0.7—0.5

* Explanation in the text.

the numerical data regarding the interaction of growth habit and sheath-hair character pairs, wherein the observed number is compared with the calculated on the following four different genetic bases: (1) segregation of spring and winter types in a 15 : 1 ratio, and independent inheritance of the genes for

growth habit and for sheath-hairs, (2) the same as in (1), but either of the spring genes linked with *hs* with 20% of recombination, (3) segregation of the two types in a 61 : 3 ratio, and three spring genes inherited idependently of *hs*, and finally (4) the same as in (3), but either of the two dominant spring genes linked with *hs* with 20% of recombination or the recessive spring gene linked with *hs* with 6.4% of recombination. As seen in table 16, however, we could not determine from the F_2 test whether two spring genes or three were involved and also which of these genes was really linked with the gene for sheath-hair character.

To solve this question, all of the winter-type plants and about one third of the spring-type plants with hairy and glabrous sheaths involved in the F_2 population were carried through the F_3 generation. The results obtained are shown separately in table 17 A, B and C. It became clear at once from the

**Table 17. Number of different genotypes in the F_2 of a Hayakiso
No. 2 × Tammi cross as determined by F_3 test.
A. Strains from the F_2 plants of winter habit.**

Items	Winter Homo.			Heterozygotes			Total	χ^2	P
	HsHs	*Hshs*	*kshs*	*HsHs*	*Hshs*	*hshs*			
Observed number	11	0	0	1	12	1	25		
Calc. as *sh—hs* 6.4% of recombination	7.30	1.00	0	1.00	14.67	1.00	25	3.39	0.7—0.5
Calc. as Sh_2 or Sh_3—*hs* 20% of recombination	5.33	2.67	0.33	10.67	5.33	0.67	25	18.78	<0.01

B. Strains from F_2 plants of spring habit having glabrous sheaths.

Items	Homo. spring	Segreg. in 61 : 3 or 15 : 1	Segreg. in 13 : 3 or 3 : 1	Total	χ^2	P
Observed number	46	3	1	50		
Calc. as *sh—hs* 6.4% recombination	46.88	1.56	1.56	50	1.55	0.5—0.3
Calc. as Sh_2 or Sh_3—*hs* 20% of recombination	39.97	6.02	4.01	50	4.68	0.1—0.05

C. Strains from F_2 plants of spring habit having hairy sheaths.

Items	Spring Homo.		61 : 3 or 15 : 1		13 : 3 or 3 : 1		Total	χ^2	P
	HsHs	*Hshs*	*HsHs*	*Hshs*	*HsHs*	*Hshs*			
Observed number	11	23	10	7	11	13	75		
Calc. as *sh—hs* 6.4% of recombination	11.70	25.06	6.62	12.50	6.62	12.50	75	7.27	0.3—0.2
Calc. as Sh_2 or Sh_3 —*hs* 20% recombinat.	12.24	28.06	3.19	13.56	7.98	9.97	75	20.81	<0.01

behaviors of the F_3 strains derived from the F_2 winter plants that the cross had included one recessive spring gene, besides two dominant ones, inasmuch as each of more than half of the strains segregated in a 1 spring : 3 winter

ratio. Existence of linkage between the recessive spring gene and *hs* for non-hairy sheath character was also confirmed by this test. The recombination value computed on this basis was found to be 6.4%, and the actual data afforded a good fit to the expected number on this basis. The assumption of linkage between *hs* and either of the dominant genes was disproved, on the other.

It is naturally expected that a similar F_3 test of the strains derived from the F_2 plants of spring habit also corroborates the above result. About 50 plants of each strain were used for the test in order to discriminate the strains which would segregate spring and winter plants in a 61 : 3 or 15 : 1 ratio from the true breeding strains and a group of strains segregating in a 13 : 3 or 3 : 1 ratio. As seen in table 17B and C, the results proved to be almost as expected, although for the case shown in B it could not be determined which of the growth habit genes were truly linked with *Hshs*.

Relation of either of the dominant spring genes involved in Tammi with Sh_n in Natsudaikon-mugi was then studied by means of the "triple cross" method stated before. If the three dominant genes under consideration were quite different, hybrid plants between F_1 (Tammi × Natsudaikon-mugi) and a winter variety, Hayakiso No. 2, would segregate spring plants and winter plants in a 7 : 1 ratio. On the other hand, if either of the dominant spring genes were allelic to Sh_n no winter plant would appear among the hybrid population. Eighty nine hybrid seeds, together with 20 seeds of each of the parents, were sown on February 25 in a glass house and grown under 24 hours of illumination. It was found from this experiment that the latter assumption was truly the case, since all the hybrid plants eared from March 29 to April 9, and Tammi and Natsudaikon-mugi also between 1 and 8 of April, whereas only a part of the winter parent, Hayakiso No. 2, eared by far later than the hybrid plants.

With respect to the allelic relation between the recessive spring genes, sh_t in Tammi and sh_m in Mensury C, no direct evidence has ever been obtained until now. But, as was shown above, a complete agreement of recombination value between sh_t and *hs* with that found in a cross between Mensury A_1 and C may be interpreted as both spring gene, sh_t and sh_m being identical. It may be safe, therefore, to conclude from these results that the spring variety, Tammi, possesses three spring gene pairs altogether, which may be represented as $shshSh_1Sh_2Sh_3Sh_3$.

B.   On the genetic behaviors of the crosses with five other spring varieties

Below are presented the results of genetic studies of the crosses involving five spring varieties, Hadostreng, Nigrinudum, Vaga, Colsess I and Olli, as they were inferred to be similar to Tammi as to the genetic constitution for growth habit. The materials consisted of the F_2 of three simple spring-winter variety crosses and two triple crosses, F_1 (Hadostreng × Shimabara) × Men-

sury C and F_1 (Olli × Hayakiso No. 2) × Mensury C. They were grown
under long photoperiodic condition and segregation of various character pairs
involved were studied.

It was first recognized that segregation of spring and winter types in
the F_2 or triple crosses with Colsess I, Hadostreng and Olli afforded good fits
to the calculated on a 61 : 3 or a 7 : 1 ratio, but not to those on a 15 : 1 or a 3 : 1
ratio, respectively, which indicated two dominant and one recessive spring
genes being involved in these crosses. The result of triple crosses with
Hadosteng and Olli revealed also that the recessive spring gene involved was
identical with sh_m in Mensury C. However, two other crosses failed to show
whether they were digenic or trigenic difference regarding growth habit.

Interaction of growth habit and sheath-hair character pairs in F_2 and
triple hybrids is shown in table 18. It is generally accepted in all of the

**Table 18. Interrelation of spring vs. winter habit and hairy vs. hairless
sheath character pairs in some F_2 and triple hybrids.**

Crosses*	Items	Spring type		Winter type		Total	χ^2	P
		Hairy	Hairless	Hairy	Hairless			
Nigrinudum × S	Obsvd. No. (corrected)	217.11	74.89	12.39	1.61	306		
	Calc. (1)**	215.16	71.72	14.34	4.78	306	2.53	
	Calc. (2)	211.14	75.74	18.36	0.76	306	3.07	0.5—0.3
	Calc. (3)	218.74	72.92	10.76	3.58	306	1.40	0.8—0.7
	Calc. (4)	215.75	75.91	13.75	0.59	306	1.92	0.7—0.5
Colsess I × H	Obsvd. No.	212	84	9	1	306		
	Calc. (1)	215.16	71.72	14.34	4.78	306	7.13	0.1—0.05
	Calc. (2)	211.14	75.74	18.36	0.76	306	5.75	0.2—0.1
	Calc. (3)	218.74	72.92	10.76	3.58	306	3.76	0.3—0.2
	Calc. (4)	215.75	75.91	13.75	0.59	306	2.86	0.5—0.3
Vaga × H	Obsvd. No.	135	47	9	0	191		
	Calc. (1)	134.30	44.77	8.95	2.98	191	3.10	0.5—0.3
	Calc. (2)	131.79	47.27	11.46	0.48	191	1.09	0.7—0.5
	Calc. (3)	136.53	45.51	6.72	2.24	191	3.08	0.5—0.3
	Calc. (4)	134.67	47.38	8.58	0.37	191	0.39	0.95—0.9
Hadostreng × S × MC	Obsvd. No.	53	67	17	0	137		
	Calc. (1)	51.38	51.38	17.12	17.12	137	21.92	small
	Calc. (2)	41.10	61.65	27.40	6.85	137	14.71	small
	Calc. (3)	59.94	59.94	8.56	8.56	137	18.52	small
	Calc. (4)	52.47	67.40	16.03	1.10	137	1.17	0.8—0.7
Olli × H × MC	Obsvd. No.	53	76	25	0	154		
	Calc. (1)	57.75	57.75	19.25	19.25	154	27.13	small
	Calc. (2)	46.20	69.30	30.80	7.70	154	10.44	<0.02
	Calc. (3)	67.375	67.375	9.625	9.625	154	38.36	small
	Calc. (4)	58.98	75.77	18.02	1.23	154	4.54	0.3—0.2

* S, H and MC stand for Shimabara, Hayakiso No. 2 and Mensury C, respectively.
** Explanation in the text.

crosses that winter types with hairy sheaths were found more and those with
hairless sheaths less in number than those expected for independent assort-
ment. Such a relation suggests existence of linkage between these two
character pairs in these crosses, for the winter parents crossed are all charac-

terized by hairy sheaths. Comparison with the calculated numbers on the bases of four possible segregations made as in the case for Tammi, however, does not give any definite indication about the genic constitutions of these spring varieties and its relation to sheath-hair character, except in two triple crosses. Further study on the F_3 segregation is, therefore, necessary for the elucidation of these relations in these three crosses, but such a test was made only for 17 strains derived from all the late and several early F_2 plants in a Vaga × Hayakiso No. 2 cross. The result was that 6 out of 9 late F_2 plants were heterozygous for the recessive spring gene pair, and 3 homozygous winter types. It may be true that Hadostreng, Olli, Vaga, and probably also Colsess I and Nigrinudum, are of the same genotype regarding their spring habit as Tammi, though the last two varieties requires further evidences in favor of the conclusion.

4. A group of spring varieties having a single dominant gene pair

There has been found a fourth genotypic group of spring varieties where each has a single dominant gene for the growth habit. They are for the most part characterized by the slight lateness in earing time under continuous illumination as compared with those spring varieties which have been dealt with in the foregoing sections and hence are ranked II grade for the spring habit. In this section will be stated the results of the crosses with these varieties. At first, genetic behavior of a cross between *Hordeum agriocrithon* var. *eu-agriocrithon* C. I. 6496 and Shimabara will be explained in some details.

