Physiological and Genetical Characters for Early Maturity in Barley and Common Wheat

Shozo YASUDA*

ABSTRACT: Physiology and genetics of early maturity in cereals are the subject of practical as well as scientific interest for agronomist and plant breeders. Thorough understanding of the true nature of such a complex character requires physiological and genetical knowledge about the internal factors, which are closely bound up with and react to some particular external or environmental factors. From the practical point of view, experiments should be conducted under controlled conditions, especially the day length and temperature, so that the genotypic differences pertaining to these factors may be discerned.

Takahashi and Yasuda (1958, 1970) maintained that at least three physiological factors were responsible for determining earliness in barley, namely, (1) spring and winter habit of growth or vernalization requirement, (2) photoperiodic response or sensitivity to short-day, and (3) earliness factor in a narrow sense or minimal vegetative growth. The same situations were true in common wheat also (Yasuda and Shimoyama, 1965).

In this report, physiology and genetics of internal factors and their relations to the time of heading in the field will be presented with some problems concerning differences in mechanism of early maturity between barley and wheat

INTERNAL FACTORS AND THEIR RELA-TIONS TO THE TIME OF HEADING IN THE FIELD

It is well known that barley and wheat have a nature with wide range of vernalization requirement from highly spring habit to extreme winter habit. We called this "grade of spring habit". Experimentally, grade of spring habit of a variety is estimated by the method that seeds of the same variety are sown at 10-or 15-day intervals from early spring to early summer when natural day-length becomes longer. Earliness and lateness of the critical sowing date for normal heading is used as the criterion of the grade of spring habit, in which the earlier the critical date, the lower the grade of spring habit. We are conventionally classified into six or seven categories denoted by Roman figures, I to VI or VII, Where I stands for most extreme spring habit and VI or VII, differing in research workers, for the extreme winter habit. According to Yasuda (1961) and Ha (1976), the

barley varieties graded II, III, IV, V and VI require 10, 20, 30 and 40 days, or more at 3-5°C, respectively, for through vernalization. Another conventional method is to estimate the grade of spring habit of a variety by the use of earliness in heading under 24-hour/day at moderately high temperature, though some inaccuracy is accompanied in the estimation.

As to effect of temperature on heading time of the plants, it was shown by Takahashi and Yasuda (1960) that there is no significant difference among barley varieties in sensitivity to temperature, in a sense that all the varieties fully vernalized or of highly spring habit are equally accerelated by a rise of temperature within a certain temperature range, when grown under continuous illumination. The same situations were recognized in wheat varieties (Yasuda and Shimoyama, 1965).

Photoperiodic response is another important internal factor that strongly affects the time of heading of barley, but its expression is highly conditional (Takahashi and Yasuda, 1960). Figure 1 shows heading response of spring varieties and fully vernalized win-

^{*} Research Institute for Bioresources, Okayama University, Kurashiki, Japan (Received May 12, 1990)

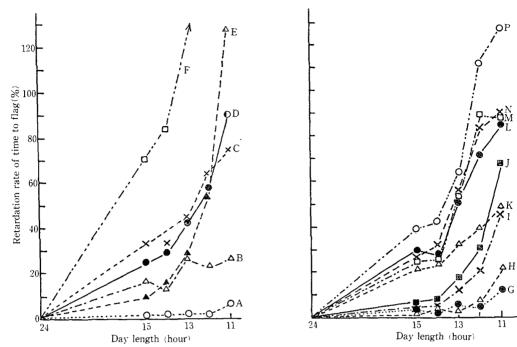


Fig. 1. Comparison of retardation rate of flag-leaf emergence under 15-to 11-hour/day against 24-hour/day. Left: spring vars.(A-F), Right: winter vars.(G-P). (Takahashi and Yasuda, 1970).

ter varieties of barley to various day-length under high temperature suitable to growth. A marked difference in heading time was observed among varieties when grown under a shortened photoperiod, whereas under 24-hour/day all of them headed out very early and almost simultaneously. In other words, some varieties are day-neutral while some are extremely long-day type or sensitive to short photoperiod, and some others respond intermediately to the more or less shortened photoperiod. It is known that barley and wheat plants with winter habit of growth can be vernalized by exposure to short photoperiod, though it is not so effective as compared with exposure to low -temperature. Therefore, determination of photoper-

iodic response of a winter barley and wheat must be preceded by full vernalization before planting.

