VARIETAL DIFFERENCES IN RESPONSES TO PHOTOPERIOD AND TEMPERATURE IN BARLEY

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I. INTRODUCTION

Superior, early maturing varieties of barley have long been hoped for and desired by the growers in the major barley producing regions of Japan, and such demands have recently become more active than ever. With a view of contributing to genetic knowledge and giving practical genetic guidance in breeding programs, the writers have been working for these past ten years on physiology and genetics of some important internal factors influencing ecology and development of barley plants. As the results we have succeeded in disclosing the mode of inheritance of spring and winter habits of growth, and also of another internal factor which was tentatively named as earliness in a narrow sense (Takahashi and Yasuda 1956). But, it was still of necessity to study further on the genetics of response to photoperiod in barley, as it was already suggested by Doroshenko (1927) that varieties of barley, like those of many other plant species, have developed photoperiodic responses which enabled them to adjust the time of maturity in their respective habitats. However, Enomoto (1929) and his followers have maintained that varieties within wheat and barley differ not only in the responses to photoperiod, but also in their "thermic" responses. And, this view has received the support of most of the Japanese agronomists although without any close scrutiny. Therefore, genetic studies have had to be preceeded by a physiological study so as to know whether and how barley varieties are differentiated with respect to their responses to photoperiod and temperature. Investigations were made to answer this question, and the results obtained are presented in this paper.

II. CHARACTERISTICS OF THE MATERIALS

A total of 15 varieties of barley was used in this experiment. The varieties are listed in Table 1. Six varieties of group A were selected among varieties possessing a characteristic of highly spring habit to cover those which have been indicated by Enomoto to be distinctly different in sensitivity to light and temperature. Nine other varieties of group B were all winter barleys, ranging from early to late maturity under ordinary, field conditions in southern Japan. These winter barleys were fully vernalized prior to planting by exposing to a low temperature of 3°C or thereabout for 73 days so as to attain complete receptiveness to photoperiod and temperature stimuli as demonstrated by Kakizaki and Suzuki (1937) and also by Cooper (1954).

Table 1. Characteristics of the experimental materials

A. Spring barleys

Variety	Grade of spring habit	Days to* heading	Leaf* number	Sensitivities to** temperature %	Sensitivities to** photoperiod %
A. Kinai No. 5	I	135	9.0	61	0
B. Tammi	I	130	7.4	—	—
C. Sächsender	I	152	13.0	41	22
D. Natsudaikon-mugi	I	151	13.7	37	55
E. Shokubi-mugi	I	148	13.4	42	48
F. Mensury C	I	163	15.6	—	—

B. Winter barleys

Variety	Grade of spring habit	Days to* heading	Leaf* number	Variety	Grade of spring habit	Days to* heading	Leaf* number
G. Kochi Wase	IV	134	11.3	L. Dairokkaku No. 1	IV	158	13.9
H. Sakigake	IV	139	13.0	M. Nagaoka	V	162	13.7
I. Hayakiso No. 2	IV	143	12.2	N. Kesajiro	VI	162	14.9
J. Sekitori	IV	146	13.8	O. Iwate Omugi No. 1	VI	170	16.1
K. Shimabara	V	149	13.0				

* Seeds sown in mid-November in the field.

** Cited from Enomoto's data (1929).

III. VARIETAL DIFFERENCE IN PHOTOPERIODIC RESPONSE

Photoperiodic responses of the spring barleys and the winter barleys listed in Table 1 were studied by two similar experiments conducted during winter to mid-spring in 1953 and 1954 in a small green house which was maintained higher than 10°C throughout the experimental periods. Seedlings of these varieties were grown in pots, 7~8 uniform plants to a pot, and subjected to the following constant day lenghs: 24, 15, 14, 13, 12, and 11 hour days. These photoperiods were provided by covering the pots with metal tins and giving appropriate exposure to day light from 7:30 A.M. to about 4:30 P.M. each day. To suppliment the natural day length, some of the plots were illuminated by 20 watt incandescent lamps suspended 30cm above the plant level. Records were taken on a single plant basis for the time of emergence of each leaf-blade from its lower sheath, the number of leaves on the main stem, and the time of heading.