Hordeum agriocrithon, a six-rowed wild spring barley, was obtained from U. S. A. with the courtesy of Dr. W. H. Leonard. The original form was found first by Åberg among a seed sample gathered at East Tibet (Åberg 1938). Since this species is generally believed as a putative ancestral type of the cultivated six-rowed barley or at least as a form allied to it, the genetic analysis may be of especial interest. The general characters of both parental varieties have been referred to in table 1. The seeds of the F_2 and their parents, along with some F_1's, were sown in two flats on February 20, and the plants were grown under 24 hours' illumination in a glass house. Date of flag-leaf emergence and the characters of the leaf-sheaths of these plants are illustrated in Fig. 8.

It was known in this experiment that the distinction of the spring type from the winter one among the F_2 plants was no less easy, in spite that both types did not differ so far physiologically as in the crosses with the varieties of the highest spring habit. The spring-type plants eared rather abruptly within ten days from 3 to 12 of April and the spring parent did simultaneously, which was followed immediately by the F_1 plants. On the other hand,
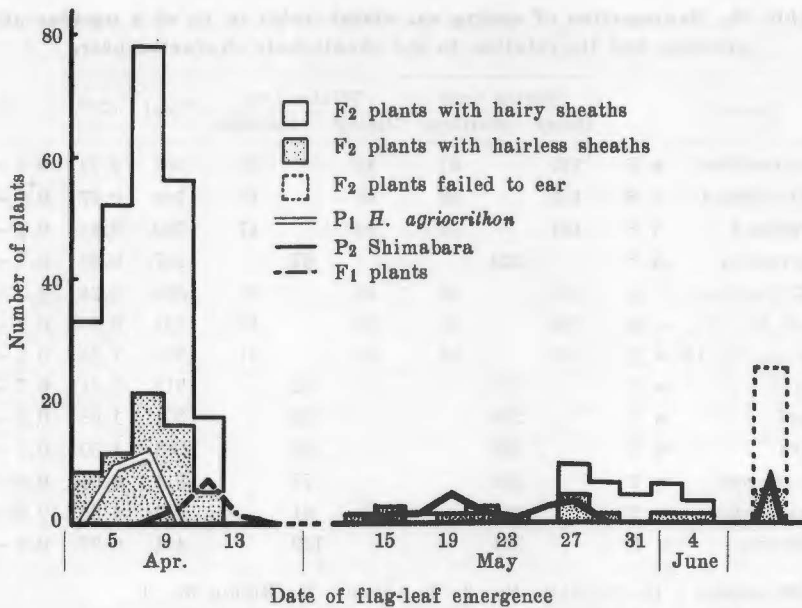
Fig. 8. Date of flag-leaf emergence of F_1 and F_2 plants from a cross between *H. agriocrithon* and Shimabara, and of their parents. Seeds were sown on February 20.

the F_2 plants of winter type, and the winter parent as well, began to ear more than one month later than the spring type and continued earing until early June, but some of them died without ear formation. This figure suggests also that there may be no association between the spring vs. winter habit and the hairy vs. hairless sheath character pairs.

The observed number of the four phenotypes in the F_2 generation is shown in the first line of table 19. The result reveals that the actual number affords a good fit to the theoretical one on the basis of independent assortment of both character pairs, each of which is segregated in a simple Mendelian ratio. The fit to the calculated for 13 spring : 3 winter segregation ratio was known to be poor (P = 0.01). It may therefore be safely concluded from the result that the spring variety, *H. agriocrithon*, has a single dominant spring gene which is independent of the gene *hs* for hairless sheath.

The F_2 result was corroborated by the F_3 progeny test. A number of the winter plants taken at random from the F_2 population were found to breed true to winter habit in their F_3 generation.

Allelic test for the spring gene in *H. agriocrithon* and Sh_n in Natsudaikon-mugi was then made by means of "triple cross" method. F_1 plants between *H. agriocrithon* and Natsudaikon-mugi were crossed with a winter variety Hayakiso No. 2, and about 30 hybrids seeds thus obtained were sown on October 2. It was found in this experiment that the earing time of the hybrid plants was almost as early as those of the two spring parents, while winter parent was belated from the hybrid plants 80 days or more in earing.

Table 19. Segregation of spring vs. winter habit in F_2 of a number of crosses, and its relation to the sheath-hair character pair.

Crosses*		Spring type		Winter type		Total	χ^2**	P
		Hairy	Hairless	Hairy	Hairless			
1. *H. agriocrithon*	× S	175	61	43	18	297	3.79	0.3 —0.2
2. Mushihchang 1	× S	152	56	57	19	284	0.87	0.9 —0.8
3. Hsinwuko 1	× S	184	45	54	17	300	3.88	0.3 —0.2
4. Sumiremochi	× S		220		67	287	0.29	0.7 —0.5
5. A 222 (Almora)	× H	169	45	58	23	295	3.24	0.5 —0.3
6. French No. 1	× H	163	51	59	18	291	0.60	0.9 —0.8
7. Kuromugi No. 148	× T	169	64	56	31	320	7.26	0.1 —0.05
8. Hozoroi	× T		229		82	311	0.31	0.7 —0.5
9. Baitori	× T		216		85	301	1.68	0.2 —0.1
10. Ohgara	× T		225		63	288	1.50	0.3 —0.2
11. Hojo (Korea)	× T		237		77	314	0.04	0.9 —0.8
12. Indian barley	× T		249		61	310	4.68	0.05—0.02
13. Ligule-less	× R		324		120	444	0.97	0.5 —0.3

  * S=Shimabara ; H=Hayakiso No. 2; T=*tonsum* ; R=Riku-u No. 1
  ** Compared with the calculated ratio of 9 : 3 : 3 : 1 or 3 : 1.

Table 20. Segregation of spring vs. winter habit and hairy vs. hairless character pairs in the four triple crosses.

Crosses*			Spring type		Winter type		Total	χ^2**	P
			Hairy	Hairless	Hairy	Hairless			
14. Marumi No. 16	× S	× MC	16	13	11	13	53	0.96	0.9 —0.8
15. Akashinriki	× S	× MC	33	22	37	40	132	5.64	0.2 —0.1
16. Tainan No. 1	× S	× MC	25	17	18	23	83	2.16	0.7 —0.5
17. Nudideficiens	× H	× MC	22	25	29	15	91	4.60	0.3 —0.2
18. Coast III	× H	× MC		36		34	70	0.06	0.9 —0.8
19. Native No. 1	× H	× MC		39		36	75	0.24	0.7 —0.5
20. Paisha-Tayeh 5	× H	× MC	21	20	19	21	81	0.14	0.99—0.98
21. Indian barley	× W	× MC	23	18	28	17	86	3.58	0.5 —0.3

  * S=Shimabara ; H=Hayakiso No. 2 ; W=Wasehadaka (Kochi) ; MC=Mensury C
  ** Compared with the calculated ratio of 1 : 1 : 1 : 1 : or 1 : 1.

The result may be interpreted as that the spring gene of *H. agriocrithon* is allelic to Sh_n in Natsudaikon-mugi. Because, if not so, the triple hybrid is to segregate the spring and winter types in a 3 : 1 ratio.

Twelve other crosses were also studied in their F_2 segregation in the same way as stated before. The parental spring varieties of these crosses are those originated chiefly from East Asia, inclusive of Japan, Korea, China Proper, and India. In deciding the cross combination, all the crosses, with one exception of Sumiremochi × Shimabara, had been planned so as to investigate the interrelation of the growth habit and sheath-hair character pairs, but it was unsuccessful for the six crosses with Paish-Tayeh 1 or

tonsum and Riku-u No. 1. The apparent shortage of plants with hairy sheaths was observed among these F_2 populations, and a similar disposition, though slight, was also recognized in a cross with Kuromugi, which might perhaps be due to incomplete penetrance of *Hs* gene as affected by the environmental condition. The cross combinations and the observed number of two or four phenotypes classified in the F_2 of the respective crosses are shown in table 19. The data shown in this table reveal that the observed number in most of these crosses fits well to the calculated for the segregation in a $3:1$ or $9:3:3:1$ ratio, but not to a 13 spring : 3 winter ratio with one exception of the cross with Indian barley. Any sign of association between spring habit and sheath-hair character pairs was not observed.

For seven other spring varieties and Indian barley genetic analyses were made by means of triple cross method: F_1 plants from spring-winter varietal crosses were again pollinated by Mensury C, and these hybrid seeds were grown under continuous illumination. The results are shown in table 20, which indicates clearly that these eight spring varieties have each a single dominant spring gene, but not the recessive spring gene in Mensury C. Agreement with the expected number on the assumption as above was ascertained as good.

Investigations were also made to answer the question whether the dominant spring genes involved in these spring varieties might be allelic to Sh_2 in Natsudaikon-mugi. The varieties examined were three naked one — Sumiremochi, Marumi No. 16 and Akashinriki, and four covered varieties — Indian barley, Kuromugi No. 148, Hozoroi and Tainan No. 1. The F_1 plants between Natsudaikon-mugi and each of these seven varieties were crossed to Hayakiso No. 2, and the behaviors of these hybrid plants were studied under continuous illumination. It was ascertained by the experiments that all the hybrid plants from these triple crosses eared as early as the spring parents, and any segregate which eared as late as the winter parent was not found at all. The results may indicate the spring genes in these varieties being allelic to Sh_2 in Natsudaikon-mugi.

Finally, a result pertaining to the linkage relation of the spring genes, particularly of the dominant one, Sh_2, will be presented. The material consists of the F_2 and F_3 plants from a cross between two spring varieties, Kuromugi No. 148 and Mensury C. As stated before, Mensury C is known to have a recessive spring gene, *shsh*, and Kuromugi No. 148 a dominant spring gene, Sh_2Sh_2, which is capable of initiating second grade of spring habit. Therefore, this cross is to involve two different spring gene pairs. About 570 F_2 plants and 100 F_3 strains randomly taken from the F_2 plants which had been harvested in the previous season were grown simultaneously from September 19 in a warm house under 24 hours' illumination.

It was confirmed in the F_2 test that spring-type plants and the winter one segregated in a $13:3$ ratio, which result was just as expected. It may

be of interest to note herewith that the spring-type plants have been clearly subdivided further into two distinct groups, the early and the medium early, since typical bi-modal frequency distribution curve regarding the date of earing was shown by the spring-type plants. Segregation of the early and medium early types was occurred in a 4 : 9 ratio, owing to the epistacy of the gene that is capable of initiating higher grade of spring habit to that for lower spring habit. Therefore, it seems as adequate to infer that the early group possesses $shsh$, and the medium early one has Sh_2Sh_2 or Sh_2sh_2 but no sh gene in homozygous condition, while the winter-type plants have neither $shsh$ nor Sh_2.

Table 21. Interrelation of the spring genes, sh and Sh_2, with some genes for visible characters in the F_2 of a cross between Kuromugi No. 148 and Mensury C.