The third internal factors will be called "earliness factor in a narrow sense". It is clearly recognized that, when the highly spring habit or fully vernalized plants of barley are grown under long photoperiodic conditions, some varieties always head out several to 10 days earlier than other varieties. These earlier varieties also develop a smaller number of leaves on the main stem. Such a difference in date of heading in response to the condition of long photoperiod has been confirmed to be a character peculiar to the variety. Quite same situations as those of barley varieties were found among wheat varieties (Yasuda and

Table 1. Three internal factors in fall-sown barley and wheat

Internal factor	Testing method
Grade of spring habit	(1) Length of treatment by low temperature
(Vernalization requirement)	2) Successive sowing in early-to late-spring
•	3) Capability of heading under 24-h/day at
	high temperature
Photoperiodic response	Earliness under short-day at high temperature
(Sensitivity to day-length	after vernalization
Earliness in a narrow sense	Earliness under long-day at high temp, after
(Minimal vegetative growth	after vernalization

Table 2. Interrelations between heading time under outdoor condition |Y| and its three internal factors $|x_1|$, $|x_2|$ and $|X_3|$

Itoma	C	ent	b^1	
Items	$\overline{X_2}$	X_3	Y	Y on x
x ₁ Grade of spring habit				
Japanese cvs	. 03	.31*	.00	04
Korean cvs	,12	.43**	.02	18
Ethiopian cvs	.68**	.69**	.66**	.09
Wheat	.24*	.32**	. 47**	. 26
x ₂ 12-hour day vernal,				
Japanese cvs		.57**	.79**	.72
Korean cvs		.74**	.78**	.51
Ethiopian cvs		.86**	.88**	. 68
Wheat		.68**	.87**	.73
x ₃ 24-hour day vernal.				
Japanese cvs			.53**	.14
Korean cvs			.60**	.27
Ethiopian cvs			.78**	.02
Wheat			.70**	.13

^{*.**:} Significant at 5% and 1% levels, respectively.

Shimoyama, 1965'. Test methods of three internal factors stated above are summarized in Table 1

In order to determine how earliness of fall-sown barley and wheat are affected by these three internal factors, four experiments were performed at Kurashiki. One of them was made using 65 barley varieties from different parts of Japan (Takahashi and Yasuda 1985'. The time of heading of each variety under the outdoors was determined by sowing on November 15 in eight years in the fieled. Photoperiodic response and earliness in a narrow sense were investigated in a greenhouse with 12- and 24-hour day conditions, respectively, after full vernalization, Second and third experiments were made using 38 barley varieties native to Korean peninsula (Ha, 1976) and 211 Ethiopian barley varieties (Yasuda, 1981), respectively. The fourth one was made using 208 wheat varieties collected from the world (Yasuda and Shimoyama, 1965'. In second to fourth experiments, each of three internal factors were investigated by the same methods as those in the first experiment, though the heading time in the outdoors of the varieties was only the result obtained in one growing season.

The relationships of heading time of fall-sown barley and wheat varieties in the field with three internal factors were shown in Table 2 including the results in four experiments.

Very high and significant correlation coefficients between Y (heading time in the outdoors) and x_2 (photoperiodic response) and also large standard partial regression coefficients of Y on x_2 indicate that photoperiodic response is the principal internal factor that determines the earliness of fall-sown barley and wheat varieties. Growth habit (X_1) , however, seems to matter little to the earliness of fall-sown barley and wheat. The correlation between Y and x_2 earliness in a narrow sense was found to be considerable, except for Korean barley varieties, but the contribution of x_2 to Y is very little as the partial regression of Y on x_2 was insignificantly small. It is to be noted that close apporoximate estimates have been obtained from different sources of data.

GENETIC STUDIES ON THE INTERNAL FACTORS

A Genetics of spring and winter habit of growth

Genetic analysis of spring and winter habit of growth or vernalization requirement in barley have

b1: Standard partial regression coefficient.

No. of cvs tested: Japan 65, Korea 38, Ethiopia 211, Wheat collected from the world 208.