The time to flag-leaf emergence and the number of leaves on the main stem of each variety under different photoperiods are shown in Table 2 for the first experiment with the spring barleys and in Table 3 for the second experiment with the winter barleys. The data shown in these tables indicate that all the varieties produced their flag-leaves very early under 24 hour day treatment with only slight differences between varieties, which were attributable to the varietal

Table 2. Days to flag-leaf emergence and leaf number on the main stem of six spring barleys grown under different photoperiods

Variety	Items	24h.	15h.	14h.	13h.	12h.	11h.
A. Kinai No. 5	Days to flag	45.0	45.0	45.1	44.9	44.3	48.3
	Leaf number	*7.0*	*7.0*	*7.0*	*7.0*	*7.0*	*7.1*
B. Tammi	Days to flag	42.6	50.0	49.0	54.0	53.2	53.7
	Leaf number	*6.7*	*7.0*	*7.0*	*7.0*	*7.2*	*7.0*
C. Sächsender	Days to flag	48.0	63.9	64.3	69.3	78.9	83.7
	Leaf number	*8.0*	*9.9*	*10.0*	*10.0*	*10.4*	*11.0*
D. Natsudaikon-mugi	Days to flag	42.1	52.5	54.0	59.9	66.3	80.6
	Leaf number	*7.0*	*7.9*	*8.0*	*8.5*	*9.0*	*10.1*
E. Shokubi-mugi	Days to flag	38.0	41.7	44.3	49.1	58.4	86.9
	Leaf number	*6.9*	*7.0*	*7.0*	*7.7*	*8.7*	*10.9*
F. Mensury C	Days to flag	42.3	72.4	78.1	121.3	—	—*
	Leaf number	*7.0*	*10.4*	*11.0*	*14.2*	*18.0*	*18+*

* Ear primordia not differentiated.

Table 3. Days to flag-leaf emergence and leaf number on the main stem of nine winter barleys grown under different photoperiods after vernalization

Variety	Item	24h.	15h.	14h.	13h.	12h.	11h.
G. Kochi Wase	Days to flag	33.8	34.1	34.4	37.0	37.4	42.4
	Leaf number	*6.4*	*6.0*	*6.2*	*6.0*	*6.0*	*6.8*
H. Sakigake	Days to flag	34.2	34.2	35.0	35.8	39.1	49.4
	Leaf number	*6.8*	*6.9*	*7.1*	*6.9*	*6.9*	*8.5*
I. Hayakiso No. 2	Days to flag	33.3	36.0	36.4	41.4	47.8	63.3
	Leaf number	*6.0*	*6.1*	*6.1*	*6.6*	*7.0*	*9.0*
J. Sekitori	Days to flag	32.6	36.4	37.6	43.9	53.2	77.2
	Leaf number	*7.9*	*7.8*	*7.9*	*7.9*	*8.6*	*11.6*
K. Shimabara	Days to flag	42.8	61.1	63.4	70.3	75.5	84.6
	Leaf number	*7.8*	*9.7*	*10.1*	*10.5*	*11.1*	*12.2*
L. Dairokkaku No. 1	Days to flag	35.1	56.5	54.1	71.5	86.7	94.8
	Leaf number	*7.0*	*9.3*	*8.9*	*10.8*	*11.1*	*11.9*
M. Nagaoka	Days to flag	34.6	54.0	56.6	72.9	91.5	97.0
	Leaf number	*6.0*	*8.0*	*8.2*	*9.4*	*11.0*	*11.0*
N. Kesajiro	Days to flag	35.2	53.1	53.1	73.8	98.1	97.7
	Leaf number	*6.6*	*8.9*	*8.5*	*10.6*	*12.2*	*11.7*
O. Iwate Omugi No. 1	Days to flag	38.3	66.0	70.3	87.6	125.3	135.7
	Leaf number	*6.8*	*9.6*	*9.6*	*10.8*	*14.3*	*14.7*

differences in earliness in a narrow sense. However, as the photoperiods became shorter, most of the varieties tended to delay more in their flaging, although there were some that showed no such tendency. Quite similar changes in the leaf numbers under different photoperiods are easily noted in these tables: all varieties required least number of leaves for maturity when grown under 24 hours exposure, and this number tended to increase proportionately with the delay in time of flag-leaf emergence.

Varietal difference which was exhibited markedly under the shorter photoperiodic conditions will be more easily understood from Figs. 1 and 2, in which the rate of retardation in flag-leaf emergence under 15 to 11 hour days as compared with the time required under 24 hours is shown for each variety: Mensury C and Iwate Omugi were retarded strikingly even under 15 hours, and the former was incapable of heading within the limits of the experimental period when grown under 12 and 11 hours, while Kinai No. 5, Kochi Wase and also Sakigake were affected little by short photoperiods. So, the latter may be called as the day-neutral or light insensitive varieties, and the former as pure long day or light sensitive ones. The other varieties of both spring and winter habit behaved more or less intermediately between these extremes. Thus, a wide and rather continuous variation regarding photoperiodic response was recognized among varieties of both spring and winter habit.