Character pairs A a	Items	Spring type		Winter type		Total	χ^2	P
		A	a	A	a			
Normal vs.	Observed number	350	109	88	23	570		
uzu ($Uzuz$)	Calc. as independent*	347.34	115.78	80.16	26.72	570	1.702	0.7—0.5
Hairy vs.	Observed number	332	127	106	5	570		
hairless sheath	Calc. as independent*	347.34	115.78	80.16	26.72	570	27.750	<0.01
($Hshs$)	Calc. sh—hs 7.7% of recombination	325.90	137.22	101.60	5.28	570	1.081	0.8—0.7
Long vs.	Observed number	350	91	56	43	540		
short-haired rachilla	Calc. as independent*	329.06	109.69	75.94	25.31	540	22.117	<0.01
(Ss)	Calc. Sh_2—s 34% of recombination	347.85	90.90	57.15	44.10	540	0.0639	>0.99

* Segregation ratio of 39 : 13 : 9 : 3.

Table 21 shows the interrelation of the genes for growth habit with those for three visible character pairs in the F_2 of this cross. It is obvious from the result that both of the growth habit genes are independent of $Uzuz$ for normal vs. uzu character pair; the observed count fits well to the calculated for independent assortment of these gene pairs. However, neither the gene pair for hairy vs. hairless sheaths nor that for long- vs. short-haired rachilla can be regarded as independent of the growth habit genes. In both cases parental types are found apparently in excess, which indicates existence of linkage between these two visible character pairs and the growth habit. It seems as pertinent to conceive that the spring gene in linkage with hs is the recessive one which has been inherited from Mensury C. It is because that previous experiments have established well a close linkage of $Hshs$ with $Shsh$ in one hand, and both of these genes are independent of Sh_2sh_2 on the other, and further that the recombination value found in this cross (7.7%) approximates closely with that found in the previous experiments (6.4%). This naturally leads us further to a supposition that the growth habit gene linked

with Ss for rachilla hair character pair may be Sh_2sh_2. The recombination value between Sh_2sh_2 and Ss was found to be 34.0 ± 3.2186 (%), and the observed number fitted very well to the calculated on this basis.

Another evidence which may be in favor of this was obtained from the F_3 progeny test. As 25 out of 100 strains tested were found to breed true in the F_3 generation to the earliest spring type and impossible to be subdivided further into different genotypes, so the data of the remaining 75 strains were used for this linkage study. The observed number of nine genotypes distinguished among these strains was as shown in table 22. It was known from the result that the observed count afforded a good fit to the calculated on the basis of 40% of recombination between Sh_2sh_2 and Ss, and also to that for independent assortment. However, it seems as probable that this is due to the loose linkage between both genes; and the result may be interpreted to show that both genes are in linkage rather than independent, since similar linkage values have been found in the F_2 of this and some other crosses.

Table 22. Number of different genotypes involved in the F_2 of a Kuromugi
No. 148 × Mensury C as determined by the F_3 generation test.

Items	F_2 genotypes*									Total	x^2	P
	AABB	AABb	AaBB	AaBb	AAbb	Aabb	aaBB	aaBb	aabb			
Obsvd. No.	5	7	7	25	3	7	3	9	9	75		
Calc. as independent	4.69	9.37	9.37	18.75	4.69	9.37	4.69	9.37	4.69	75	9.226	0.5—0.3
Calc. as 40% of recomb.	6.75	9.00	9.00	19.50	3.00	9.00	3.00	9.00	6.75	75	4.088	0.9—0.8

* Aa and Bb stand for Sh_2^{II} sh_2 and Ss, respectively.

A better fit to the calculated on the basis of linkage with 40% of recombination than to that for independent assortment may support this view. If this is true, we can calculate a weighted P-value from the F_2 and F_3 results obtained in the above experiment. It is $36.4 \pm 2.4949\%$. This value approximates closely with that obtained in a back-cross, F_1 (Vladivostok × Sakigake) × Sakigake (38.5%).

The results of a series of experiments made with the use of a number of spring varieties which have originated mostly from East Asia and are characterized by somewhat lower grade of spring habit (grade II) may be summed as follows: Each of these varieties possesses only a single dominant spring gene pair, Sh_2Sh_2. The gene in some of these varieties proved to be allelic to the dominant gene involved in Natsudaikon-mugi, and inherited independently of $Hshs$ for sheath-hair character pair. The spring gene in Kuromugi No. 148, which is capable of initiating second grade of spring habit and make plants to ear later than $shsh$ in Mensury C, has been shown to be linked with Ss for rachilla hair character with 36.4% of recombination.

5. A variety with two dominant spring gene pairs

It is not impossible to suppose that among various spring barleys there exist seven kinds of genotypes arising from the possible combination of three kinds of genes, sh, Sh_2 and Sh_3, each responsible for spring habit of growth. And, we are successful in finding one more in addition to the four genotypes reported above, but the other two have not yet been discovered.

The variety having this genotype is Brachytic, which was obtained by the courtesy of Dr. W. H. Leonard as a linkage tester. The original form of Brachytic was first found by Stadler as a spontaneous mutant arisen from Himalaya, a long-awned naked variety (var. *coelesta*). The characteristics of this mutant were informed in detail by Swenson (1940), and suffice it to mention here that this is of the II grade in spring habit and has glabrous leaf-sheaths. This was crossed to Hayakiso No. 2, a winter variety, and the F_2 and their parents were sown twice, on November 22 in 1954 and February 25 in 1955. They were, of course, grown under continuous illumination as usual.

The date of flag-leaf emergence and the condition of sheath hair of the F_2 plants in the first experiment are shown in Fig. 9 A. The variation histogram of F_2 plants with respect to earing date is typically tri-modal, and early, medium early and late groups are possibly classified before and after
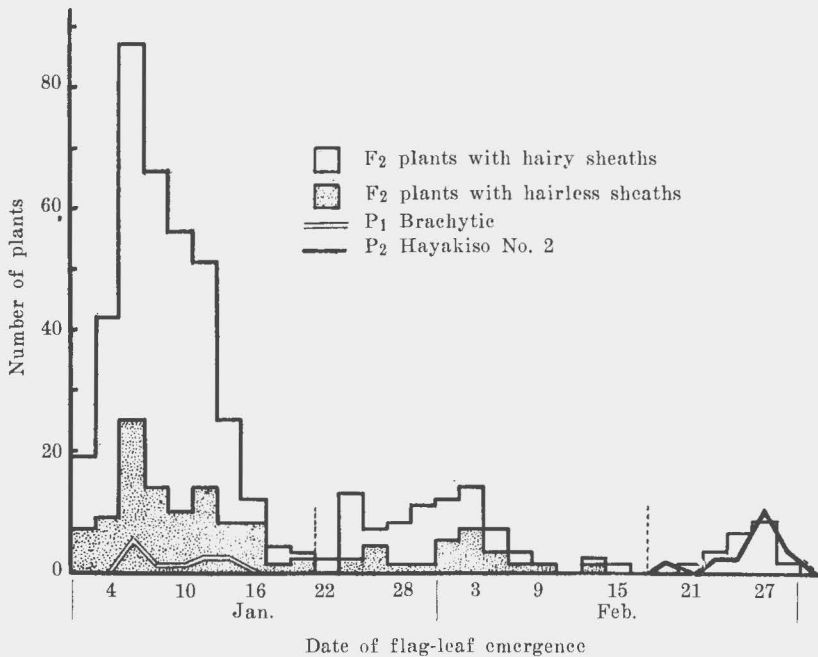

Fig. 9A. Frequency distribution histogram as regards the date of flag-leaf emergence of F_2 segregates having hairy and non-hairy sheaths in F_2 of a Hayakiso No. 2 × Brachytic cross. Seeds were sown on November 22.

21 of January and 18 of February, both of which correspond at large to the
bottoms of trimodal variation histogram.   It is noted also in this figure that
the early-F_2 plants and the spring parent, Brachytic, have eared almost
simultaneously, and the late-F_2 group and the winter parent, Hayakiso
No. 2, have done so on the other.   It may be reasonable to conceive the late
group of F_2 as winter type and the other including both the early and the
medium-early groups as spring type.   The actual numbers of both types as
classified on this basis proved to fit well to 15 : 1 and 61 : 3 ratios.   Hereupon,
it is remembered that an almost similar segregation ratio has been found in
the crosses of Tammi and other spring barleys, each of which was shown to
have three spring genes altogether. In the cross under consideration, however,
there seems to be no sign of linkage between spring habit and sheath-hair
character pairs, which suggests that a recessive spring gene, sh, is not invol-
ved in this cross.   Quite the same result was obtained in the second experi-
ment.

A more exact knowledge of the genotypic consitituion of Brachytic was
obtained from the result of experiment with a triple cross, in which F_1 be-
tween Brachytic and Hayakiso No. 2 was crossed again by Mensury C. As
stated before repeatedly, Mensury C is a variety that has glabrous leaf-
sheath, the gene for which is linked closely with the recessive spring gene,
sh. The hybrid seeds and parental ones were sown on February 25 in 1955,
and they were reared under continuous illumination in a glass house.   Fig. 9
B shows the date of flag-leaf emergence in relation to the characteristic of
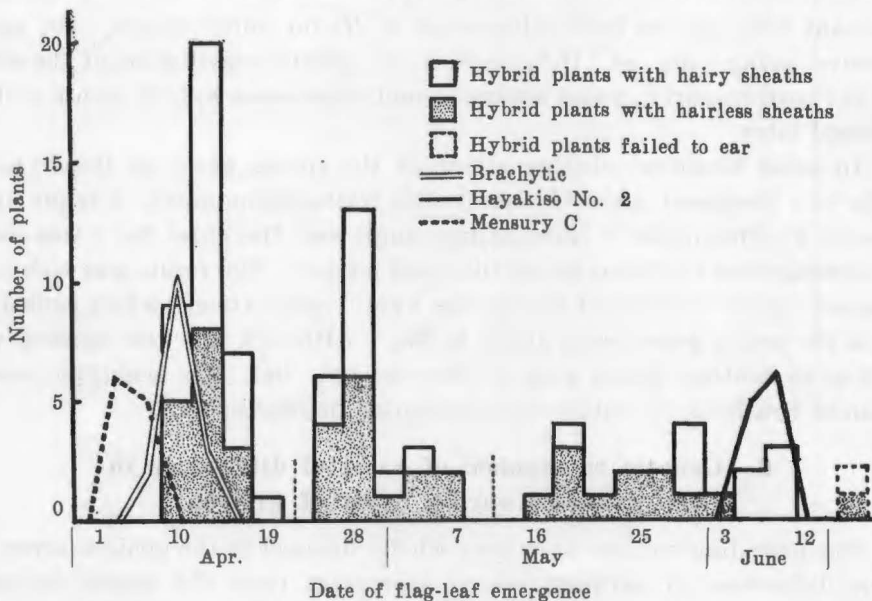

Fig. 9B. Frequency distribution as regards the date of flag-leaf emergence of the
hybrid plants and three parental varieties in a triple cross, F_1 (Hayakiso No. 2 ×
Brachytic) × Mensury C. Seeds were sown on February 25.

leaf-sheaths of each plant. It is evident in this figure that the earing time of this hybrid plants, too, shows a typically trimodal variation histogram, and the early group has eared almost simultaneously with Brachytic, while the late group is somewhat earlier or almost as late as the winter parent. Mensury C has eared rather earlier than the early group. Independent inheritance of spring habit and sheath-hair character pairs is evident, because hairy and non-hairy character pair has segregated in almost in a 1 : 1 ratio in each of the three different classes of the hybrid. If Brachytic had a gene, sh, instead, this hybrid would segregate in a 7 spring : 1 winter ratio, with preponderance of hairy-sheathed plants among the late plants of the hybrid. The numerical data of this triple cross, together with F_2 hybrid stated above, are shown in table 23, which indicate clearly that Brachytic possesses two

Table 23. Segregation of spring vs. winter habit of growth and hairy vs. hairless sheath character pairs in F_2 of a Brachytic × Hayakiso No. 2 cross and also in a triple cross between the F_1 and Mensury C.

