

ANALYSIS OF INTERNAL FACTORS INFLUENCING THE HEADING TIME OF WHEAT VARIETIES

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I. INTRODUCTION

It is generally believed that wheat is much more winter hardy and also tolerant to high temperature than barley. Also it differs from barley in that some of the winter wheat requires longer pretreatment for vernalization. However, there has never been tried to compare the physiological nature between wheat and barley closely and precisely.

The senior author has already shown in a series of experiments with barley varieties that three internal factors, namely, spring and winter habit of growth, photoperiodic response (response of vernalized plants to short-day) and earliness in a narrow sense (response of vernalized plants to long-day) are responsible for the heading time of barley plants (Takahashi and Yasuda, 1957, 1958, 1960). To the fall-sown barley, the photoperiodic response among others was shown to be the chief agent for earliness or lateness of heading. But, the other two internal factors affect little the earliness under outdoor condition. It may be reasonable to suppose that the heading time of wheat plants, too, is controlled by the three internal factors as above-stated, but the relative importance of these three internal factors might be more or less different between wheat and barley. Response of wheat plant to temperature might also be different to some extent from that of barley.

In order to disclose the possible differences between wheat and barley in their physiological nature, especially, those which concern ecology and/or heading time, some experiments were carried out. The results will be presented below.

II. RESPONSE TO TEMPERATURE

For the investigation of the response to temperature, ten spring wheat varieties were used. Their physiological characteristics are summed and given in Table 1; namely, they are almost the same as to their grade of spring habit, but different from each other regarding the heading time under both open field and short-day conditions. Seven uniform seeds of each of these varieties were sown in a pot, and grown outdoors subjecting to various temperature of different seasons and continuous illumination with 100 watt incandescent lamps. Such sowing was made 21 times at 30 days interval from October of 1962 to June of 1964. Daily record was taken on a single plant basis for date of flag-leaf emergence and number of

TABLE 1
Characteristics of the experimental materials

Variety	Grade of spring habit	Days to flag. under 24 hr. day	Time of* heading (Outdoors)	Days to flag.** under 24 hr. day (Vernal.)	Days to flag.*** under 12 hr. day (Vernal.)
Konosu No. 25	I†	32.0	24	26.3	31.8
Saitama No. 27	I	35.0	29	30.5	32.9
Toyama-Wasekomugi	I	36.8	30	25.6	35.0
Taichung No. 17	I	37.0	32	27.5	34.1
Taichung No. 23	I	33.5	28	25.3	32.2
Euston	I	34.2	26	26.5	36.8
Italian No. 64	I	38.2	46	32.8	77.6
Itallian No. 70	I	34.5	33	29.6	30.7
Progress C. I. 6902	I	34.3	38	30.4	67.4
Russian No. 25	I	35.7	47	31.3	71.7

* Number of days from April 1st. ** Earliness in a narrow sense. *** Photoperiodic response.
† Highly spring habit.

leaves on the main stem. Daily temperature was represented by air temperature taken at 9 A M.

In Fig. 1 are shown the seasonal variation curves of days to flag-leaf emergence of the five representative varieties tested.

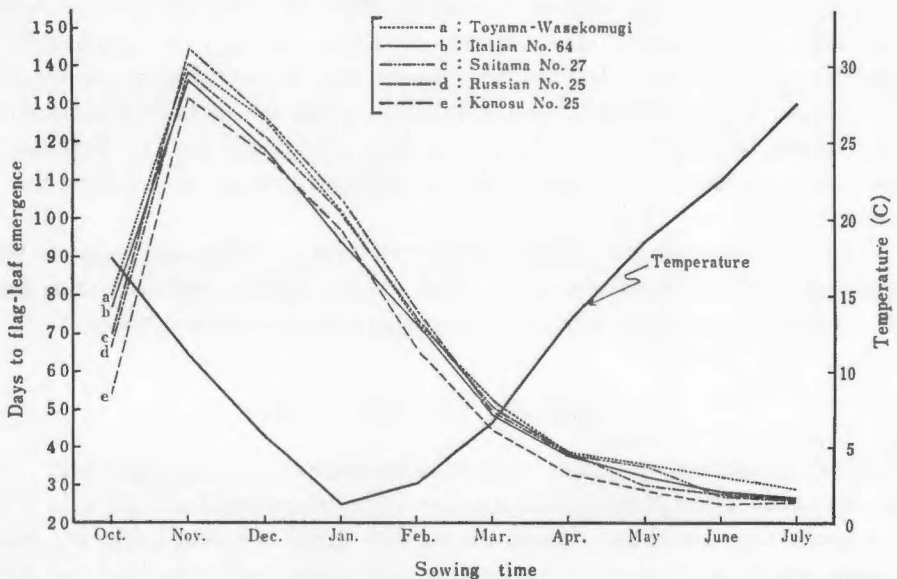


Fig. 1. Changes of days to flag-leaf emergence in spring wheat varieties which were sown at 30 days intervals and grown outdoors under 24 hour day.