Table 3. Five spring genotypes and segregation ratios in F_2 s crossed between spring and winter cultivars in barley

T.	C	Segregation ratio
Type	Genotype	Spring : Winter
1. One dominant	$Sh \cdot Sh_2 \cdot sh_3$	3:1
2. Two dominant	Sh Sh_2 Sh_3	15:1
3. One recessive	$sh - sh_2$ sh_3	1:3
4. Two genes	$sh Sh_2 (sh_3)$	13:3
5. Three genes	$sh\ Sh_2\ Sh_3$	61:3
Winter type	$Sh = sh_2 + sh_3$	

^{*} Shsh: Chromosome 4, Sh_2sh_2 : Chromosome 7, Sh_3sh_3 : Chromosome 5.

been made under 24-hour illumination in a greenhouse. Until now, we have determined the genetic constition of more than 400 spring barleys originating in various regions of the world. The results lead to the following conclusion: Three pairs of genes, Shsh, Shsh, and Sh_3sh_3 , are responsible for the growth habit of barley. The gene sh, Sh_2 and Sh_3 are all for the spring habit. and their allelic genes for the winter habit. Since both Sh_2 and Sh_3 are epistatic to the dominant winter gene Sh, and the recessive spring gene sh is epistatic to both sh_2 and sh_3 for winter habit, only a single genotype, ShShsh₂sh₂sh₃sh₃, is capable of exhibiting winter habit. Although seven possible genotypes are expected to be of spring habit, only the following five genotypes have been found among the existing spring barley varieties: 1. $(Sh) Sh_2(sh_3)$, 2. $(Sh) Sh_2Sh_3$, 3. $sh(sh_2sh_3)$, 4, $shSh_2(sh_3)$ and 5, $shSh_2Sh_3$, Segregation of spring and winter type plants in F2 crossed between spring and winter varieties fitted any one of five ratios according to the genotypes of spring varieties tested (Table 3)

Furthermore, linkage studies of the three genes, sh, Sh_2 and Sh_3 , have shown that they are on chromosome 4, 7 and 5, respectively (Takahashi and Yasuda, 1956, 1958, and Yasuda, 1969). As to the relation between the spring genes and the grade of

Table 4. Genotypic constitution for response to vernalization in wheat cultivars McIntosh, 1983

Stock	Genotype	Vernalization response		
Triple Dirk	Vm-1 Vm-2	No		
Kolben	Vm-1	No		
Festiguay	Vm-2	Yes		
Gabo	Vm-2 $Vm-4$	Yes		
Chinese Spring	Vrn-3	Yes		

Vrn-1 5A , Vrn-3 5D , Vrn-5 7B .

spring growth habit, it may be noted that there is a multiple allelic series on the Sh_2 locus, and that are responsible for the grade of spring growth habit. On this basis, the genes Sh_2 and Sh_2 denote the spring genes with high grade (grade I) and moderate grade grade II) of spring growth habit, respectively.

In wheat, five dominant spring genes, Vm-1, chromosome 5A), Vm-2, Vm-3 chromosome 5D), Vm-4 and Vm-5 (chromosome 7B) have so far been reported (McIntosh, 1983). Wheat cultivars possessing Vm-1 are insensitive to vernalization, and Vm-1 is epistatic to other spring genes (Table 4: McIntosh, 1983). Winter cultivars carry recessive alleles at all loci (Yasuda, 1968, Pugsley, 1983), and differences among winter wheats with respect to vernalization requirements seem to be due to multiple recessive alleles (Pugsley 1983).

B) Photoperiodic response

Yasuda carried out genetic studies on photoperiodic response using very early barley varieties, and found the gene ca_k for insensitivity to day length from a variety kinai 5 which was known to be day-neutral and very early heading under field condition at Kurashiki (Takanashi and Yasuda, 1960). The ea_k is on chromosome 5, and the same as mutant gene for very early heading from Chikurin Ibaragi 1 (Ukai, 1983) and also the gene ea-a included in very early Swedish variety, Mari (Yasuda, 1977).

In wheat, at least three pairs of genes are responsible for photoperiodic response. According to Welsh et al. (1973), the gene *Ppd*-1 on chromosome 2D is dominant epistatic for insensitivity, and the gene *Ppd*-2 on chromosome 2B is dominant for partial insensitivity. The third gene of insensitivity, *Ppd-3*, is on

chromosome 2A (Law et al. 1978).