Items	Spring type		Winter type		Total	χ^2	P
	Hairy	Hairless	Hairy	Hairless			
Obsvd. No. (F_2)	321	124	16	3	464		
Calc. on Indep.*	326.25	108.75	21.75	7.25	464	6.234	0.2 —0.1
Obsvd. No. in triple cross	32	31	10	12	85		
Calc. No. **	31.875	31.875	10.625	10.625	85	0.239	0.98—0.95

  * Based on the 45 : 15 : 3 : 1 segregation ratio.
  ** Based on the 3 : 3 : 1 : 1 segregation ratio.

dominant spring genes both independent of Hs for hairy sheath, but not a recessive spring gene, sh. Differences in the genetic constitution of the early and the medium early groups among F_2 and triple cross hybrid plants will be discussed later.

In order to know whether either of the spring genes in Brachytic is allelic to a dominant gene Sh_n, involved in Natsudaikon-mugi, a triple cross between F_1 (Brachytic × Natsudaikon-mugi) and Hayakiso No. 2 was made and investigated the behavior by the usual method. The result was such that no winter plant was found among the hybrid population, which indicated one of the spring genes being allelic to Sh_n. Although any test as such was made as to another spring gene of this variety, but, the genotypic constitution of Brachytic is tentatively represented $Sh_2Sh_2Sh_3Sh_3$.

6. Genetic mechanism of varietal difference in the grade of spring habit of growth

The preceding sections have been wholly devoted to the genic analyses of major differences in earliness among segregates from the crosses between varieties of pure spring and winter habit of growth. Thorough understanding of hybrid behaviors, however, requires further investigations in detail of their earing reaction. In the physiological studies of spring vs. winter

habit of growth, Enomoto and others found that two extremities of spring and winter types were connected by a series of intergrades, in which any two closely allied variants were differentiated in a slight physiological reaction. Therefore, elucidation of the genetic mechanism for the intergradation of growth habit constitutes another problem of scientific as well as practical importance.

An attempt to approach to this problem was made with the use of seven varieties differing in the grade of spring habit. They are Indian barley (I), Kuromugi No. 148 (II), Chinko No. 83 and Shirochinko, both being closely akin to each other and equally of III grade of spring habit, Sekitori Sai No. 1 (IV), Shimabara (V), and Iwate Omugi No. 1 (VI), in which numerals in parenthesis signify the grade of spring habit of the respective varieties. Crossings were made between an intermediate form, either Chinko No. 83 or Shirochinko, and five other varieties. For the sake of convenience, experiments were conducted in two different seasons. In the first experiment were tested two crosses with Indian barley and Kuromugi No. 148, both being higher in the spring grade than the female parent, Chinko No. 83. The seeds of the F_2 from these two crosses and of their parents were sown on September 29, 1953. Three other crosses with varieties of lower grade of spring habit were sown January 14, 1955. All of them received best care under continuous illumination in a warm house.

Since parental varieties of some of the crosses differ less in their earing reaction than those of the crosses hitherto tested, we were not sure whether we were able to distinguish successfully the early- and the late-type plants. Nevertheless, the distinction between the two types proved to be clear and easy in all cases, and moreover, F_3 progeny tests made for some of the early and the late F_2 segregates revealed also the classification in F_2 being quite right.

Number of early and late plants, together with the mean days from seeding to flag-leaf emergence of both types and their parents of these crosses are shown in table 24. In aid for better comprehension of the state of matter, frequency curves regarding the earing date of these five crosses are illustrated in Fig. 10 and 11 separately for the first and second experiments, respectively.

The results in these figures and the table indicate an interesting fact. It is that earliness is dominant over the lateness irrespectively as to whether intermediate parent, Chinko No. 83 or Shirochinko, has been crossed to the earlier or the later forms. In the crosses with Indian barley and Kuromugi No. 148, the early segregates began to ear almost simultaneously with the respective spring male parent, while the late ones behaved almost the same as the inermediate parent. On the other hand, in the crosses with varieties of lower spring habit than Chinko No. 83 or Shirochinko, the early plants have eared in general at the same time with the intermediate parent, and

Table 24. Number of early and late F₂ plants (a) and mean days from seeding to flag-leaf emergence of both types and their parents (b) in the five crosses between Chinko No. 83 or Shirochinko (III grade) and five varieties differing each in the grade of spring habit.

*Chinko No. 83 or Shirochinko (III) crossed with		P̄	F₂ plants		χ²**	P
			Early	Late		
Indian barley (I)	(a)		277	76	2.2672	0.1—0.05
	(b)	(36.2)	(42.7)	(130.7)		
Kuromugi No. 148	(a)		256	93	0.5052	0.5—0.2
(II)	(b)	(51.9)	(54.1)	(129.2)		
Chinko No. 83 (III) parent	(b)	(127.8)				
Sekitori Sai	(a)		217	63	0.933	0.5—0.2
No. 1 (IV)	(b)	(105.1)	(65.0)	(102.9)		
Shimabara (V)	(a)		199	73	0.490	0.5—0.2
	(b)	(107.2)	(69.8)	(104.1)		
Iwate Omugi No. 1	(a)		231	70	0.488	0.5—0.2
(VI)	(b)	(not eared)	(74.3)	(not eared)***		
Chinko No. 83 (III)	(b)	(69.2)				
Shirochinko	(b)	(73.3)				

* Iwate Omugi was crossed with Shirochinko, others with Chinko No. 83
** Compared with the calculated on a 3 : 1 segregation ratio.
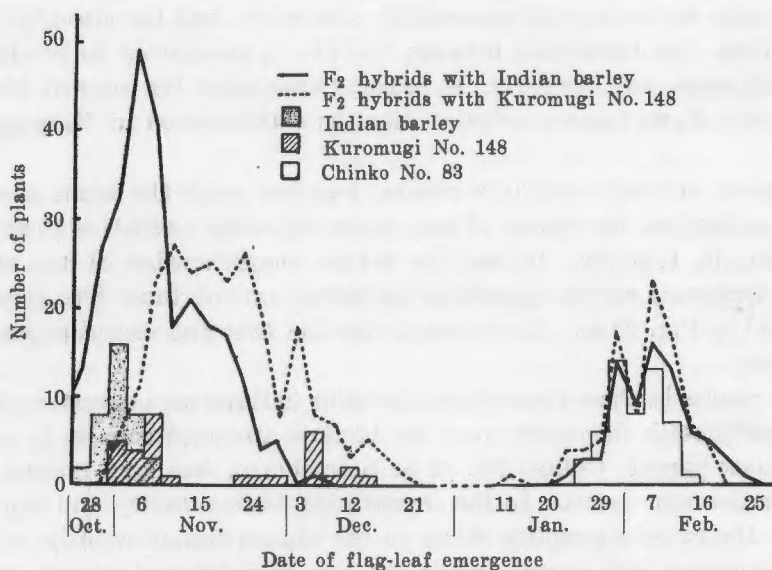*** With 6 exceptions which eared about 130 days after sowing.

Fig. 10. Frequency distribution as regards the date of flag-leaf emergence of the F₂ hybrid plants and their parents in two crosses of Chinko No. 83 (III grade) with Indian barley (I grade) and Kuromugi No. 148 (II grade). Seeds were sown on September 29.
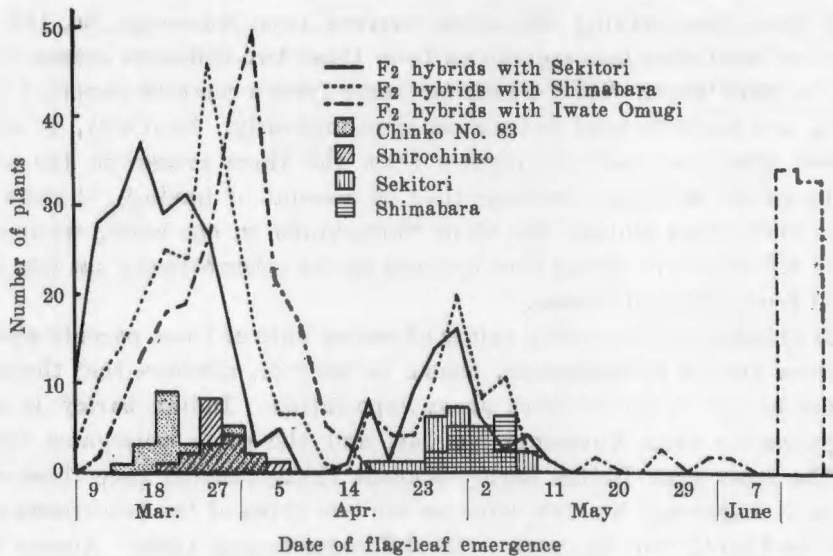
Fig. 11. Frequency distribution as regards the date of flag-leaf emergence of the F₂ hybrid plants and their parents in three crosses of Chinko No. 83 or Shirochinko (III grade) with Sekitori (IV grade), Shimabara (V grade) and Iwate Omugi No. 1 (VI grade). Seeds were sown on January 14.

the late plants with the respective winter parents. In these circumstances, the earlier group was by far larger in number than the later group without exception. As seen in table 24, the observed counts of both types in each of the crosses fit well to a 3 : 1 ratio, with earlier type being dominant over the late one. Although the actual count of the F_2 from a cross with Indian barley fitted also to a 13 : 3 ratio, all of the strains derived from the late plants in F_2 generation bred true to lateness in F_3 generation, indicating the variety having no recessive spring gene pair.

It has already been shown that Indian barley and Kuromugi No. 148 has each a single dominant spring gene, Sh_2 or such like, both being allelic to Sh_v in Natsudaikon-mugi. Therefore, it may be safe to conclude that Chinko No. 83 possess a gene pair allelic to Sh_2, which is however less effective in initiating spring growth habit than those in Indian barley and Kuromigi No. 148. If so, then, a supposition may be possible that each of three other winter varieties, Sekitori Sai No. 1, Shimabara and Iwate Omugi, possesses also an allelic gene, which is still more ineffective for initiating spring habit than that of Chinko No. 83. These are expressed in other words that a multiple allelic series are responsible for the physiologic minor differences between these varieties differing in the grade of spring habit of growth.