As apparent in Fig. 1, the time needed for the flag-leaf emergence of five varieties varied with time of sowing. It is the largest for those which have been sown in November, and has gradually decreased with the change of sowing time

from winter to summer. This apparently indicates that the emergence of flag-leaf of these spring varieties tends to be accelerated with the rise of temperature.

The relation between time to flag and temperature during growing period has been studied by plotting hereupon the logarithm of time to flag against the logarithm of the corresponding average temperature of the respective growing period, which have been shown in Fig. 2. Since their relations were found to be almost

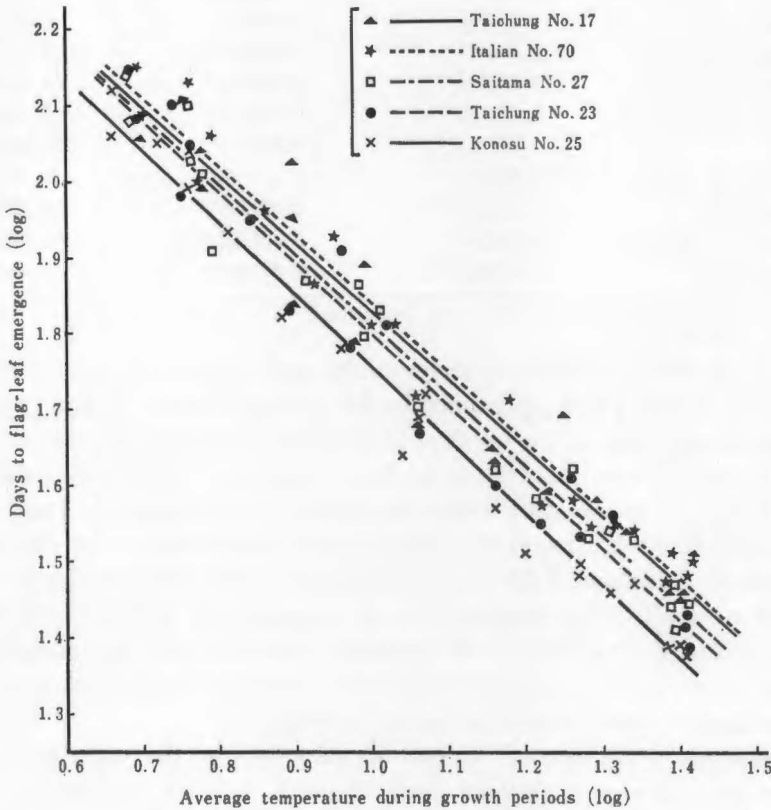


Fig. 2. Relations between time to flag-leaf emergence and average temperature during growth periods in five spring wheat varieties.

linear, Bělehrádek's temperature coefficients (1926) or linear regression coefficients of time to flag on temperature were calculated for each variety. According to Table 2, the estimates of the coefficients are much the same and highly significant. Moreover, significant differences were not found between any two of these estimates in *t*-test. It can be considered, therefore, that at least within the range of $5^{\circ}\sim 27^{\circ}\text{C}$, temperature is the most important external factor determining earliness of spring wheat grown under long-day condition. Furthermore, it must be noted that varietal differences of heading response to temperature are not observed in this condition.

Time to flag-leaf emergence may be represented by the product of the growth

TABLE 2
Regression coefficients of days to flag-leaf emergence (log), growth rate of leaves (log) and number of leaves on average temperature during growing periods (log)

Variety	Days to flag (log)	Growth rate of leaves (log)	Number of leaves
Konosu No. 25	-0.961844**	-0.895179**	-0.301055
Saitama No. 27	-0.932583**	-0.932307**	+0.255325
Toyama-Wasekomugi	-0.831482**	-0.891679**	+1.136637*
Taichung No. 17	-0.899067**	-0.917478**	+0.413037
Taichung No. 23	-0.944115**	-0.941409**	-0.032376
Euston	-0.837611**	-0.857576**	+1.229590*
Italian No. 64	-0.923156**	-0.893508**	-0.373961
Italian No. 70	-0.898220**	-0.889948**	-0.109794
Progress C. I. 6902	-0.992565**	-0.884762**	-1.382115*
Russian No. 25	-1.010255**	-0.880798**	-1.903597*

* and ** significant at 5% and 1% levels, respectively.

rate of leaves and the number of leaves on the main stem. In this experiment, the growth rate of leaves was represented by the average number of days required for development of a leaf or the quotient of days from sowing to flag-leaf emergence divided by the leaf number of the same plant. Regression coefficients of the growth rate of leaves on temperature were calculated by the logarithmic scale, because their relationships were found to be almost linear when their scales were changed to logarithm. As seen in Table 2, the temperature coefficients for the growth rate of leaves were all highly significant, and no significant differences were found among each of the varieties. It is apparent, therefore, that the growth rates of leaves are accelerated uniformly with the rise of temperature, which are quite the same tendency as those in time to flag-leaf emergence.