(C) Earliness in a narrow sense

Genetic studies on the earliness in a narrow sense of barley showed that this character was controlled by so -called polygenes (Takahashi and Yasuda, 1958). Yasuda (1970) selected early and late type plants from a F_2 population grown under 24-hour day at high -temperature, and fixed them after selfing up to five generations. The F_2 plants from a cross between the early and late type selections showed clear-cut segregation fitting well to the ratio of 3 ealy to 1 late type plants, when grown under 24-hour day at high temperature. This may indicate that the character under consideration proved to be a pair of genes with a minor effect.

Few studies on earliness in a narrow sense are found in wheat so far.

DIFFERENCES OF MECHANISM FOR EARLY MATURITY BETWEEN BARLEY AND WHEAT

A new wheat variety with a little earlier maturity has long been desired by the farmers in western and central Japan. The main reasons are to escape damage by rainy season and, also to cope with the recent trend of earlier planting of rice after winter cereal crops.

The study was carried out to know the reason for the difficulty in developing wheat varieties as early as the barley varieties with early maturity (Yasuda, 1984, 1989). Outlines of this study will be stated bellow.

A) Effects of short-day and low-temperature on the development of the ear primordium or shoot apex

The developmental courses of ear primordia or shoot apicies of six varieties each of barley and wheat with various grades of spring and winter habit were investigated after they were sown at mid-November in the field of Kurashiki. Six plants from each variety were sampled every 10 days, and their stages of differentiation or development of shoot apex was

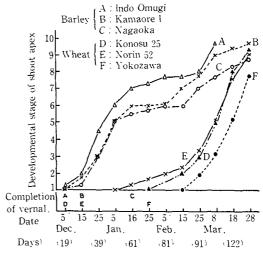


Fig. 2. Development of shoot apex in barley and wheat cultivars when sown outdoors in fall at Kurashiki Date: date of observation, Days: number of days from sowing. Completion of vernalization: critical time of completion of vernalization. (Yasuda, 1989)

decided by Inamura and Nonaka's standard (1955) including 10 stages from differentiation of leaf primordia (1st stage) to late stage of floret development (10 th stage) in which double ridge stage was represented as 7th stage.

In barley plants, the elongation of the shoot apex began in mid-December followed by rapid differentiation, and most of the varieties tested attained to the early to middle or double ridge stages of spikelet development (Fig. 2). After this, however, the development of the shoot apex was retarded or interrupted for about one month, and after which it continued vigorously (late-February~early-March). In wheat plants, regardless of the varieties, shoot apex started to elongate between late-January and mid-February, which was later the time when elongation started in barley plants. However, the shoot apex of the wheat plants differentiated successively and they were at the middle stage of spike development (7th stage) in mid-to late-March.

In this experiment, it was recognized in both wheat and barley that no relation has been found in critical time of completion of vernalization. It can be safely said, therefore, that in Kurashiki, spike primordia

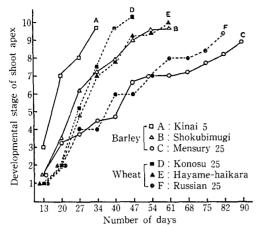


Fig. 3. Development of shoot apex in barley and wheat cultivars grown under a 12-h photoperiod at a high temperature (greenhouse). (Yasuda, 1984)

differentiation of wheat and barley plants sown in fall is not affected by the grades of their growth habit.

As a next step, two experiments were conducted to know whether the differences in shoot apex development between wheat and barley plants were attributable to the effects of either short-day or low-temperature prevailing in the winter months. First experiment

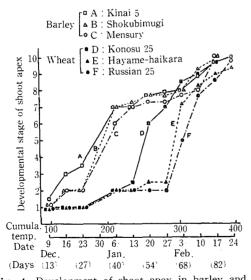


Fig. 4. Development of shoot apex in barley and wheat cultivars grown under 24-h photoperiod at a high temperature.

Cumulative temperature: see text. Date: date of observation, Days: number of days form sowing (Yasuda, 1984)

was made for short-day in which early to late varieties with spring habit of barley and wheat were used as the materials. Fig. 3 shows the weekly changes in shoot apex development of three each of wheat and barley varieties which were grown under 12-hour photoperiod in the greenhouse (17-23°C). Both barley and wheat included early and late developmental types of shoot apex. This suggests that there are no fundamental differences in the developmental pattern between barley and wheat.