On the basis of this hypothesis, the alleles involved in Indian barley, Kuromugi No. 148, Chinko No. 83 or Shirochinko, and other varieties will be symbolized as Sh_2^{I}, Sh_2^{II}, $Sh_2^{III} \cdots Sh_2^{VI}$. Then, F_2 plants inheriting an allele, Sh_2^{I}, from Indian barley are expected to be earlier under continuous illumi-

nation than those having Sh_2^{II} allele derived from Kuromugi No. 148. On
the other hand, the late segregates from these two different crosses are to
have the same allele, Sh_2^{III}, which has come from a common parent, Chinko
No. 83, and hence to head out almost simultaneously. Similarly, it will be
expected that the early segregates from the three crosses in the second
experiment ear at almost the same time on account of having the same or a
similar allele from Chinko No. 83 or Shirochinko on one hand, while consi-
derable differences in earing time are seen on the other between the late types
derived from different crosses.

Examination of the mean values of earing date of these parents and the
two types among F_2 segregates, shown in table 24, discloses that the actual
data are almost in accord with above expectation: Indian barley is about
15 days earlier than Kuromugi No. 148, and the early segregates derived
from the cross with Indian barley is about 11 days earlier than those of the
cross with Kuromugi No. 148, whereas the late types of the two crosses eared
as late as Chinko No. 83, with little difference among them. Among three
other parental varieties, Sekitori Sai No. 1 and Shimabara differed only
slightly, but were apparently earlier than Iwate Omugi No. 1 which com-
pletely failed to ear and died from high temperature. The behaviors of the
late F_2 segregates of these three crosses were recognized to be almost similar
to the respective winter parent and those of the early segregates to the inter-
mediate parents, Chinko No. 83 or Shirochinko. These results thus obtained
may be a strong evidence in favor of the view that varietal differences in the
grade of spring (winter) habit of growth in barley are chiefly governed by
a multiple allelic series sited perhaps at Sh_2 locus.

Another evidence in favor of this multiple allelic hypothesis will be
presented here. This was afforded by a series of experiments which were
made to investigated the relation of the dominant spring genes involved in
each of the different spring varieties with Sh_n in Natsudaikon-mugi. As
stated before, F_1 hybrids between any one of these spring varieties to be
tested and Natsudaikon-mugi were crossed again to a winter parent, Haya-
kiso No. 2, and these triple hybrid plants were grown simultaneously under
long photoperiodic condition. The results showed that all the hybrid plants,
without exception, behaved similar to the spring parents, indicating that
the dominant spring genes involved in the spring varieties tested were allelic
to Sh_n in Natsudaikon-mugi.

It must be confessed, however, that the time and especially the range of
period of earing were different to an extent with the cross combinations. In
Fig. 12 are shown the frequency distribution histograms of eight crosses as
regards the date of flag-leaf emergence. They can be classified into two
groups, namely, hybrids with Tammi, H. E. 3649 and Shokubi-mugi, all of
which are of the first grade of spring habit, and hybrids with Sumiremochi,
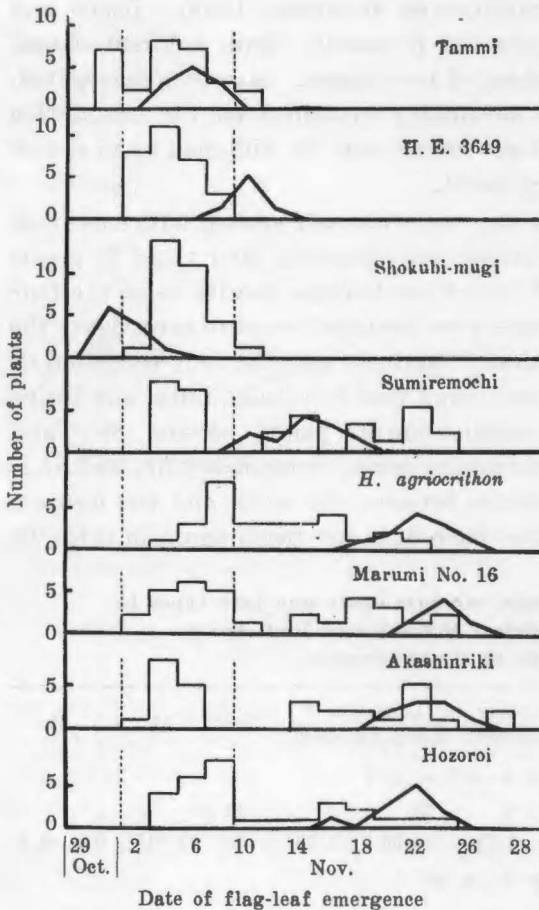*H. agriocrithon*, Marumi No. 16, Akashinriki and Hozoroi, all of which are

Fig. 12. Frequency distribution histograms of the hybrid plants derived from eight triple crosses in respect to the date of flag-leaf emergence. Date of flag-leaf emergence of the respective parental varieties is shown by frequency curves, and limits of earing date of a common spring parent, Natsudaikon-mugi, by the vertical dotted lines. Seeds were sown simultaneously on October 2.

of second grade of spring habit.

It is perceived obviously in this figure that the distribution histograms of the first three crosses are all typically uni-modal, the range of earing period being narrow, while those of the other five crosses are in general bi-modal, spreading far wider than in the former group of crosses. Furthermore, as to the earing time the earlier classes of these hybrid plants are recognized to be almost in accord with Natsudaikon-mugi, a common spring parent, and also with Tammi, H. E. 3649 and Shokubi-mugi, while the later classes which are found only in the five crosses do so with another spring parents of second grade of spring habit. And, the number of early and late spring plants segregated from the five crosses is almost equal. Hereupon, it is natural to conceive that such a differential behavior of two groups of crosses is due to the difference in the nature of the dominant spring genes derived from the eight parents differing in the grade of spring habit, since the two other parents, Na-

tsudaikon-mugi and Hayakiso No. 2, are common to all the crosses: that is to say, the dominant spring genes involved in Natsudaikon-mugi and also in Tammi, H. E. 3649 and Shokubi-mugi are regarded to be all identical, i. e, Sh_2^I, and hence no segregation has occurred in their triple hybrids. On the other hand, the spring genes in Sumiremochi and four others are to be Sh_2^{II}, and therefore two different alleles, Sh_2^I derived from Natsudaikon-mugi and Sh_2^{II} from another parent involved in the five triple crosses have resulted in the segregation of the early and the late spring types.

In connection with this, it is also of some interest that the five triple or

simple crosses with such spring varieties as Svanhals, Lutai, Ihsien and Brachytic have shown an unusual behavior; namely, three different classes, early, medium early and late, instead of two classes, have been segregated. Because, such a behavior may be adequately explained on the assumption that two spring genes involved in these crosses may be different to an extent in their ability to express the spring habit.

As was already stated, these spring varieties were crossed with a common winter variety, Hayakiso No. 2, having hairy sheaths, and their F_1 plants were again crossed with Mensury C which has hairless sheaths as in the four spring varieties. Thus, the materials were prepared so as to investigate the interrelation between character pairs of earliness and the hair condition on leaf sheaths. From the results, it was found that Svanhals, Lutai and Ihsien possessed one dominant and one recessive spring genes, sh and Sh_2, and Brachytic two independent dominant spring genes, presumably Sh_2 and Sh_3.

In order to make clear the relation between the early and the medium early segregates in these crosses, the same data are listed again in table 25,

Table 25. Segregation of early, medium early and late types in relation to hairy vs. hairless character of leaf-sheaths in five triple or simple crosses.

Items	Early type		Medium early		Late type		Total	χ^2	P.
	Hairy	Hairless	Hairy	Hairless	Hairy	Hairless			
F_1 (Svanhals × H)* × MC*									
Obsvd. No.	1	40	19	0	21	0	81		
Calc. No. **	2.58	37.92	18.96	1.29	18.96	1.29	81	3.881	0.7—0.5
F_1 (Lutai × H) × MC									
Obsvd. No.	3	39	21	0	18	0	81		
Calc. No. **	2.58	37.92	18.96	1.29	18.96	1.29	81	2.947	0.8—0.7
F_1 (Ihsien × H) × MC									
Obsvd. No.	4	43	31	2	23	1	104		
Calc. No. **	3.33	48.67	24.34	1.66	24.34	1.66	104	3.024	0.7—0.5
F_1 (Brachytic × H) × MC									
Obsvd. No.	21	16	11	15	10	12	85		
Calc. No. ***	21.25	21.25	10.125	10.125	10.125	10.125	85	3.329	0.7—0.5
Brachytic × H (F_2)									
Obsvd. No.	266	98	55	26	16	3	464		
Calc. No. ***	261	87	65.25	21.75	21.75	7.25	464	7.938	0.2—0.1

* H stands for Hayakiso No. 2 and MC for Mensury.

** On the basis of a recessive gene, sh, being linked with hs with 6.4% of recombination.

*** On the basis of independent assortment of spring genes and hairy gene.

however in which are shown number of individuals falling into the three different earing types each further subdivided into hairy and hairless classes.

It is obvious in this table that the segregation of the early, the medium early and the late types occurred almost in a $2:1:1$ ratio in the first four triple crosses, and in the last F_2 hybrid in a $12:3:1$ ratio. And, in the first three crosses the early types consisted for the most part of hairless plants, while the medium early and the late types chiefly of hairy ones. This is evidently indicative of the early type consisting of plants with the recessive spring gene, sh, in homozygous condition, as the gene has been known to be closely linked with hs for hairless sheaths. If so, the medium early type will naturally be thought to be $ShshSh_2sh_2$, while the late type is $Shshsh_2sh_2$. The actual data fitted well to the calculated on such a basis. Therefore, it will safely be concluded that the dominant spring gene involved in Svanhals, Lutai and Ihsien is less effective for the expression of spring habit than the recessive spring gene, sh, which is capable of expressing first grade of spring habit, and hence it may be adequate to symbolize this as Sh_2^{II}.

A quite similar behavior to these crosses was observed in F_2 of a cross between Kuromugi No. 148 and Mensury C. The result was stated before in some detail, and suffice it to mention that, as the result of interaction of $shshsh_2sh_2$ in Mensury C and $ShShSh_2^{II}Sh_2^{II}$ in Kuromugi No. 148, the early, medium early and late type plants have segregated in a $4:9:3$ ratio in their F_2 generation.

Situations are somewhat different for the crosses with Brachytic. This variety is certainly lower to an extent in the grade of spring habit than those varieties stated above; under continuous illumination this variety eared slightly later than Kuromugi No. 148 and almost simultaneously with Marumi No. 16, both of the varieties having ranked as II grade of spring habit. In Fig. 9 A and B was already shown the date of flag-leaf emergence of hybrid plants from the simple and the triple crosses with Brachytic. According to these figures, the earing time of the early group of the hybrid plants was almost in accord with that of Brachytic, while the medium early group of the hybrid plants was 15 to 20 days later than the former group. In a F_3 test made with the strains derived from a number of medium early and late F_2 plants, it was recognized that the medium early type eared almost simultaneously with Chinko No. 83 which was grown at the same time with the hybrid plants. It seems appropriate therefore to conceive that the dominant spring genes involved in Brachytic are those which are capable of initiating second and third grade of spring habit of growth, and that one of them may perhaps be Sh_2^{II}. It is not certain, however, whether the other gene for the second grade of spring habit is truly Sh_3 or not.