Regression coefficients of the number of leaves on the main stem on temperature (log), however, differed markedly with varieties. Significant negative values—the implication of which is that number of leaves decreases with rise of temperature—was only found in two varieties, Progress C. I. 6902 and Russian No. 25. Toyama-Wasekomugi and Euston, on the contrary, indicated significant positive values, and the coefficients of the other six varieties were insignificant. Thus, the results obtained in wheat differed considerably from those in barley, where the values were negative in all varieties tested (Takahashi and Yasuda, 1960).

To obtain additional informations concerning the number of leaves, correlation coefficients between the number of leaves and the days to flag-leaf emergence were calculated in both wheat and barley, and given in Table 3. It is apparent in this table that the barley varieties show a marked tendency to increase leaf number with the increases of the days to flag-leaf emergence. In wheat, this is true only for three varieties, and correlation coefficients of the other seven varieties are all

TABLE 3
Correlation coefficients of days to flag-leaf emergence with number of leaves on the main stem in wheat and barley varieties

(A) Wheat

Variety	Correlation coefficient	Variety	Correlation coefficient
Konosu No. 25	+0.754**	Euston	-0.183
Saitama No. 27	-0.035	Italian No. 64	+0.164
Toyama-Wasekomugi	-0.226	Italian No. 70	+0.024
Taichung No. 17	-0.068	Progress C. I. 6902	+0.610**
Taichung No. 23	+0.150	Russian No. 25	+0.569**

(B) Barley

Variety	Correlation coefficient	Variety	Correlation coefficient
Kinai No. 5	+0.727*	Natsudaikon-Mugi	+0.909**
Tammi	+0.657*	Shokubimugi	+0.904**
Sächseder	+0.677*	Mensury C	+0.836**

* Exceeds the 5% level. ** Exceeds the 1% level.

insignificant. The reason is, perhaps, due to the limited range of seasonal changes in number of leaves of wheat varieties. It may also be explained, at least partially, by the fact that seasonal changes in number of leaves on main stem are not always parallel with changes in days to flag-leaf emergence and in average temperature during growth period. In fact, the range of the seasonal changes in number of leaves was only one or two leaves in the majority of the wheat varieties tested. In connection with this, the number of days for complete appearance of each leaf blade from its lower sheath were further investigated in the present study. This is explained in Fig. 3, by two varieties, Konosu No. 25 and Taichung No. 17 as typical examples.

As seen in Fig. 3, the expansion of the 1st and 2nd leaves required much more days when sown in winter months than when sown in

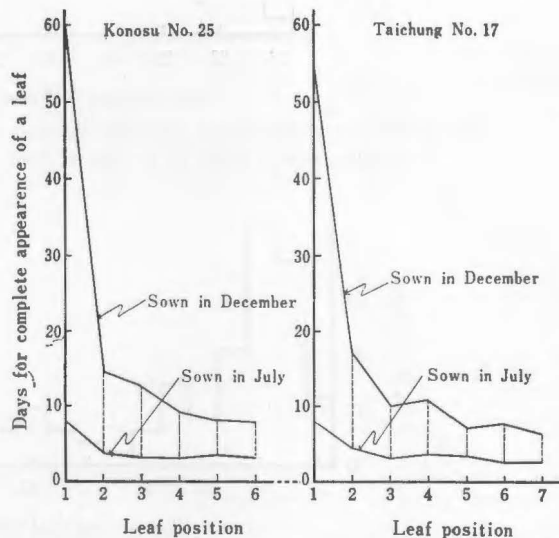


Fig. 3. Number of days for complete appearance of each blade from its lower sheath

summer. It is considered, therefore, that the differences in days to flag-leaf emergence between both conditions shown in Fig. 3 are considerably affected by the growth rate in their seedlings. However, it seems to be noteworthy that in spring wheat varieties there are little or no seasonal changes in number of leaves on the main stem, in spite of the sowing time, provided they are grown under continuous illumination.

III. RESPONSES OF VERNALIZED PLANTS TO PHOTOPERIOD

For the investigation of the differences in sensitivities to photoperiod among varieties, it is necessary to convert their winter growth habit into spring one before photoperiodic treatments. A total of 208 wheat varieties collected from various regions of the world are used as materials. Slightly sprouted seeds of each variety were fully vernalized by exposing them to low-temperature of 1~3°C for 70 days, and grown in a greenhouse under both 24 hour and 12 hour day conditions, respectively. The date of flag-leaf emergence and number of leaves on the main stem were recorded on the single plant basis.