Effects of low-temperature on shoot apex of wheat and barley plants with highly spring habit were investigated under outdoor condition with 24-hour photoperiod. The air-temperature in the open field at 9 a.m. after mid-November was bellow 10°C, and from December to mid-February about 4°C, the daily minimum temperature being below 2°C in December.

Fig. 4 illustrated the changes in shoot apex development in three each of wheat and barley varieties. As seen in this figure, the wheat varieties did not show any significant change in size or form of shoot apex during the first 45 to 60 days after sowing, but within about 10 days after that date the shoot apices abruptly developed up to the 7th stage, and during the subsequent 3 weeks they reached the 10th stage, whereas the shoot apices of all the barley varieties began to develop as 13 days after sowing and reached the 7th stage within subsequent 30-40 days.

This figure also shows the relationship between shoot apex developement and the cumulative temperature which is the sum of the daily temperature upper than 5°C at 9 a.m. during the growth period from early -December to late-February. Shoot apex development in wheat varieties progressed rapidly when the cumulative temperature exceeded 250°. In barley varieties, on the other hand, rapid differentiation of shoot apex occurred when the cumulative temperature was about 150°.

(B) Comparison between wheat and barley at developmental stages from initiation of ear primordium to maturity

In order to obtain further information about the differences in growth and development between wheat and barley, thirty cultivars each were selected among

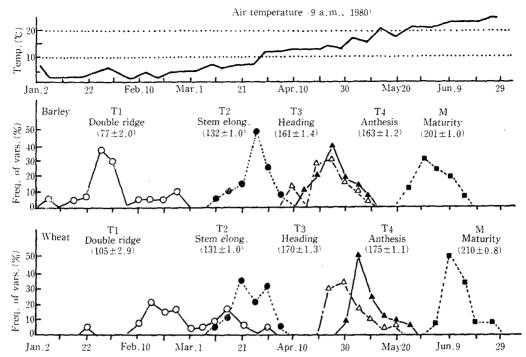


Fig 5. Growth and development in 30 cultivars each of wheat and barley, when sown outdoors on November 15, 1979.
T1 ○ : time of double ridge stage, T2 • · · · · · : onset of stem elongation, T3 △ - - : time of heading,

T4 ▲—: time of anthesis, M ■……: maturation time. Numerals in parentheses represent mean days from sowing and standard errors of the means. (Yasuda, 1989)

Table 5. Correlation coefficients among five development times (TI-T4, M) and two kinds of standard partial regression coefficients (A and B) using 30 cultivars each of wheat and barley. (Yasuda, 1989)

Character C	Crop	T2 Stem elon.	T3 Heading	b' (A) 1)	T4 Anthesis	M Maturation	(B) 1)
T1 Double ridge stage	Wheat Barley	.914** .784**	.869** .774**	. 985 . 354	.863** .807**	.789** .723**	.061 .093
T2 Stem elongation Onset	Wheat Barley		.773** .813**	.128 .536	.762** .838**	.677** .693**	137 228
T3 Heading time	Wheat Barley				.989** .971**	.928** .919**	.835 .873
T4 Anthesis	Wheat Barley					.894** .896**	.148

^{**} Significant at the 1% level.

wheat and barley varieties ranging from extremely early to late maturing types. They were all sown simultaneously in the field of Kurashiki at mid -November.

As seen in Fig. 5, the double ridge stage (T1) of ear primordium differentiation in wheat was markedly

retarded as compared with that in barley. In spite of difference in the onset of stem elongation (T2) between wheat and barley, in the case of the wheat varieties the time of heading (T3), anthesis (T4) and maturation (M) occurred later than in barley.

Table 5 shows correlation coefficients among the

 $^{^{11}}$ b' $[A \ \] \ x_3$ on x_1 and $x_2, \ R^2$] wheat .767, barley .714.

b'(B): Y on $x_1 \sim x_4$, R^2 : wheat .867, barley .859.