The foregoing experimental results may be summarized as follows : Varietal difference in the grade of spring (winter) habit of growth is chiefly determined by a multiple allelic series sited perhaps at Sh_2 locus. Segregation of the early, medium early and late types in the segregating generations of some spring-winter varietal crosses seems to be adequately explained on the

assumption that two spring genes involved in the spring parent are differentiated as to the capacity of initiating spring habit of growth.

7. Interaction of the growth habit genes

Some data pertaining to the interaction of the growth habit genes are presented below. As stated in sections 2 and 3 of this chapter, a considerable number of the F_2 plants from the two crosses, Shimabara × Natsudaikon-mugi and Hayakiso No. 2 × Tammi, were subjected to the F_3 progeny tests, which enabled us to presume, though not exactly, the genetic constitution of each F_2 plants regarding spring vs. winter habit. A close linkage between *Hshs* for sheath-hair condition and one of the growth habit gene pair, *Shsh*, was useful for the classification of the genotypes. In table 26 are shown the mean days from sowing to flag-leaf emergence of various genotypes classified among the F_2 populations of the cross between Shimabara and Natsudaikon-mugi.

Table 26. Mean days from sowing to the emergence of flag-leaves and its probable errors of various genotypes involved in F_2 of a Shimabara × Natsudaikon-mugi cross.

	Spring type in F_2 (phenotype)		Winter type in F_2 (phenotype)	
	Homozygous spring type	Heterozygous types for growth habit	Winter homo. (AAbb)	Heterozygous (Aabb)
HsHs	34.9±0.389 (AABB)[1]	40.4±0.435 (AABb)	179.7±0.800	183.3 —
Hshs	35.4±0.384 (AaBB)	39.5±0.388 (AaBb)	185.6 —	182.8±0.636
hshs	35.1±0.282 (aa—)	39.0 — (AaBb)	—	184.7 —
Mean	35.1±0.145	39.8±0.318	180.7±0.882	183.0±0.693
Difference	4.7**		2.3	

(1) Aa and Bb stand for the gene pairs *Shsh* and *Sh₂sh₂*, respectively. The genotypic constitution shown in parenthesis were inferred from the close linkage of *Shsh* with *Hshs*.

** Significant on 1% level.

According to table 26, there is no marked difference in earliness among three genotypes involving either of the spring genes, *shsh* or Sh_2Sh_2, in homozygous condition, and also among three others which are all heterozygous for Sh_2sh_2 gene pair. However, the homozygous types for Sh_2 are 4.7 days earlier in average than the heterozygous types, the difference being significant on 1% level, whereas no significant difference has been found between the homozygotes and the heterozygotes for *Shsh* gene pair, which are differentiated among the spring and the winter plants. The result indicates an interesting fact that Sh_2 is incompletely dominant over sh_2, and slightly lower grade of spring habit is exhibited by the heterozygote for Sh_2sh_2 gene pair, while Sh_2Sh_2, and *shsh* as well, is capable of initiating the highest grade of spring habit.

It is to be expected that a more complicated state of interaction between growth habit genes is manifested in a cross between Hayakiso No. 2 and Tammi, in which three pairs of genes are involved. With a technical reason, however, complete discrimination of various genotypes involved in this cross was very difficult, and only eleven types were distinguished according to their behaviors in the F_3 generation. In table 27 are shown the mean days from seeding to flag-leaf emergence of these different types.

Table 27.　Mean days from sowing to flag-leaf emergence of various types differentiated in F_2 of a cross between Hayakiso No. 2 and Tammi.

	Spring type (F_2)				Winter type (F_2)	
	Bred true	Segreg. in 61 : 3 or 15 : 1	Segreg. in 13 : 3 or 3 : 1	Mean	Bred true	Segreg. in 1 : 3
HsHs	29.4±1.208	29.7±0.953	39.8±1.426	32.8±0.875	155.8±1.744	163.0　—
Hshs	27.4±0.603	30.1±1.204	33.8±1.067	29.7±0.565		145.7±2.730
hshs	26.8±0.515			26.8±0.515		155.0　—
Mean	28.0±0.571[1]	29.6±0.713	36.3±0.916		155.3±1.744	147.7±2.232

(1) Calculated excluding *hshs* type.

Comparison of the mean values of the seven types distinguished among the spring-type plants in F_2 revealed that F_2 plants which segregated in F_3 in a 3 spring : 1 winter ratio were the latest of all, and those which segregated in F_3 in a 13 spring : 3 winter ratio were somewhat earlier than the former. The other five types were all significantly earlier than these two, but no difference was recognized statistically among them. Since the latest type has only either of the dominant spring genes, Sh_2 or Sh_3, in heterozygous condition and the next late type is heterozygous for both the recessive spring gene and either of the dominant ones, it seems probable that either of the dominant spring genes or both are incompletely dominant, making plants slightly later in heterozygous condition than in homozygous condition. On the contrary, Sh gene in heterozygous condition seems to make plants somewhat earlier than those which are homozygous for this gene pair. Judged from the condition of *Hshs* gene pair which is known to be closely linked with *Shsh*, *shsh*-type seems to be the earliest of all. It is also interesting to note that two dominant spring genes, Sh_2 and Sh_3, present both in heterozygous condition are similar in effect on earliness to either or both of them present in homozygous condition.

8.　Modifiers of the growth habit genes — Polygenic inheritance of earliness of vernalized hybrid plants grown under long photoperiodic condition

Spring vs. winter habit of growth is certainly the most important factor which determine the earliness of cereals grown under long photoperiodic

condition. But, it seems also as true that the growth habit is not a unique inner factor, and the date of earing under such a condition is affected to an extent by the other factor or factors for which may be given a general term, "earliness" factor in narrow sense. This will be justified by the result of an experiment stated below.

As was already stated in section 1, we studied the F_2 behaviors of six crosses made between different winter varieties and a common spring variety, Mensury C, under 24 hours' illumination in a glass house, and found that each of these crosses segregated spring and winter plants in a 1 : 3 ratio. It must be confessed, however, that the earing time of the hybrid plants was somewhat different with the crosses.

In table 28 are shown the mean days from sowing to flag-leaf emergence

Table 28. **Mean days from sowing to flag-leaf emergence.**

Mensury C crossed with	$\bar{P} \pm P.E$	F_2 segregates	
		Early	Late
Sekitori (IV)	161.2 ±2.4271	56.8±1.3996	156.7± 6.2948
Sakigake (IV)	161.6 ±0.9251	43.8±1.0858	151.8±13.1981
Dairokkaku No. 1 (IV)	162.2 ±1.0958	68.6±1.5156	161.8± 6.6737
Shimabara (V)	170.3 ±2.7988	60.4±1.3583	162.8± 5.8329
Kesajiro (VI)	183.5*± —	83.1±1.6483	170.3±13.4798
Iwate Omugi No. 1 (VI)	189.5 ±3.8529	73.9±0.8290	177.3± 7.0539
Mensury C (I)	77.8 ±0.7545		

* Calc. on only two plants.

of early and late types of F_2 and their parents in each cross. As seen in this table, the late-F_2 segregates of each cross behaved almost alike to their respective winter parent, though the former eared in general several days earlier than the latter. Discrepancies between these late segregates from these different crosses regarding earing date seem to be explained adequately on the basis of the different alleles which has each inherited from the respective winter parents differing in the grade of spring habit.

It was expected, on the other hand, that behaviors of all the early-F_2 segregates from these different crosses would be almost alike to that of Mensury C. Because, they had been inherited the same gene, *shsh*, from the common parent, Mensury C. However, these early-F_2 types from different crosses differed considerably regarding their earing time. For example, mean days to earing of the early type from the cross with Sakigake was only 43.8 days, which was 34 days earlier than Mensury C, while that of the cross with Kesajiro was 83.1 days and about 5 days later than Mensury C. Therefore, these marked difference in earing date is apparently indifferent of spring vs. winter habit, and it must necessarily be attributed to some certain other genetic causes.

In order to make the situation more clear, an experiment was conducted with the same materials as above. This time, however, all the germinated seeds of hybrids and parents were sufficiently vernalized by means of exposing them to low temperature of 3°C for 50 days or more. Thus, the materials were prepared so as to be free from any degree of winter habit of growth which might otherwise influence so much to earing date as to make the physiological difference under consideration obscure. Three hundred and twenty F_2 plants from each cross and 40 plants of each of the parents were raised in spring from April 3 to early June under 24 hours' illumination in a glass house.

Earing reaction of these hybrids and their parents was, as a matter of course, different entirely from that arose in a similar experiment made with the unvernalized materials; all plants finished earing by June 3, about two months after sowing. The frequency distribution of F_2 plants from each cross was of normal type. In table 29 are shown mean days from sowing to

Table 29. Mean days from sowing to flag-leaf emergence under continuous illumination of sufficiently vernalized plants from various F_2 and their parents, and heritability percent for earliness.

Cross combination	$\overline{P} \pm$ P.E.	Mid-parent	$\overline{F_2} \pm$ P.E.	Heritability percent
Sekitori Mensury C	31.6±0.1635 36.7±0.2848	34.1	34.0±0.1941	84.79
Sakigake Mensury C	31.3±0.1802 37.0±0.1844	34.2	31.4±0.1757	84.39
Dairokkaku 1 Mensury C	40.2±0.3352 36.8±0.3181	38.5	39.7±0.1880	65.26
Shimabara Mensury C	39.1±0.2503 37.4±0.3847	38.2	39.5±0.2720	85.83
Kesajiro Mensury C	47.5±0.6769 38.4±0.3430	43.0	44.8±0.2937	67.91
Iwate Omugi 1 Mensury C	45.9±0.5034 35.1±0.2703	40.5	40.5±0.2937	33.11

flag-leaf emergence of F_2 plants from these crosses and their parents. Heritability percent in broad sense was also calculated separately from the available data and listed together in the table.

As apparent in table 29, most of the F_2 means of these crosses differ significantly each from other. And, in each cross F_2 mean is recognizable to be almost alike to the value of its mid-parent, with one exception of the cross with Sakigake, in which the former value is somewhat smaller than the latter. It seems, therefore, that, if the difference between any two of these crosses were under genetic control, it may chiefly attributed to the genetic difference between the winter varieties crossed with a common parent.