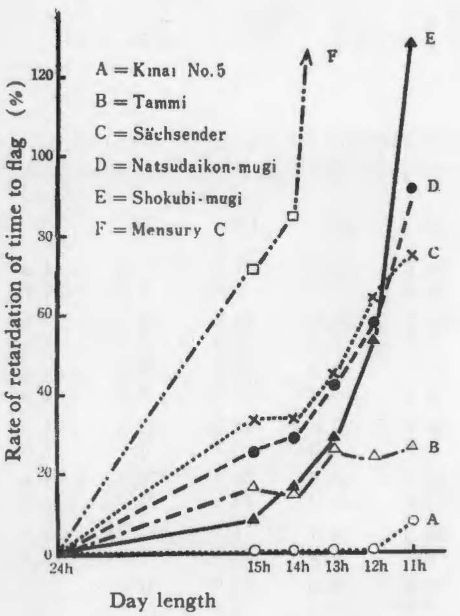

Fig. 1 Comparison of 6 spring barleys in their responses to short photoperiods as indicated by the retardation rate of flag-leaf emergence under 15~11 hour days to the time to flag of the respective variety under 24 hour day.

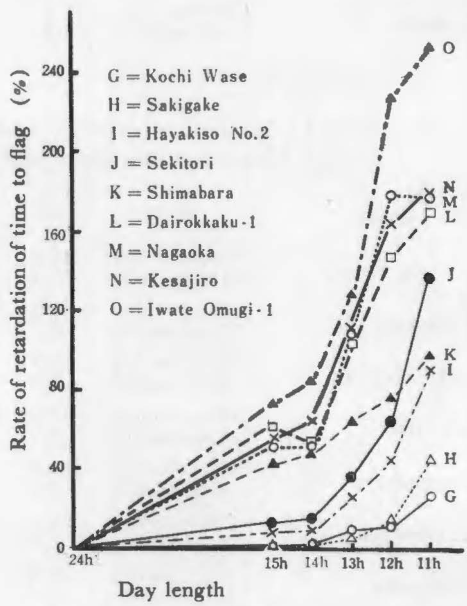

Fig. 2. Comparison of 9 winter barleys (vernalized) in their responses to short photoperiods as indicated by the retardation rate of flag-leaf emergence under 15~11 hour days to the time to flag of the respective variety under 24 hour day.

IV. RESPONSE TO TEMPERATURE

Responses of the six spring barleys to different temperatures were studied under 24 hour photoperiod, a condition that was suggested by the previous experiment to be most favorable for heading of all of these varieties without exception. Seeds of each variety were sown 11 times at 30 days intervals from February 8th of 1953 to the following February inclusive, excepting July and August when temperature was too high to allow normal growth of barley, and these plants were reared under outdoor condition, subjecting to various tem-

Table 4. Days to flag-leaf emergence and number of leaves on the main stem of six spring barleys which were sown at 30 days intervals and grown outdoors under 24 hours illumination. Average temperatures of the growing periods of each sowings are also indicated

Variety	Items	Feb.	Mar.	Apr.	May	June	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.
Kinai No. 5	Days to flag	72.7	56.6	42.4	39.7	38.2	39.0	42.7	92.3	107.6	89.0	67.6
	Leaf number	*8.0*	*8.0*	*8.0*	*7.0*	*7.0*	*7.0*	*7.0*	*8.0*	*8.0*	*8.1*	*8.0*
Tammi	Days to flag	66.0	51.3	36.0	35.9	30.1	33.8	41.8	78.0	98.8	85.2	64.7
	Leaf number	*7.0*	*7.0*	*6.6*	*6.0*	*6.0*	*6.7*	*7.0*	*7.0*	*7.0*	*7.0*	*6.8*
Sächsender	Days to flag	78.7	58.0	45.9	40.0	45.5	45.9	51.5	114.9	114.3	96.3	73.5
	Leaf number	*10.0*	*9.4*	*8.0*	*8.0*	*8.3*	*9.0*	*9.5*	*9.0*	*10.4*	*10.0*	*9.0*
Natsudaikon-mugi	Days to flag	68.2	51.8	38.6	35.5	32.3	33.4	34.8	77.0	101.2	88.7	63.9
	Leaf number	*8.3*	*8.0*	*7.9*	*7.0*	*7.0*	*7.0*	*7.4*	*8.0*	*9.0*	*8.9*	*7.7*
Shokubi-mugi	Days to flag	61.7	50.4	35.2	28.5	24.8	26.3	28.9	68.0	96.5	83.3	62.9
	Leaf number	*7.8*	*7.0*	*7.0*	*6.0*	*6.0*	*6.0*	*6.1*	*6.9*	*8.0*	*7.9*	*7.1*
Mensury C	Days to flag	74.0	56.4	40.4	37.9	34.7	43.1	50.1	104.6	112.2	92.2	72.1
	Leaf number	*9.5*	*9.2*	*8.0*	*7.0*	*8.0*	*8.0*	*9.0*	*9.4*	*10.0*	*10.5*	*9.0*
Average temperature(C)		10.4°	13.3°	16.6°	21.3°	24.6°	23.5°	17.7°	9.4°	7.8°	8.4°	10.4°