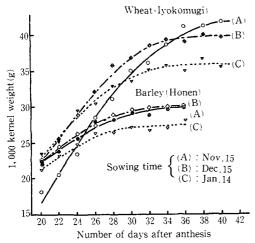


Fig. 6. Increase of 1000 kernel weight after anthesis in wheat and barley cultivars. (Yasuda, 1989)

times of these developmental stages and standard partial regression coefficients of T3 and M on the two and four stages, respectively. The T1 was most closely related to the heading time (T3) in wheat, while in barley T_2 was. In both wheat and barley, however, T3 was most closely related to the matuartion (M).

(\mathbb{C}) Differences in maturation period between wheat and barley varieties

As the next step of the study, the experiment was conducted in order to obtain information about the kernel filling process in relation to differences in the time of anthesis (Yasuda, 1989). In this experiment, seven cultivars each of wheat an barley were selected so as to present different grades of maturation time. They were sown three times from mid-November to mid-January at one month's interval. Time of anthesis and heading was investigated every other day on a single stem basis, and five heads per variety were harvested at two day intervals after anthesis.

Fig. 6 shows the trend of the daily increase of kernel weight after anthesis in a variety each of both wheat and barley which was taken as a representative of the tested varieties. It appears that the kernel weight increased lineally until about 30 days after anthesis in barley and about 35 days in wheat, respectively, and thereafter the rates of increase became gradually lower in both wheat and barley. In this

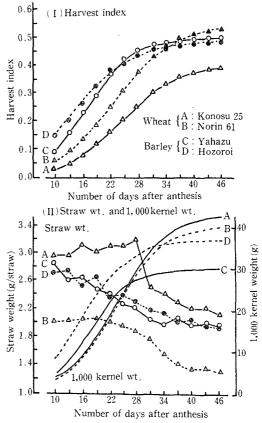


Fig. 7. Changes in harvest index (I) and straw weight (per straw) and 1000 kernel weight (II) after anthesis in wheat and barley cultivars. (Yasuda, 1989)

experiment, the maturation time was represented by the number of days from anthesis to the time when the maximum weight of 1,000 kernels was reached. The wheat varieties always required 3-5 days more for kernel filling than those of barley regardless of the anthesis time. At the same time, the rates of increase of the 1,000 kernel weight during 20-30 day period after anthesis were significantly larger in the wheat varieties. The accumulated temperature during the kernel filling period which was represented by the sum of the values of air temperature at 9 a. m. was 70°C or more higher in the wheat varieties than in the barley varieties.

In order to analyze the differences in grain filling between wheat and barley in more detail, two cultivars each of wheat and barley were selected as the materials and sown in a field at mid-November.

Table 6 . Harvest index and 1000 kernel weight estimated from simple logistic curves Yasuda, 1989	Table 6	Harvest index and	1000 kernel weigh	it estimated from simple	logistic curves	Yasuda, 1989
--	---------	-------------------	-------------------	--------------------------	-----------------	--------------

			Harvest index				1000 kernel weight			
Crop	Name of cvs.	Anthesis	Max,	Days to K	10days* K(%)	Accum, temp,	Max. (K)	Days to K	10days*	Accum temp,
Wheat	Konosu 25 Norin 61	Apr.29 May 1	0.406 0.547	46 47	8.1 11.4	897 932	44.5 40.7	48 47	7.7 8.6	942 932
Barley	Yahazu Hozoroi	Apr.24 Apr.29	0.497 0.487	35 37	19.1 30.2	627 702	30.3 37.4	37 38	15.8 24.6	668 723
	1.s.d. 5%		0.015	1.7	2.2	37	1.2	6.8	2.0	145

^{*} Ten days after anthesis K in percent.

The results shown in Fig. 7 indicated that in barley varieties the rates of increase of the harvest indices were high immediately after anthesis. On the other hand, in the wheat varieties, the rates of increase of harvest indices were rather low until two or three weeks after anthesis. About the same tendencies were recognized in the rates of increase of 1,000 kernel weight in barley and wheat. Table 6 shows estimates of harvest index and 1,000 kernel weight, which were calculated from the simple logistic curve. The number of days required to reach maximum values of harvest indices were about 10 days less in the barley varieties than in the wheat varieties. In the barley vareieties, 20° or more of the maximum values of the harvest index was reached at 10 days after anthesis, while in the wheat ones the values were only half of those obtained in the barley varieties. Accumulated temperatures at 9 a. m. during the period when the maximum value of harvest index was reached were markedly lower in the barley varieties than in wheat ones. The changes in the 1.000 kernel weight with the increase in the number of days after anthesis were similar to those of the harvest index.