Figs. 4 and 5 show the frequency distributions of 208 varieties regarding the average days to flag-leaf emergence under each of the conditions of 24 hour and

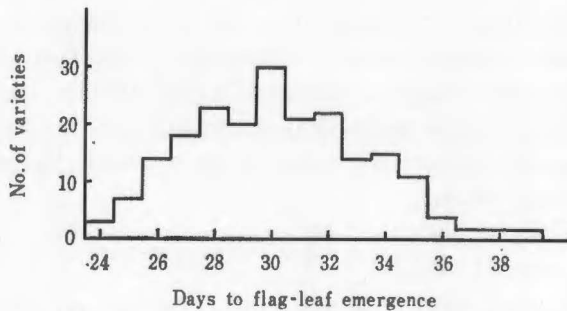


Fig. 4. Frequency distribution regarding the days to flag-leaf emergence of wheat varieties grown under 24 hr. day at high temperature after vernalization.

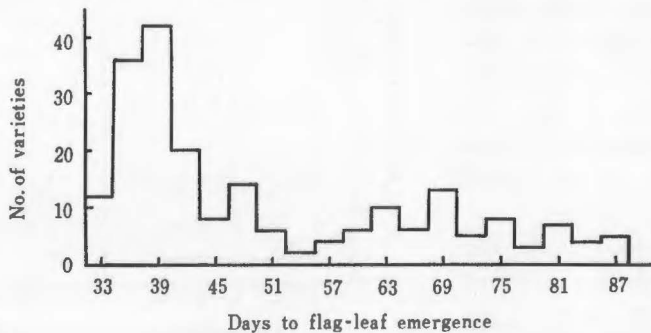


Fig. 5. Frequency distribution regarding the days to flag-leaf emergence of wheat varieties grown under 12 hr. day at high temperature after vernalization.

12 hour day after vernalization, respectively. Under continuous illumination at high temperature after vernalization, as seen in Fig. 4, the variations of average days to flag among varieties are completely continuous and indicate uni-modal curve as a whole. However, the differences in sensitivity to long photoperiod among varieties are not so marked, though about two weeks differences are found in days to flag between the earliest and the latest variety.

The average days to flag under short photoperiod, on the other hand, indicated nearly bi-modal curve in their frequency distribution; the varieties belonging to earlier group were found to be much larger in number than those of later group (Fig. 5). This may imply that majority of the varieties tested are less sensitive to the retarding effect of short photoperiod. However, from the fact that the difference between the earliest and the latest was 50 or more days, it would appear that even in wheat varietal differences in sensitivity to short photoperiod were great as in barley which was confirmed by Takahashi and Yasuda (1960).

IV. THE GRADE OF SPRING AND WINTER HABIT OF GROWTH

Varietal differences in spring and winter habit of growth of barley and wheat should not be represented by only two groups of spring and winter types. As was demonstrated by Enomoto (1929), barley and wheat varieties represent a rather continuous series of gradation from typical spring to extremely winter types. These gradations of growth habit, generally called the grade of spring growth habit, can be distinguished by the critical time of sowing in early spring to permit normal heading, and also by the differences in periods of cold-pretreatment required for vernalization (Enomoto 1929, Kakizaki and Suzuki 1937). In this experiment, the grades of spring growth habit in wheat varieties have been determined by the number of days to flag-leaf emergence under continuous illumination at high temperature. It has already been known in barley varieties that the time of flag-leaf emergence under continuous illumination at high temperature correlated closely with the grade of spring growth habit (Takahashi 1943, Takahashi and Yasuda 1956)

The materials used are the same varieties as used in the investigation of the sensitivities to photoperiod. Ten or more plants of each variety were reared in a greenhouse under continuous illumination, and time of flag-leaf emergence was recorded on a single plant basis. In the present study, a series of standard varieties with a known grade of spring growth habit were grown together for the classification of varieties to be tested. The frequency distribution of average days to flag-leaf emergence is shown in Fig. 6. In this figure, the grades of spring habit of standard varieties have been expressed by the conventional symbols, I, II, . . . VII, where I stands for the highest and VII the lowest degree of spring habit, respectively.

It is apparent, in Fig. 6, that the days to flag-leaf emergence of the standard

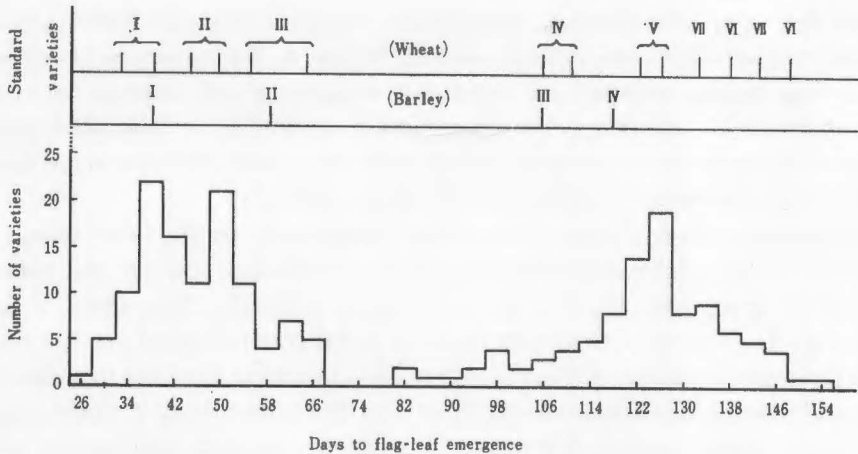


Fig. 6. Frequency distribution regarding the days to flag-leaf emergence of wheat varieties grown under continuous illumination at high temperature. Heading behaviors of standard varieties of wheat and barley are shown in the upper side; I stands for the highest and VII the lowest grade of spring habit, respectively.