Table 6. Days to flag-leaf emergence and number of leaves on the main stem of six spring barleys which were sown at 30 days intervals and grown outdoors under natural day length

Variety	Items	Feb.	Mar.	Apr.	May	June	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.
Kinai No. 5	Days to flag	74.6	56.3	42.8	39.0	35.1	43.5	45.0	104.0	113.2	89.7	67.8
	Leaf number	*8.0*	*8.0*	*8.0*	*7.0*	*7.0*	*7.0*	*7.2*	*8.5*	*9.0*	*8.5*	*8.1*
Tammi	Days to flag	70.5	54.3	39.8	39.6	40.0	53.0	61.3	103.1	107.6	87.1	66.1
	Leaf number	*7.0*	*7.0*	*6.9*	*6.0*	*7.0*	*7.0*	*8.0*	*7.3*	*7.0*	*6.9*	*7.0*
Sächsender	Days to flag	85.0	65.0	54.4	46.5	46.3	80.3	103.5	142.0	127.9	105.1	84.1
	Leaf number	*10.0*	*10.0*	*9.0*	*8.7*	*9.0*	*10.3*	*10.4*	*10.9*	*12.1*	*11.6*	*9.5*
Natsudaikon-mugi	Days to flag	87.4	64.0	45.0	—	—	159.7	133.3	147.2	126.8	105.7	82.7
	Leaf number	*13.2*	*10.2*	*10.0*	—	—	*12.2*	*11.9*	*12.6*	*12.9*	*12.4*	*9.5*
Shokubi-mugi	Days to flag	78.6	57.0	46.3	40.9	30.7	104.4	113.9	144.0	123.1	98.7	81.1
	Leaf number	*9.6*	*8.8*	*8.2*	*7.0*	*6.0*	*11.0*	*10.6*	*11.5*	*11.9*	*11.2*	*9.4*
Mensury C	Days to flag	93.6	75.1	56.7	54.5	—	221.6	191.8	164.4	157.8	111.5	103.1
	Leaf number	*12.5*	*9.5*	*10.0*	*8.0*	—	*17.8*	*17.3*	*15.2*	*13.6*	*12.1*	*11.5*

peratures of different seasons and continuous illumination with 100 watt incandescent lamps. Records were taken for the time of flag-leaf emergence and the number of leaves on the main stem on single plant level.

In Table 4 are shown the results, together with averages of temperature at 10 A.M. during the periods from sowing to flag-leaf emergence of the six varieties for each sowing time. The data indicate that the time to flag tended to be increased remarkably in all of the varieties as temperature during the respective growing period became lower. When the logarithm of time to flag was plotted against the logarithm of the corresponding temperature of the respective period, their relationship was found to be almost linear, though the points for June and September sowings fell somewhat apart from the line, probably because temperature was still too high in these seasons. Excluding these two cases, Bělehrádek's temperature coefficients (1926) or linear regression coefficients of time to flag on temperature was calculated for each variety. The estimates of the coefficients

Table 5. Regression coefficients of days to flag-leaf emergence (log), leaf number, and growth rate of leaves (log) on average temperature during growing periods (log)

Variety	Days to flag (log)	Leaf number	Growth rate of leaves (log)
Kinai No. 5	-1. 01845**	-2. 18764*	-0. 88344**
Tammi	-1. 09312**	-1. 47691*	-0. 91062**
Sächsender	-1. 15055**	-4. 24110**	-0. 91847**
Natsudaikon-mugi	-1. 13569**	-3. 72175**	-0. 87986**
Shokubi-mugi	-1. 20455**	-4. 16674**	-0. 93562**
Mensury C	-1. 16710**	-6. 23491**	-0. 83109**

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

are shown in Table 5. Since they were found to be highly significant, it is possible to conceive that, at least within the range of 8° to 21°C, the temperature is a unique factor determining earliness of barley grown under long day condition.

However, whether there exists an appreciable difference among barley varieties in response to temperature will constitute another problem. By definition, the temperature coefficient signifies the rate of decrease in time to flag-leaf emergence with the rise of average temperature during growth period, so it follows that, if these varieties responded differently to temperature, the estimates of temperature coefficient for these varieties should be significantly different. Outcome of the *t*-tests between any two of these estimates did not show the existence of any significant difference. This naturally leads us to the conclusion that all the varieties tested respond almost similarly to a wide range of temperature which allows barley more or less vivid development.

The time to flag-leaf emergence may be represented by the product of the number of leaves and average days required for development of a leaf or simply growth rate of the leaves. The effects of temperature on these two components of earliness were studied further.