It is obvious, however, that such a minor difference can not be analysed by means of ordinary Mendelian method. The continuous nature of the variation of F_2 plants in its frequency distribution indicates it being under

the control of polygenes. And, agreement of the values of mid-parents and
F_2's means in most of the crosses suggests that no dominance or epistasis is
involved, and at the same time the effects of the polygenes are simply additive.
Therefore, heritability percent was calculated for each cross according to
the following formula, which are as listed in the last column of the table 29.

$$\frac{V_{F_2} - \frac{1}{2}(V_{P_1} + V_{P_2})}{V_{F_2}} \times 100$$

As the result, heritability of the "earliness" differentiated between parents,
was found to be considerably high in five out of six crosses, indicating ob-
viously that the difference in earliness was in the most part under genetical
control. As the consequence, the differences between these crosses which is
in fine those between the winter varieties included in these crosses, are
possibly conceived to have arisen by the polygenic differences.

In conclusion, all the evidence available indicates that there is an inner
physiologic factor which affects earliness independently of spring vs. winter
habit of growth, and that this factor is under the control of polygenes.

It seems pertinent to give an account here of a fact that earliness under
long photoperiodic condition is modified to an extent by a certain qualitative
gene or by those in linkage to it. This was first found by chance in the
course of an experiment with the use of a Shimabara × Natsudaikon-mugi
cross. To show the situation clearly, F_2 plants of this cross were classified
into six types by three contrasted characters, namely, normal vs. uzu growth
habit, hairy vs. hairlessness on basal sheaths, and also spring vs. winter
habit, and mean days to flag-leaf emergence of these types were calculated
and listed in table 30. It is obvious in the table that uzu-type plants need a

**Table 30. Mean days from seeding to flag-leaf emergence of normal
and uzu plants subdivided each into three different types
in F_2 of a Shimabara × Natsudaikon-mugi cross.**

| | Spring type | | Winter type |
	Hairy	Hairless	Hairy
Normal	37.0±0.165	35.7±0.192	181.3±0.589
Uzu	42.1±0.341	39.2±0.447	184.8±0.705
Difference	−5.1*	−3.5**	−3.5*

* and ** indicate to be significant on 5% and 1% level, respectively.

few days longer time to ear than the contrasted normal-type plants, the
difference between two types in each column being statistically significant.
Moreover, with respect to the number of leaves on the main stem plants of
uzu type have in general one or two more leaves than those of the normal
type, which may be an evidence supporting above fact. And, it is possible
to assert that this has not occurred by accident, but is very common, because

quite a similar relation has been confirmed in the F_3 families of this cross
and many others which included a gene pair for normal vs. uzu character.

V. GEOGRAPHIC REGULARITIES IN THE DISTRIBUTION
OF THE GENES FOR SPRING GROWTH HABIT

It is convincing that among the numerous genetic changes that affect
adaptability of barley to various climatic conditions, those responsible for
spring and winter habit of growth may be the most important. In places
where grounds are covered with heavy snow for a long time or have severe
cold winter, barley are generally sown in spring, and naturally, varieties of
high spring habit are required exclusively. On the other hand, barleys sown
in the fall are variable with respect to the growth habit. There are, however,
such regularities in their geographic distribution as follows : In the northern-
most part of fall-sown regions varieties should have the highest degree of
winter habit in order that ear will not be formed before exposure to low
temperature and short photoperiod for long time and thereby overwinter
safely. Down to south where the winter climate is more or less warm varie-
ties with intermediate growth habit are mostly required. In the subtropical
zone, however, pure spring type is preferred, because warm winter climate
may, otherwise, make the plants unable to form normal ears. The details
will be stated in other opportunity.

Meanwhile, a considerable number of spring varieties originated from
different regions of the world were subjected to the genic analysis, and their
genic constitutions for growth habit were disclosed. Summing up these data
varietal frequencies of four main genotypes in different countries or regions
of the world are shown in table 31. This may show also well geographic
distribution of three different genes for spring habit of growth.

Table 31. Geographic distribution of spring barleys with different genotypes.

Countries or Regions	$shSh_2Sh_3$	$shSh_2$	Sh_2Sh_3	sh	Sh_2	Total
U. S. A.	2		1		2	5
Europe	4	4			1	9
Russia		3				3
Manchuria & N. China		4				4
North Korea		4		1		5
India		1			1	2
Central China & S. Korea					5*	5
Formosa					3	3
Japan {exotic		5		2		7
Japan {endemic					8	8
Total	6	21	1	3	20	51

* Inclusive of a wild barley, *H. agriocrithon.*.

It is perceived in the table that in south-eastern Asia wherein barley is generally sown in the fall, are distributed spring varieties with a single dominant gene, Sh_2Sh_2. It may be noted also that most of them are somewhat lower in the grade of spring habit. Besides them, there exist a few in which each have a single recessive spring gene, $shsh$, but they are all suspected to have arisen by hybridization with some foreign barleys. The remaining vast regions of the Old World, where spring-sowing is generally practised, is chiefly occupied by varieties with two or three pairs of spring genes, namely, $shshSh_2Sh_2$ or $shshSh_2Sh_2Sh_3Sh_3$, together with a few exceptions which have one or two pairs of dominant spring genes. Thus, in the distribution of the genes for spring habit of growth there is such a geographic regularity that in the "Oriental" region are found exclusively one of the dominant genes, Sh_2, and its allelic series, while in the "Occidental" region are spread widely a recessive gene, sh, and sometimes another dominant gene, Sh_3, which are always associated with Sh_2, a gene common to the Oriental barleys.

Although data hitherto obtained are insufficient, the following supposition may be warranted. Since a type of *Hordeum agriocrithon*, a putative ancestor of cultivated barley, collected from East Tibet, is known to have Sh_2 gene, the gene may have been inherited further by the cultivated barley forms now grown in Oriental and perhaps also in Occidental regions. Limited geographic distribution of sh gene suggests, on the other hand, that it might have originated somewhere within Occidental region perhaps by mutation occurred in cultivated form or forms. As to the origin of Sh_3 gene which is confined to northern Europe, a similar thought also occurs to our mind. Another speculation is that the gene, Sh_3, has been derived from a two-rowed wild barley, *Hordeum spontaneum*, which includes many varieties of winter type and, according to Vavilov, some of spring type as well. Anyhow, it is not impossible to suppose that the composite genotypes involving these spring genes altogether or these new spring genes themselves might have played a part in spreading barley crops northwards. Because, barley is originally a crop plant of temperate zone where comparatively short day is prevailing during its growing period.

In connection with this, following relations may be worth while considering. As already demonstrated previously by one of the authors, there is a geographic regularity in the distribution of two recessive genes, s and hs, for short-haired rachilla and hairless condition of leaf-sheath, respectively; namely, barleys with short-haired rachilla are distributed all-over the "Occidental" region, whereas varieties in the "Oriental" region are all characterized by long-haired rachilla. Distribution of hairless sheath character is somewhat complicated, but it is possible to point out that most of the spring varieties in the Occidental region are hairless in the sheath, while one half of the winter are hairy (Takahashi *et al*. 1947, 1948). It was apparently difficult, however, to conjecture the ecologic or some certain implication

of these geographic regularities because both of these character pairs are
seemingly indifferent at all of adaptation or agronomic usefulness. But, a
finding that *hs* is closely linked with *sh*, and *s* is also linked with Sh_2 enabled
us to suppose that these neutral characters might have spread over the
Occidental region accompanied by these ecologically important genes. In this
case, it must of course be presumed that genotypes having *sh* and *hs*, and
also Sh_2 and *s* in linked condition had been established before or during their
spreading.

It should be granted, however, that these are rather speculative, and
require more evidences in favor of them. Studies on the interrelation between
these spring barleys and some spring types of *Hordeum spontaneum*, and
also on the ecological significance of the composite genotypes as well, may
throw light upon these problems.

VI. DISCUSSION

Purvis and Gregory (1937) postulated a hypothesis regarding the physio-
logical nature of spring and winter habit of growth, the sum and substance
of which is as follows: In a spring rye a hypothetical "flower-forming"
substance or its precursor is already present in high concentration, but only
long days do the early members of the series of labile primordia form
spikelets. It appears, therefore, two stages are involved in the process. A
precursor depends for its formation on a genetic factor in spring rye and on
low temperature of germination in winter rye. A second stage in the process
involves reaction depending on day length. They showed also that date of
earing of winter plants was hastened by exposing to short days for a few
weeks at its young stage, whereas in spring plants it was always retarded
by the same treatment. This hypothesis is not new at present, and progress
of physiological and physico-chemical studies may necessitate some alteration.
A thought that the plant is tending in the direction of flowering at all times
but is kept from doing so by the production of flower-inhibiting substance,
instead of assuming flower-forming substance, may be right (Nayler 1953).
Apart from this point of question, however, this hypothesis is still of
importance as this correctly points out the general nature of spring and
winter habit of growth in cereals. From genetical point of view, this may
be interpreted as such that a typical spring plant possesses a gene or genes
responsible for the formation of sufficient precursor of ear-forming substance,
while its allelic gene or genes involved in a winter plant are not or less effec-
tive in producing such precursor unless exposed to low temperature. If so,
and taking into consideration of the existence of various intergrades between
typical spring and winter habit, it may be conceivable in fine that difference
between spring and winter habit is concerned with the quantitative difference
in productivity of such precursor (or flower-inhibiting substance). The

hypothesis suggests also that whether a plant has a spring gene or not is to be inferred from its earing reaction under long photoperiodic condition. In fact, it has been well-established in various winter cereals that a spring plant and a winter one are differentiated by the earing reaction under a condition of long photoperiod and high temperature, and this is also true to the case of any two intermediate types existing between typical spring and typical winter ones.

It should be emphasized herein that the environmental condition, especially day length and temperature, must be arranged to answer the purpose as well as possible. That the results of outdoor experiments made in spring without any control of light and temperature sometimes fail to tell the truth were demonstrated by Bell (1939), Hoffmann (1944) and also by us. Furthermore, according to our unpublished data, responses of vernalized barley plants to a more or less shortened photoperiod are governed by a genetic system quite different from that for responses to the condition of 24 hours' illumination. These are the reason why we made our experiments under a controlled condition.

As stated before, most of the published data by various authors are those obtained from outdoor experiments. Materials used are also different from ours. It is no wonder, therefore, that some results contradict to ours or are difficult to explain on the basis of the hypothesis deduced from our experiments. Nevertheless, most of these authors have confirmed that spring vs. winter habit of growth is governed by a major gene or a few major genes, with dominance of spring habit over winter one. There are also some results indicating the existence of another recessive spring gene. This suggests that some winter plants may be possibly segregated from a cross between spring varieties. In fact, it has been confirmed that a cross between two spring varieties, Mensury C and Kuromugi No. 148, has segregated in F_2 generation winter-type plants in a ratio of 3 against 13 spring type. Linkage of some of the spring genes with smooth-awnedness and also with sheath-hair characters has been also suggested by some authors. Since these facts or suggestions have been well established by us also, there may be no need to discuss about them here again.