In this experiment, another noticeable difference between barley and wheat is the changes in straw weight after anthesis. The straw weight of the barley varieties decreased lineally with the increase in the number of days after anthesis, while in the wheat varieties, the straw weight did not change during the 20 to 30 day period after anthesis. Fig 7).

These facts suggests that the differences in the duration of the kernel filling period between the wheat and barley varieties may be due to differences in the translocation of photosynthetic substances from stems and leaves to kernels. This may be the main con-

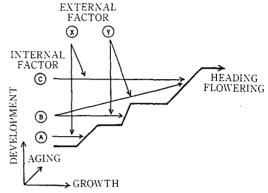


Fig. 8. Relations between internal and external factors influencing heading or flowering in crop plants.

(Yasuda, 1987)

straint on the breeding of wheat cultivars as early in maturity as the barley ones.

CONCLUSION

The internal factors stated above will exerte influence on the crop plants at specific stages or phases of growth and development, and the effects of internal factors will be expressed as the results of interaction between internal or physiological and genetical factors and external or environmental factors (Fig. 8).

From practical point of view, breeders will have selectively to take up the internal factors according to his breeding purpose, though the effects of environment on the internal factors vary with the relation between times of manifestation of the internal factors and seasonal change of climate.

As an example in Japan, the relations between internal and external factors in the fall-sown barley may be explained as follows, so far as heading time is concerned (Yasuda, 1963, 1964):

In northern region like Tohoku district, barley plants are necessary to have at least a nature of relatively late heading with winter habit. If earlier varieties are needed, the winter habit should be combined with a nature of earlier heading under long-day after vernalization or earlier in the earliness factor in a narrow sense. On the other hand, early to mediumearly type plants with either of spring and winter habit are more adaptive to central and southern regions generally including from Kanto to northern Kyushu. Southernmost region like south of Kyushu district is favorable for early and medium early type plant combined with spring habit but not for extremely early and late and also winter type plants. For breeding of earlier varieties adaptive to the regions south to Kanto district inclusive, day-neutral type plants seem to be useful. The earliness in a narrow sense is not so important for this purpose, however.

The second problem stated here is to make clear about the reason for difficulty in developing common wheat varieties as early as barley varieties with early maturity.

To contribute the purpose, different stages of developmental course from onset of differentiation of ear primordia to maturity were investigated under natural fall-sowing condition using 30 cultivars each of barley and wheat. Especially, it was analysed more in detail that effects of different grades of spring and winter growth habit, day-length and temperature of differentiation of ear primordia in barley and wheat. As the results, differences between barley and wheat are markedly recognized in each stage of development. Among the differences, however, it was considered that internal factors which most closely related to the differences in maturity between barley and wheat may be the characters connected with translocation of the photosynthetic substances from stem and leaves to kernels. Exerimentally, it was confirmed that straw and leaf weight of the barley varieties decreased lineally with the increase in the number of days after anthesis, while in wheat varieties, the straw and leaf weight did not change during the 20 to 30 day period after anthesis. These facts may partly be supported by the studies made by

Takahashi et al. (1988), Stoy (1965) and Bindinger et al. (1977).

Assuming that the physiological differences in the translocation of stored assimilates from stems and leaves to kernels account for the inherent difference between barley and wheat, it is considered that the breeding of wheat cultivars as early as barley ones may be difficult to realize at the present.