According to Table 4, variations in the number of leaves on the main stem are not so marked as those in the time to flag-leaf emergence. But, it is still possible to find out the regularity in seasonal change of leaf numbers: The least number of leaves is developed by plants which have been sown in May when temperature is considerably high, although with some exceptions, while leaf number is the largest on those sown in December or January when it is cool. Thus, the leaf number tends to increase as temperature becomes lower. More interesting is the fact that the increased number of leaves at low temperature varies with variety: for instance, difference in leaf number between the largest and the least is only one in Tammi and Kinai No. 5, while in Mensury C it is 3.5. The adequacy of these statements was tested by calculating regression coefficients of the leaf number on temperature during growing period for each of the varieties tested and then by subjecting these estimates to the tests of significance. In these calculations, the data for June and September sowings were excluded owing to their abnormal growth. Coefficients of linear regression by converting into logarithm only for temperature are shown in Table 5. They were all found to be significant on either 1% or 5% levels, and further that the coefficient for Mensury C proved to be significantly larger than those for Tammi and Kinai No. 5 at 1% and 5% levels, respectively. A simple interpretation of the results will be such that temperature affects to an extent leaf number of spring barley grown under continuous illumination, and the effect of temperature on the leaf number varies with variety. But, this may not be necessarily be pertinent because of the fact that varieties senstive to short photoperiod are liable to increase their leaf number by being exposed to lower temperature more than those which are insensitive to photoperiod. Another interpretation, which might probably be more plausible, will then be such that the favorable effect of long photoperiod on leaf number is no longer so active at lower temperature as it is at higher temperature, resulting in a condition that is substantially similar to more or less shortened photoperiodic condition.

Effect of temperature on the growth rate of the leaves was investigated by a similar method as was applied for the aforementioned tests. The growth rate of leaves was represented by the quotient of days from sowing to flag-leaf emergence divided by the leaf number of the same plant. The regression coefficient of the growth rate of leaves on temperature for each variety thus obtained are listed in Table 5. These estimates are all highly significant, and are so closely approximate with each other in magnitude that the differences between them are statistically insignificant.

V. INTERACTION OF PHOTOPERIOD AND TEMPERATURE

It is desirable to perform experiments under controlled condition of light and temperature for acquiring precise knowledge about the combined effects of photoperiod and temperature. But, lack of such facilities forced us to approach this problem by the experiments under natural conditions. In parallel with the aforementioned experiment in which six spring barleys were sown 11 times at 30 days intervals and grown outdoors under continuous illumination, the same materials were sown at the same time and plants were reared without supplimental illumination, subjecintg to natural day length. In Table 6 are given the data, arranged in the same manner as in Table 4, and for the sake of convenient comparison, the table is placed below Table 4.

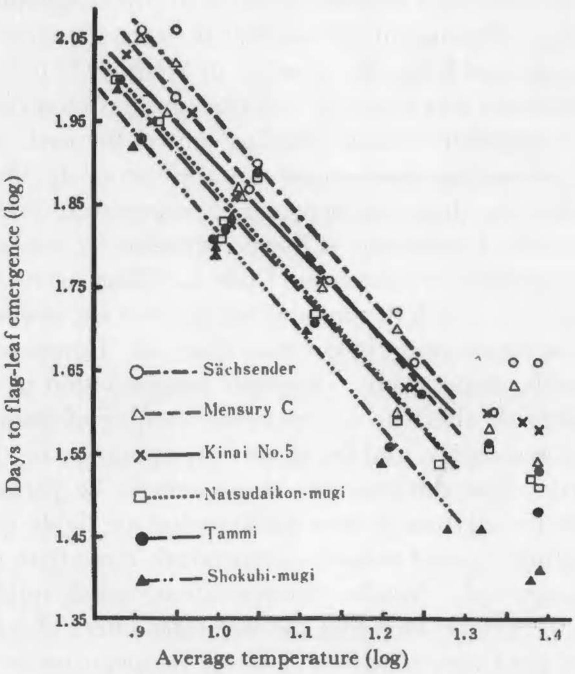

Fig. 3. Relations between time to flag-leaf emergence and average temperature during growth periods.

As indicated in the previous paragraph, the time to flag-leaf emergence under continuous illumination mostly depends upon height of temperature of growing condition, but is irrespective of sensitivities of the varieties to photoperiod, while under natural day length it will be affected not only by temperature but also by photoperiod. So, it follows that the difference in time of flag-leaf emergence between two contrasting plots under natural and long photoperiods may suggest extent of interaction between temperature and photoperiod, or extent of effect of photoperiod under different temperatures. In Fig. 4 are shown the seasonal variation curves of the said difference for each of the six varieties, together with those of natural day length and also average temperatures of ten day-periods during experiment in Kurashiki.