Standard varieties:

Wheat; (I) Konosu No. 25, Saitama No. 27, (II) Shinchunaga, Iga-Chikugo, (III) Norin No. 52, Akabozu, (IV) Tokorozawa, Gifu-wase, (V) Velvet, Nishimura, (VI) Akakawa-aka, Yokosawa, (VII) Akasabishirazu No. 1, Hokuei

Barley; (I) Indian Barley, (II) Kuromugi No. 148, (III) Chinko No. 83, (IV) Hayakiso No. 2

varieties indicate a tendency to become larger with increase of the grade from highly spring (I) to extremely winter growth habit (VII). The frequency distribution of the varieties regarding average days to flag represented nearly a interrupted bi-modal curve, and coincidence was recognized between the early group and the standard varieties with spring growth habit (grade I~III) in one hand, and between the late one and the standard varieties with winter growth habit (grade IV~VII), on the other. Fig. 6 has further indicated that although marked difference in days to flag is found between standard variety with the grade III (spring type) and those with the grade IV (winter type), a few varieties tested are intermediate type between them.

V. INTERRELATIONS BETWEEN EARLINESS UNDER NATURAL CONDITION AND THE THREE INTERNAL FACTORS

Earliness under natural condition was investigated using the same varieties as those in the studies of sensitivities to photoperiod and spring and winter habit of growth. Following our conventional cultural method, seeds of each variety were simultaneously sown in mid-November of 1961. The time of heading of each variety was recorded when about 80 per cent of heads of the varieties had appeared from their sheaths. In Fig. 7 is shown frequency distribution of heading date in

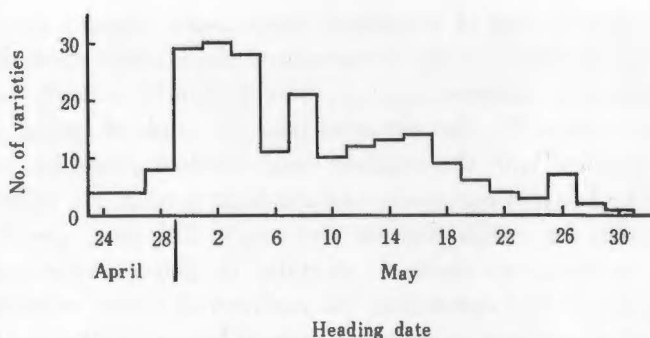


Fig. 7. Frequency distribution regarding the heading date of wheat varieties. Seeds were sown outdoors in November 15 at Kurashiki.

wheat varieties, which reveals that earlier heading varieties, rather than late ones, predominate though variation curve in heading date is continuous. It may be said, therefore, that this tendency is almost similar to that of days to flag under 12 hour day after vernalization, as shown in Fig. 5.

In order to know interrelations of the earliness under outdoor condition with three internal factors (the sensitivities of vernalized plants to long and short photoperiod and the grade of spring growth habit), correlation coefficients between these four variables, together with standard partial regression coefficients of heading time under outdoor condition on the three internal factors, are calculated using the four kinds of data of 208 varieties as above-mentioned. The results are shown in Table 4, together with those obtained in barley varieties (Takahashi and Yasuda, 1957).

TABLE 4

Interr. lations between heading time under outdoor condition (Y) and its three internal factors, the grade of spring habit (x_1), responses to 24 hr. (x_2) and 12 hr. (x_3) photoperiod after vernalization. The results of barley varieties were cited from the paper of Takahashi and Yasuda (1957)

Item	Correlation coefficient			b' Y on x	
	x_2 Response to 24 hr. (vernal.)	x_3 Response to 12 hr. (vernal.)	Y Heading time outdoors		
x_1 Grade of spring habit	{Wheat	+0.317**	+0.235**	+0.467**	+0.257**
	{Barley	+0.306*	+0.030	+0.0001	-0.040
x_2 Response to 24 hour day (vernal.)	{Wheat		+0.684**	+0.704**	+0.125**
	{Barley		+0.573**	+0.530**	+0.139**
x_3 Response to 12 hour day (vernal.)	{Wheat			+0.873**	+0.727**
	{Barley			+0.794**	+0.716**

* Exceeds the 5% level of significance.

** Exceeds the 1% level of significance.

b' = Standard partial regression coefficient.