Although little has been discussed as to the interaction of the genes for growth habit in barley, several authors have obtained results suggesting that the genes for spring habit are in general epistatic to the non-allelic genes for winter habit of growth. As stated before, Gaines' result (1917), which was accounted for by assuming a dominant winter gene and its inhibitor, may also be explained on the basis of epistasis of dominant and recessive genes for spring habit to the winter genes. Neatby (1929), Huber (1932), Kuckuck (1933) and Grevennikov (1935) are of opinion that all or almost all of the genes for growth habit or earliness should be recessive for the expression of winter habit of growth. This implies the spring genes being epistatic to the

non-allelic winter genes. Furthermore, it has been proved by Neatby (1929) that there is a negative correlation (r = −0.4053) between the proportion of winter plants in F_3 lines and the earliness of the F_2 plants of spring type from which they have been derived. This indicates that more than one of the winter habit factors are concerned in the growth period of the spring plants. A similar relation was also confirmed by Kuckuck (1933). In this connection, Powers' result (1934) appears to be more instructive and interesting for us. He made a close examination of interaction of the growth habit genes in a wheat cross involving two dominant and one recessive spring genes, A, B and c, and postulated a working hypothesis for the nature and interaction of the growth habit genes. According to this hypothesis, AA is epistatic to bb and CC, BB to aa and CC, and cc to aa and bb. These gene pairs for growth habit are not duplicate genes as regards their effect upon earliness, and earliness is dependent upon quantity and kind of the growth habit genes present: AA is a gene for early maturity, causing plants to ripen earlier than $aaBBcc$, which causes plants to be of medium early. $aaBBCC$ and $aabbcc$ cause to be late in ripening and $aabbCC$ causes winter habit of growth. The interaction of BB and CC is such that BB is only partially epistatic to CC as to earliness. It was also indicated that spring genes in homozygous condition make plants ripen earlier than the genes in heterozygous does. These results have led him to a conception that the reaction of AA, BB and cc are rate factors in development, the strength of the reaction process depending upon the initiating factor.

In the majority of the spring-winter varietal crosses tested in our experiments, it has been confirmed that the spring-type plants and the winter ones eared at quite different periods, forming two discrete groups as regards their earing time. Furthermore, these two types were found to segregate in 13 : 3, 61 : 3 or 15 : 1 ratios in most of the crosses involving two or more spring genes. These facts immediately suggest us that a plant having at least a single or one pair of spring gene is always of spring nature and ready to head out without any delay under continuous illumination at moderately high temperature, and this is true irrespective of the kind and number of the spring genes involved in it. Winter habit of growth, on the other hand, is exhibited only when a plant has none of these spring genes. For example, a genotype, $shshsh_2sh_2sh_3sh_3$, is of spring type in spite of the presence of two winter genes, sh_2sh_2 and sh_3sh_3, and can ear as early as $shsh\ Sh_2Sh_2Sh_3Sh_3$, as the former has a single pair of spring gene, $shsh$. This will be expressed as such that any one of the spring genes is epistatic to the non-allelic winter gene or genes ; for example, that $shsh$ is epistatic to $sh_2sh_2sh_3sh_3$ in the above instance.

It is not difficult to present a number of instances similar to these. As shown in section 6 of chapter IV, the early group of the hybrid plants from the triple crosses involving two spring genes, sh and Sh_2^{II}, were composed of

two kinds of genotypes, namely, $shshSh_2^{II}sh_2$ and $shshsh_2sh_2$, and both of the genotypes eared more than 25 days earlier than the medium early group with a constitution of $ShshSh_2^{II}sh_2$. The result clearly indicates that the weaker spring gene Sh_2^{II} in this case, does not affect the earing date when associated with a stronger gene, $shsh$, or simply that $shsh$ is epistatic to Sh_2^{II}. The same was true to the case of two dominant spring genes, presumably Sh_3 and Sh_2^{III}, involved in the simple and triple crosses with Brachytic, in which Sh_3 for second grade of spring habit has been epistatic to Sh_2^{III} for third grade of spring habit. In the absence of the stronger gene, however, Sh_2^{III} was capable of exhibiting its own physiological reaction, making plant to behave as a medium early type. Thus, it seems to be general that the stronger gene for expressing spring habit is always epistatic to the weaker ones.

It is also of interest in this connection to note that in the experiments dealing with various crosses between varieties differentiated in the grade of spring or winter habit of growth, the alleles capable of initiating higher grade of spring habit have been found to be always dominant, though not completely as shown below, over those for lower grade of spring habit, but, the latter alleles in the homozygous condition were able to exhibit its physiological reaction and have made plants to behave in accordance with the respective grades of spring or winter habit of growth, unless other stronger gene coexisted.

These results suggest us that the effects of these growth habit genes are not cumulative, and earing reaction under long photoperiod, or grade of spring habit, of a certain genotype is determined only by the gene with strongest capacity of initiating spring habit, irrespectively of whether the other genes involved are those for spring or winter habit of growth.

Studies of the F_3 behaviors in a few crosses indicated also that the gene pairs for growth habit are incompletely dominant in general. Furthermore, $ShshSh_2sh_2Sh_3sh_3$, $ShShSh_2sh_2Sh_3sh_3$ and also $Shshsh_2sh_2Sh_3sh_3$ proved to be slightly earlier than $ShshSh_2sh_2sh_3sh_3$ or $Shshsh_2sh_2Sh_3sh_3$, which were, however, somewhat earlier than $ShShSh_2sh_2sh_3sh_3$ or $ShShsh_2sh_2Sh_3sh_3$. These behavior may be interpreted as similar to those found by Neatby (1929) and Kuckuck (1933), as well as that confirmed by Powers. It may be noted, however, that these intra-and inter-allelic interaction of the growth habit genes affects earliness so slightly as to make impossible in detecting it, unless a considerable number of plants are available. It was also shown that a number of minor genes are also repsonsible for the earliness under long photoperiodic condition. Although these data are insufficient, it may be right to consider at any rate that earliness under long photoperiodic condition or grade of spring habit is modified, though slightly, by quantity of the growth habit genes and also by a number of minor genes independent of these major genes. The major determinant of the growth habit is doubtlessly the quality of the growth habit genes.

The various results discussed above indicates interaction of these growth habit genes being rather simple.   All the evidences afforded by our experiments seem to lead conformably to a simple conclusion that these three gene pairs for growth habit including a series of multiple alleles may interact each with others as if all of them were alleles sited on a single locus of a chromosome. This is almost the same as what Powers (1934) has attained from his experiment on a wheat cross. Consequently, a working hypothesis may be possibly suggested that these three pairs of growth habit genes may affect one and the same physiological process, in determining quantitatively the productivity of a hypothetical precursor of flower initiating or flower inhibiting substance.

There remains a question how and why such growth habit genes on different locus have differentiated in cultivated barley which has only the basic number of chromosomes. An approach to the problem may be possible through ecological and phylogenetical studies.

VII. SUMMARY

For the partial fulfilment of our aim to have a deeper insight into the physiological and genetical nature of ear emergence in barly and wheat, and thereby to contribute to the breeding of early varieties, a study was made on the inheritance of spring vs. winter habit of growth in barley. As the materials more than ninety crosses involving 52 spring and 13 winter varieties of barley, which were originated from various parts of the world were used. For the sake of obtaining accurate data, almost all of these crosses were grown under 24 hours' illumination in a glass house, which was sometimes heated if necessary in winter. For the economy of space, an intensive method of growing barley plants was devised. The results obtained may be summed up as follows.

1.   At least three kinds of major gene pairs are responsible for the spring vs. winter habit of growth in barley. They are designated as $Shsh$, Sh_2sh_2 and Sh_3sh_3. Any one pair of the genes, $shsh$, Sh_2Sh_2, and Sh_3Sh_3, or two or three pairs of them involved in a genotype causes plants to express spring habit of growth. For the expression of winter habit are necessary all of the three genes, Sh, sh_2 and sh_3, in homozygous condition or in heterozygous only for the recessive spring gene, sh.

2.   The spring varieties tested are possibly classified into the following five groups, consisted of almost all possible combination of three spring genes, $shsh$, Sh_2Sh_2 and Sh_3Sh_3; namely, (1) $shsh$, (2) Sh_2Sh_2, (3) $shshSh_2Sh_2$, (4) $shshSh_2Sh_2Sh_3Sh_3$ and (5) $Sh_2Sh_2Sh_3Sh_3$. No variety having Sh_3Sh_3 or $shshSh_3Sh_3$ genotype has been found, however.

3.   A recessive spring gene and also one of the dominant spring genes, each involved in a number of different spring varieties tested, proved to be

identical with or at least allelic to each other, namely they are Sh_2 and sh, respectively.

4. Linkage of two gene pairs, $Shsh$ and Sh_2sh_2, with some morphological character pairs were established; $Shsh$ was linked with $Hshs$ for sheath-hair character pair with the recombination value of 6.4% in average. Their linkage groups has not been ascertained. Sh_2sh_2 is located in linkage group V. The recombination percentage with Ss for long- vs. short-haired rachilla was found to be 38.5% or 36.4% or 20%, while that with Rr for rough vs. smooth awn was 14%. Independent inheritance of Sh_2sh_2 with Vv for non-six-row vs. six-row and Ee for normal vs. elongated outer glume, both in group I, Nn for covered vs. naked grains and Ll for lax vs. dense ear, both in group III, and also with $Uzuz$ for normal vs. uzu growth habit in group VI was ascertained.

5. A multiple allelic series sited at Sh_2 locus are found to be responsible for the difference in earing reaction between varieties differentiated with respect to the grade of spring (winter) habit of growth. They are tentatively symbolized Sh_2^I, Sh_2^{II}, and so on. Varieties having any one pair of these intergraded alleles together with $ShSh$ and sh_3sh_3 both for winter habit, are capable of exhibiting its corresponding grade of spring habit, and hence ear more or less later than typical spring form under long photoperiodic condition. Several varieties were found to have each $Sh_2^{II}Sh_2^{II}$ or $Sh_2^{III}Sh_2^{III}$ together with $shsh$ or Sh_3Sh_3, which, however, expressed the highest degree of spring habit — earing very early.

6. It seems that the effects of these growth habit genes are not cumulative, and that a gene which effect is stronger for the expression of spring habit is in general epistatic to the other weaker genes. Consequently, the grade of spring habit of a certain genotype is determined only by the gene with the strongest effect.

7. A slight difference in earing time was recognized between plants having a single spring gene in homozygous condition and those in heterozygous condition, indicating incompleteness of dominance of growth habit genes.

8. Earliness under long photoperiodic condition seems to be affected to an extent by a physiological factor which may be called as "earliness" factor in narrow sense, besides by spring vs. winter habit of growth. It was shown that such a minor difference in earing time was governed by a polygenic system and also by $Uzuz$ gene pairs itself or those linked with this gene.

9. There are geographic regularities in the distribution of the genes for spring habit; spring barleys distributed in south-eastern Asia are those having some one of allelic series of Sh_2 only, while in the other parts of the Old World are spread the recessive spring genes, sh, widely, and also Sh_3 rather rarely, which are always associated with Sh_2^I or Sh_2^{II}.

10. Interaction of the growth habit gene pairs was discussed from the physiolgical point of view.

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