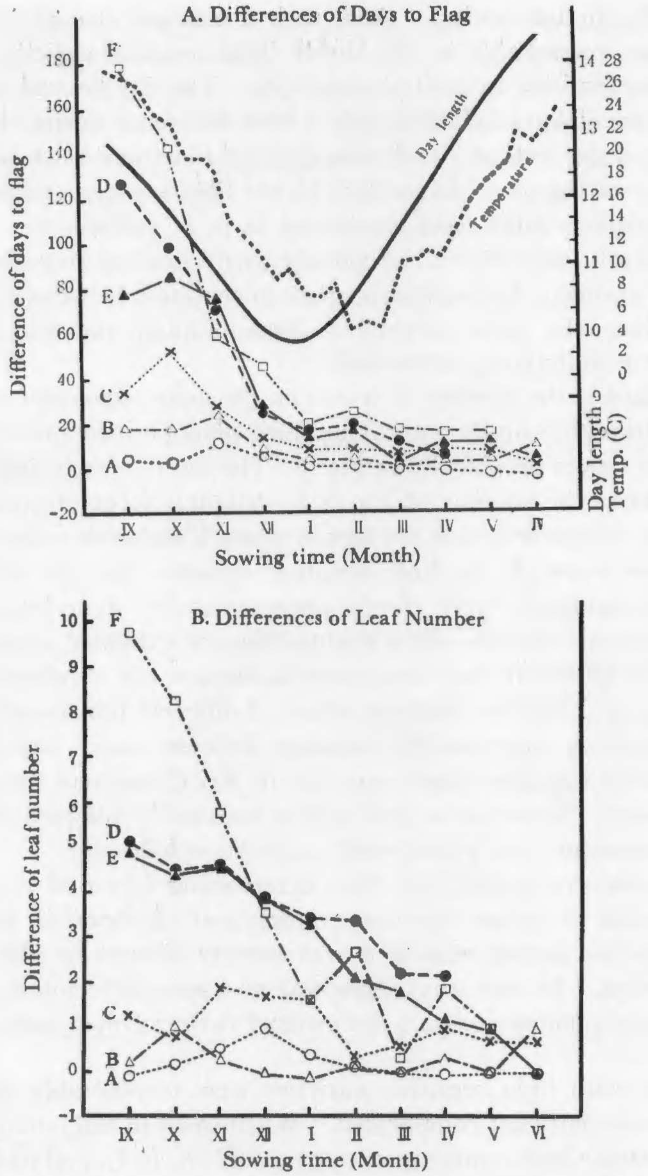

Fig. 4. Changes of differences of (A) time to flag-leaf emergence and (B) leaf number on the main stem between plants subjected to natural day length and 24 hour day. Six spring barleys were sown outdoors at 30 days intervals.
A. Kinai No. 5　C. Sächsender　E. Shokubi-mugi
B. Tammi　D. Natsudaikon-mugi　F. Mensury C

It is apparent in this figure that the differences in time to flag-leaf emergence between plants grown under natural and long photoperiods varies considerably with variety and also with time of sowing of each variety. Namely, the largest differences are found in those which have been sown in September to November, but the differences become smaller and smaller when sown in winter and especially in late spring. And, such a seasonal change in difference as above is more remarkable in the highly light sensitive varieties than in those which are less sensitive to short photoperiods. The day-neutral varieties, Kinai No. 5 and Tammi, have exhibited only a little difference in time to flag between plants grown under long day and those exposed to natural photoperiod, indifferently of their sowing time. In contrast, highly light sensitive varieties, Mensury C and Natsudaikon-mugi, have manifested as large differences as 178 and 126 days, respectively, when sown in September, with gradual decrease in the difference at later sowings. Almost intermediate in condition between those mentioned above are shown by such varieties as Shokubi-mugi and Sächsender, which respond intermediately to photoperiod.

With regard to the number of leaves on the main stem quite a similar comparison between plots under natural and long photoperiods was undertaken, and its results are shown graphically in Fig. 5. The figure clearly indicates that the said difference in the number of leaves is strikingly larger at autumnal sowing than at either winter or spring sowings in general, and such a seasonal change is exhibited more evidently by light sensitive varieties than by light insensitive ones. These conditions were closely approximated to those found for the time to flag-leaf emergence with only a slight difference exhibited at winter sowing.

It must be admitted that these experiments are not necessarily satisfactory for estimating in detail the combined effects of different temperatures and photoperiods on heading time and leaf number, because under natural conditions both temperature and day length vary day by day throughout the whole periods of barley growth. Nevertheless, it would be reasonably inferred that the interaction of temperature and photoperiod might be as follows:

For a day-neutral variety the chief determining factor of time to heading and growth rate of leaves was temperature, and photoperiod mattered little. Number of leaves on the main stem was scarcely affected by both temperature and photoperiod. In any way, there was no appreciable interaction between temperature and photoperiod on a day-neutral variety grown under natural conditions.