It is recognized, from Table 4, that interrelations among four variables do not so differ from those in barley varieties, without a few exceptions. Two in-

ternal factors, days to flag of vernalized plants under long-day or earliness in a narrow sense (x_2) and days to flag of vernalized plants under short-day or photoperiodic response (x_3), always correlate, to considerable extent, with heading time of fall-sown wheat (Y). But the other one, the grade of spring growth habit (x_1), did not correlate with the earliness under outdoor condition, so markedly. However, standard partial regression coefficients of Y on x are highest in that of Y on x_3 . The other two coefficients are very small. This may, therefore, suggest the sensitivity of vernalized plants to short-day or photoperiodic response is the most important factor that determines the earliness of wheat varieties sown outdoors in fall, and that effects of the other internal factors, spring and winter habit of growth and earliness in a narrow sense, on earliness of fall-sown wheat are not so evident.

In wheat varieties tested here, however, correlation coefficient between the grade of spring growth habit (x_1) and heading time under outdoors (Y) was considerably higher than that established with the barley varieties (Table 4). In Fig. 8, where the relation between these two characters of wheat is shown, no correla-

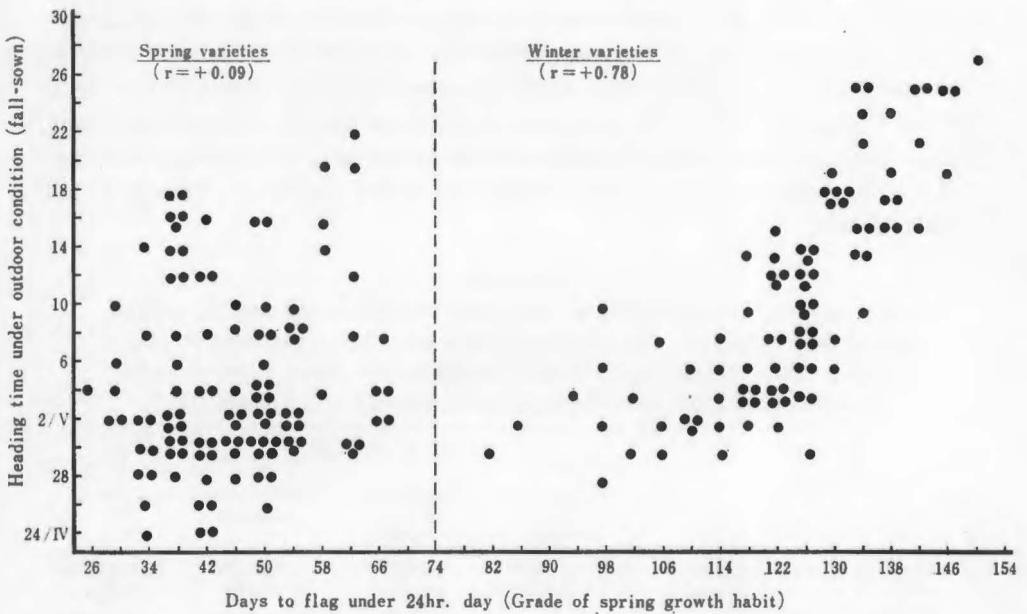


Fig. 8. Relations between heading time under outdoor condition and days to flag under continuous illumination at high temperature (the grade of spring growth habit)

tion is recognized within group of the spring varieties with the grade I~III, while within group of the winter varieties with the grade IV~VII, highly positive correlation coefficient is found, which suggests that heading time under outdoor condition differs with different grade among winter varieties. From these facts, the relations of growth habit (x_1) with the other two internal factors (x_2 , x_3) and also with

the earliness under outdoor conditions (Y) have further been studied in order to know whether the effects on these characters differ or not between the spring and the winter varieties. The results are given in Table 5.

TABLE 5
Interrelations between heading time of wheat under outdoor condition (Y)
and its three internal factors, x_1 , x_2 and x_3 , in two groups of spring
and winter varieties

Item	Correlation coefficient			b' Y on x	
	x_1 Response to 24 hr. (vernal.)	x_2 Response to 12 hr. (vernal.)	Y Heading time outdoors		
x_1 Grade of spring habit	{ Spring var.	+0.195*	+0.037	+0.085	+0.017
	{ Winter var.	+0.489**	+0.670**	+0.777**	+0.320**
x_2 Response to 24 hour day (vernal.)	{ Spring var.		+0.679**	+0.673**	+0.224**
	{ Winter var.		+0.655**	+0.610**	+0.012
x_3 Response to 12 hour day (vernal.)	{ Spring var.			+0.810**	+0.658**
	{ Winter var.			+0.896**	+0.674**

* Exceeds 5% level of significance.

** Exceeds 1% level of significance.

b' = Standard partial regression coefficient.

According to Table 5, it is obvious that photoperiodic response has the most intimate bearing on the earliness under outdoor condition, regardless of the difference in growth habit between the spring and the winter types. However, correlation coefficients of the grade of spring habit with the responses of vernalized plants to long-day and to short-day and also with the earliness under outdoor condition were markedly different between groups of the spring and the winter varieties. These three coefficients are always higher in the group of the winter varieties, though such differences are not found in correlation coefficients between the responses to long day and to short-day, and also between those two internal factors and the earliness under outdoor condition. It may, therefore, be necessary to distinguish winter varieties from spring ones when the effects of spring and winter habit of growth on earliness of fall-sown wheat are investigated.