LITERATURE CITED

- Bindinger, F., Musgrave, R.B. and Fischer, R. A. 1977. Contribution of stored pre-anthesis assimilate to grain yield in wheat and barley. Nature 270: 431-433.
- Ha, Y.W. 1976. Studies of some basic problems in barley breeding in Korea, with special reference to the geographical variations of the morphological and ecological characters of native and commercial varieties. Kinki Chugoku Agr. Res. 53: 2-92. (in Japanese)
- Inamura, H. and Nonaka, S. 1955. Standared for investigation of developmental process of ear primordium in barley and wheat. Tech. Bull. Agr. Sci. 62:1-16. (in Japanses)
- Law, C. N., Sutka, J. and Worland, A. J. 1978. A genetic study of day length response in wheat. Heredity 41: 185-191.
- McIntosh, R.A. 1983. A catalogue of gene symbols for wheat (1983 edition): Proc. 6th Intern.
 Wheat Genet. Symp. Kyoto 1983: 1197-1254.
- Pugsley, A.T. 1973. Control of developmental patterns in wheat through breeding. Proc. 4th Intern. Wheat Genet. Symp. Columbia Mo.: 857-859.
- Pugsley, A. T. 1983. Identification and management of major gense monitoring yield and adaptation. Proc. 6th Intern. Wheat Genet. Symp. Kyoto: 917-974.
- Stoy, V. 1965. Photosynthesis, respiration, and carbohydrate accumulation in spring wheat in relation to yield. Physiol. Plant. Suppl. IV: 1-125.
- 9. Takahashi, T., Nakaseko, K. and Goto, K.

- 1988. Differences in productivity between short -and long-culm varieties and their relationships with cell wall and cellular components of culm in spring wheat. Japan. J. Crop Sci. 57: 53-58.
- Takahashi, R and Yasuda, S. 1956. Genetic studies of spring and winter habit of growth in barley. Ber. Ohara Inst. landw. Biol. Okayama Univ. 10: 245-308.
- 11. Takahashi, R. and Yasuda, S. 1958. Genetic studies on heading date in barley, with some considerations of selection early maturing varieties. In "Studies on the Bulk Method of Plant Breeding" ed. by Sakai, Takahashi and Akemine, 44-64. Yokendo, Tokyo. (in Japanese)
- 12. Takahashi, R. and Yasuda, S. 1960. Varietal differences in responses to photoperiod and temperature in barley. Ber. Ohara Inst. landw. Biol. Okayama Univ. 11:365-384.
- Takahashi, R. and Yasuda, S. 1970. Genetics of earliness and growth habit in barley. Barley Genetics II: 388-408.
- Ukai, Y. 1983. Early maturing mutations as germplasm stocks for barley breeding. Gamma Field Symposia 22: 49-72.
- Welsh, J.R., Keim, D.L., Pirasteh, B. and Richards, R.D. 1973. Genetic control of photoperiod response in wheat. Proc. 4th Intern. Wheat Genet. Symp. Columbia Mo.: 879-884.
- 16 Yasuda, S. 1961. Studies on heading time in barley. pp234. Dr. Thesis. (in Japanese)
- 17. Yasuda, S. 1963. Experimental studies on natural selection for time of heading and its inner factors in some barley hybrid populations. Ber. Ohara Inst. landw. Biol. Okayama Univ. 12: 42-64.
- 18. Yasuda, S. 1964. Experimental studies on natural

- selection for time of heading and its inner factors in some barley hybrid populations. II. Genotypic constitutions of selection lines derived from the population grown at different locations. Ber. Ohara Inst. landw Biol. Okayama Univ. 12: 197-215.
- 19. Yasuda, S. 1968. Physiology and genetics of ear emergence in barley and wheat. VII. The mode of inheritance of spring and winter habit of growth in common wheat. Nogaku Kenkyu 52: 79-88. (in Japanese)
- Yasuda, S. 1969. Linkage and pleiotropic effects on agronomic characters of the genes for spring growth habit. Barley Genetics Newsletter 12: 57-58.
- Yasuda, S. 1977. Linkage of the barley earliness gene ea_k and its pleiotropic effects under different growth conditions. Ber. Ohara Inst. landw. Biol. Okayama Univ. 17: 15-28.
- 22. Yasuda, S. 1981. The physiology of earliness in barley. Barley Genetics IV: 507-517.
- 23. Yasuda, S. 1984. Comparative studies on the development of spike primordia between cultivars of common wheat and barley. Ber. Ohara Inst. landw. Biol. Okayama Univ. 18: 211-225.
- Yasuda, S. 1987. Genetics of ecological characters in barley. Iden (The Heredity) 41(5): 39-43.
 (in Jaanese)
- 25. Yasuda, S. 1989. Dfferences in mechanism of early maturity between cultivated common wheat and barley. Japan. J. Breed. 39: 327-335.
- Yasuda, S. and Shimoyama, H. 1965. Analysis of internal factors influencing the heading time of wheat varieties. Ber. Ohara Inst. landw. Biol. Okayama Univ. 13: 23-38.