The cases with light sensitive varieties were considerably different from above and were somewhat complicated. When sown in fall, young plants were subjected to rather high temperature, ranging 25° to 10°C, and such short photoperiod as below 12 hour day for more than one month. Probably on *this* account, heading time of light sensitive varieties was much retarded in one hand, and, if photoperiod was supplimented by artificial illumination, their headings were extremely enhanced on the other. The above supposition might be evidenced by the following experiment: Vernalized seeds of 78 barley varieties were divided into two, and one set of them was grown from September 20 under 12 hour day in a glass house in one hand, and another set under natural day length and temperature on the other. The data from this experiment indicated that the correlation coefficient of the time to flag-leaf emergence under natural and artificial conditions was as high as + 0.947. It may be noted also that these fall-sown barleys were allowed to continue development and heading even under outdoor conditions of winter months in Kurashiki.

Although short photoperiod below 11 hour day and low temperature mostly below 10°C prevailed throughout the winter months (December to February), these light sensitive varieties sown in this season came into heads much earlier than the same varieties sown in fall. This suggests that short day accompanied by low temperature was rather favorable for heading of these varieties as compared with the high temperature and short photoperiodic conditions in fall (Table 6). In contrast, under long day condition winter-sown barleys were much later than those sown in fall (Table 4). These will explain almost simultaneous heading of winter-sown barleys grown under natural and long photoperiodic conditions. Almost similar situations were found with regard to the number of leaves on the main stem.

In spring, day length becomes longer than 12 hours and temperature higher than 10°C, so spring-sown barleys came into heads under natural conditions as early as those grown under 24 hour day.

VI. DISCUSSION

Variability in response to short photoperiod of varieties of barley has already been suggested by Doroshenko (1927) and Enomoto (1929). Our first experiment with 15 varieties of both spring and winter habits has also shown this being true. The plants of these varieties behaved almost similarly under 24 hour day, but flag-leaf emergence was retarded and leaf number was increased in varying degree with variety under short photoperiod. Thus, some varieties behaved as day-neutral ones, and some did as strictly long-day plants, and others manifested more or less intermediate responses to short photoperiod.

By using seven species of mints, a long day plant, Allard (1941) has observed that a species has failed to flower even under 14 hour day, and in some species somewhat lower photoperiodic threshold has been indicated, and in an extreme species any delay of flower initiation has occurred even under 10 hour day. Almost similar results have been reported by Doroshenko (1927), Yatsuyanagi (1946), Cooper (1956) and Riddle and Gries (1958) for spring wheat and vernalized winter wheat; by Wiggans and Frey (1955) for oats; and by Cooper (1952) for ryegrasses.

Next, let us consider about variation in response to temperature and the effect of temperature on photoperiodic response. There is no doubt that temperature affects strongly flowering of any kinds of plants, but whether varieties of a plant species respond differently to temperature is another problem. Temperature and photoperiod exert their influences on plant growth as the environment as a whole, and hence these two are by no means separable in our experimental processes. The only possible measures to allow us to approach the problem under consideration may be the following two: One is, as Oka (1954) has tried in his experiment with rice plants, to use such materials as are entirely insensitive to photoperiod. However, this may not be applicable so widely to various plant