VI. DISCUSSION

Certainly there is no doubt about the importance of temperature and day-length in regulating flower initiation, but it is difficult to analyze separately the effect of each of these external factors, because they always operate together and exert their influence as a whole. Therefore, if you want to know varietal differences in flower response to temperature, the experiment should be run under photoperiodic condition most favorable to all of the varieties, to avoid any modifying effect upon response to temperature. Taking these consideration into account, Takahashi and Yasuda (1960) have investigated the differences of responses of six

spring barley varieties to different temperature by growing them under the condition of 24 hour day known to be most favorable to heading of all spring barley varieties. Since it is considered that the situation will be quite the same for spring wheat varieties, varietal differences in responses to temperature have been investigated under the condition of 24 hour day. The results, as seen in Table 2, indicated that temperature coefficients or regression coefficients of days to flag on average temperature during growing periods of each variety were much the same and all highly significant. Furthermore, quite the same situations were found in the temperature coefficients regarding growth rate or average days required for expansion of each leaf on main stem. These imply that heading and growth rate of leaves in spring wheats, regardless of the varieties, are uniformly accelerated with the rise of temperature, and that there is no appreciable differences in sensitivity to temperature among them. These results in spring wheat were in strict accordance with those obtained in spring barley varieties (Takahashi and Yasuda, 1960). However, the range of temperature, from approximately 5° to 27°C, which allows wheat more or less vivid development is much larger than those of barley with the range of 8° to 21°C. This may suggest that wheat is much tolerant to temperature than barley. Enomoto (1929), Wada and Akihama (1934) and also Kakizaki and Suzuki (1944) have maintained that varieties within wheat and barley differ not only in the responses to photoperiod, but also in their "thermic" responses. However, those facts could not be found in the present study. Their studies have been made under natural (short) day-length from late fall to spring, so that such thermic responses seem to have strongly been affected by interactions between temperature and short-day. Therefore, it seems that varietal differences in such thermic response can not be attributed to only different sensitivities to temperature. Under short photoperiod, indeed, heading time of barley is strongly affected by its photoperiodic sensitivity (Takahashi and Yasuda, 1960). This fact may suggest that varietal differences in the thermic response of wheat are mainly due to the differences in sensitivity to short photoperiod.

Gries and his co-workers (1956, 1958) carried out a series of studies on responses of spring wheat varieties to both temperature and day-length, and found that when two varieties, White Federation 38 and Chinese, the former an early and the latter a late maturing type, were grown under various kinds of the conditions of temperature and day-length, optimum temperature for flowering differed with day-length conditions. Especially, under the conditions of 20 hour day at a range of temperature from 60° to 80°F., White Federation 38 tended to become earlier with the rise of temperature, but the reverse was true for Chinese. Among ten spring wheat varieties tested in the present study, however, such variety as Chinese could not be found. Chinese, according to Gries *et al.* (1956), varies from very early to late in flowering depending upon on the planting date and season. This variety may, therefore, be considered to be peculiar type favorable to cool-temperature, though it remains to be confirmed because of the relatively limited number of the varieties tested here. It may be noted that a variety like Chinese

has never been found even in barleys (Takahashi and Yasuda, 1960).

In the present study, significant correlation coefficients of number of leaves on a main stem with days to flag-leaf emergence were not recognized except for a few varieties (Table 3). On the other hand, high and significant coefficients were always found in barley varieties. This suggests that the extents of the changes in number of leaves being accompanied by the variations of days to flag are smaller in wheat varieties than in barley ones, when grown under the condition of continuous illumination. Although this fact absorbs much interest, the details will be reserved for discussion in another paper after careful analysis of the problems.

As has already been stated above, responses of spring wheat to temperature were not different among varieties, at least, within a certain range of temperature, approximately 5° to 27°C. Consequently, interrelations between earliness of wheat varieties sown outdoors in fall and the three internal factors other than sensitivity to temperature were investigated. The analytical methods were used along the same lines as was applied for barley varieties by Takahashi and Yasuda (1957, 1958). The results obtained reveal that both of the internal factors, earliness in a narrow sense or response of vernalized plants to long-day (x_1) and photoperiodic response or response of vernalized plants to short-day (x_2), correlate to considerable extent with earliness under natural condition (Y) (Table 4). However, these two factors do not always affect time of heading under outdoor condition similarly. According to the standard partial regression coefficients of Y on x calculated at the same time, it is appreciated further that photoperiodic response is more important an internal factor that determines the earliness of fall-sown wheats than earliness in a narrow sense. This is almost the same results established with the cultivated barley varieties (Takahashi and Yasuda 1957, 1958, Konishi and Sugishima 1964), and also with wild barleys collected from south western Asia (Takahashi *et al.* 1963).

From all these considerations, it seems that such interrelations as above-mentioned can be explained from quite the same ecological viewpoint as that presented about earliness of fall-sown barleys by Takahashi and Yasuda (1957). Namely, the fall-sown wheat and barley are exposed to comparatively severe climate even in southern district like Kurashiki, so that they are vernalized almost completely by low-temperature and short-day during winter. Consequently, those plants thus vernalized will be capable of initiating ear formation if temperature is sufficiently high and day-length is long. To develop ear primordia, however, day-length in the early spring is too short for plants sensitive to short-day. Only plants insensitive to short-day or day-neutral can develop ear. It may, therefore, be safe to conclude that earliness of the fall-sown wheat will almost wholly depend upon its sensitivity to short photoperiod after vernalization. Although Kakizaki and Suzuki (1937) called an earliness of vernalized wheat "absolute earliness", photoperiodic response stated here may be considered to constitute the most essential part of this nature.

However, it must be mentioned that interrelations among four characters

tested were found to be more or less different in some points between two groups of the spring and winter varieties. Correlation coefficients of the grade of spring habit represented by days to flag under continuous illumination at high temperature (x_1) with other three characters, x_2 , x_3 and Y , are always higher in winter varieties than in spring ones (Table 5). This is most remarkable between x_1 and Y , which may suggest that earliness of winter wheat sown outdoors in fall is more or less attributed to residual winter growth habit of plants vernalized insufficiently during winter periods. This is the reason why the close correlation of response of vernalized plants to short-day with the grade of spring growth habit, found in the group of winter varieties, can not be well explained. Therefore, this may imply that the genes for sensitivity to short photoperiod have some connections with those for the grade of winter growth habit. In any way, for breeding of earlier varieties with winter growth habit, it may be necessary to give such relations as above-mentioned careful considerations. In barley, however, it has already been confirmed by Takahashi (1943) that earlier types are mostly found among the varieties with winter growth habit rather than in those with spring growth habit, so far as Japanese barley varieties are concerned.

Using some barley hybrid populations which had been grown in bulk during several successive generations at different locations, Yasuda (1961, 1964) has found that natural selection had a remarkable influence upon heading time under outdoor conditions and its internal factors, spring and winter habit of growth and sensitivities to photoperiod after vernalization. The plants with certain genotypes for these characters, if they were non-adaptive to the location, were rapidly eliminated from the populations. It may be considered that the same holds good of wheat, because the relative importance among these internal factors influencing the heading time under outdoor condition, as stated above, are not so much different between wheat and barley.

VII. SUMMARY

A study has been made to know what kinds of physiological internal factors are most important in determining the earliness of fall-sown wheats. Four characters, sensitivity to temperature, sensitivities of vernalized plants to long and short photoperiod and the grade of spring growth habit, were taken as internal factors, and were investigated along the same lines as was applied for barley by Takahashi and Yasuda (1957, 1958, 1960). The results may be summarized as follows:

(1) Response to temperature was investigated using ten wheat varieties with highly spring growth habit. These varieties were sown 21 times at 30 days intervals under outdoor condition with continuous illumination. Temperature coefficients, regression coefficients of days to flag-leaf emergence (log) on average temperature during growing period (log), were all highly significant and much the same among varieties. Quite the same situations were found in the temperature coefficients regarding growth rate or average days required for expansion of a leaf on

main stem. These imply that heading and growth rate of leaves in spring wheat, regardless of the varieties, are uniformly accelerated with the rise of temperature, approximately 5° to 27°C; in a word, there are no appreciable differences in sensitivity to temperature among them within a certain range of temperature. Under these conditions, however, changes in number of leaves being accompanied by the variations of days to flag were very small in the extents, and the temperature coefficients differed markedly with varieties.

(2) A total of 208 varieties collected from various regions of the world were used to investigate the interrelations of earliness of fall-sown wheats with the other internal factors except for sensitivity to temperature. The results have indicated that photoperiodic response to short-day (days to flag under 12 hour day at high temperature after vernalization, x_3) is the most important internal factor determining the heading time of wheat sown outdoors in fall at Kurashiki, whereas the other two factors, earliness in a narrow sense (days to flag under 24 hour day at high temperature after vernalization, x_2) and the grade of spring growth habit (days to flag under 24 hour day at high temperature, x_1), do not so strongly affect earliness under outdoor condition.

(3) Correlation coefficients of the grade of spring growth habit with the other two internal factors (x_2 and x_1) and also with earliness under outdoor condition are always higher markedly in winter varieties than in spring varieties. For breeding of earlier varieties with winter growth habit, therefore, such relations must be considered carefully.

(4) The results obtained in the present study were almost the same as those in barley (Takahashi and Yasuda, 1957, 1958), except for some details.

Acknowledgement. The authors deeply indebted to Dr. Ryuhei Takahashi Professor of The Ohara Institute for Agricultural Biology, Okayama University, whose kind guidance and encouragement. The authors are also grateful to Dr. Koji Ogawara, Professor of Faculty of Education, Okayama University, for his kindness in correcting the manuscript.

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