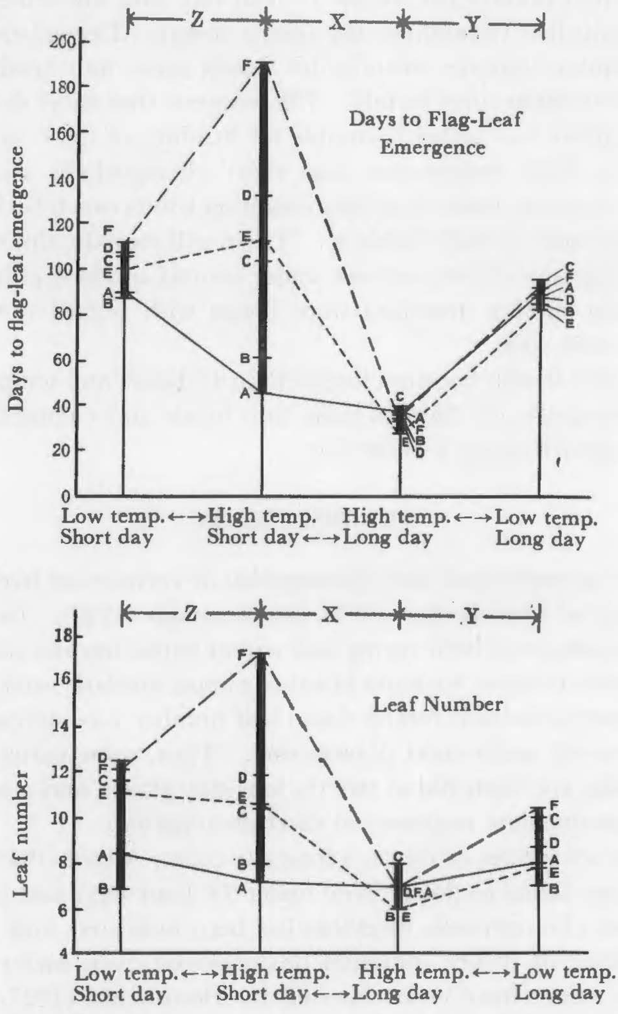

Fig. 5. Days to flag-leaf emergence (upper) and leaf number (lower) of the following 6 spring barleys grown under different combinations of photopiriod and temperature.

A. Kinai No. 5. C. Sächsender E. Shokubi-mugi
B. Tammi D. Natsudaikon-mugi F. Mensury C

species, because of the difficulties in securing sufficient materials as such. The alternative, that has been suggested by Suenaga (1936), is to arrange photoperiodic condition to be similarly most favorable to all of the varieties and not to exert any modifying effect upon response to temperature. Taking this into consideration, responses of six spring varieties to different temperature were compared under 24 hour day, a condition that may conform to the above requirement. The results have indicated that flag-leaves of these varieties emerged earlier and their growth rate of leaves were accelerated with the rise of temperature, but the temperature coefficients of these varieties for both items do not differed significantly from each others. This naturally leads to a conclusion that there is no appreciable difference in sensitivity to temperature among them. The same relation as above stated was found by Steinberg and Garner (1936) in soybeans and also by Muraoka *et al.* (1956) in tobacco. However, it must be noted here that the relation is consistent within the range of temperature, from approximately 21° to 8° C, as estimated from our experimental result, but responses to extremely higher temperature seem to be different with variety.

Number of leaves on the main stem varied only a little when plants were grown under continuous illumination for the large changes of temperature. Nevertheless, it was recognized that lowering of temperature was always accompanied by a slight increase of leaf number, and further that the rate of increase in leaf number was proportionate to the sensitivity of variety to short photoperiod. This may suggest that low temperature inactivates to an extent the favorable effect of long photoperiod so that the plants under cool, long day behave somewhat alike to those are subjected to short photoperiod. If so, it follows that the long photoperiod may not always be conceived as the most favorable similarly to all the varieties when the temperature is low. Despite this, it is still certain that the interaction of temperature and long photoperiod is not so strong that it does not bring about significant difference between the temperature coefficients regarding time to flag-leaf emergence which is the product of leaf number and growth rate of the leaves.

As pointed out by Murneek (1948), the sensitivity of many plants to the duration of light is affected very much by temperature, and contrariwise, the photoperiod influences the responses of plants to temperature. In short, temperature and photoperiod interact intricately with each other. And, the effects of their interactions on time to heading seem to be somewhat different from those on leaf number. To illustrate the situations as simply as possible Fig. 5 was prepared, in which number of days to flag and leaf numbers of six varieties under the following four combinations of light and temperature are represented. The actual data were cited from Tables 4 and 6 listed before.

Long day at high temperature: May-sowing under 24 hour day
Long day at low temperature: January-sowing under 24 hour day
Short day at high temperature: October-sowing under natural day length
Short day at low temperature: January-sowing under natural day length

The central, X, section of Fig. 5 may represent the behaviors of the plants of the six spring varieties grown under varying conditions of photoperiods at high temperature, and the right, Y, section the responses of the plants to the conditions of varying temperatures at constant, long photoperiod. By refering to the left, Z, section, we can further understand how to change time to flag-leaf emergence and leaf numbers of these varieties when grown under short day at varying conditions of temperature. As the situations represented by X, Y and Z sections of this figure are apparently similar to those discussed in detail in chapters III, IV and V, respectively, there is no need to add comments. However, it may be adequate to make some remarks about the general matters, which are as follows:

Under the condition of high temperature and long photoperiod, spring barleys come into heads most rapidly with the least number of leaves, and if vernalized, winter barleys behave similarly. So, it may be possibly considered that barley plants with highly spring growth habit are high temperature long day plants. With the fall of temperature, however, the heading time of these varieties are considerably delayed, and their leaf numbers are increased, though very slightly, even under long day condition. Judging from the relative earliness of these varieties, the chief internal factor that determines time of heading under long photoperiod, irrespective of temperature, seems to be, according to the definition given in our previous paper (Takahashi and Yasuda, 1956), the earliness factor in a narrow sense, and photoperiodic sensitivity matters little. But, as differential responses of these varieties to cool, long day are evident with respect to leaf number, so the photoperiodic sensitivity is conceived to be evoked to act to some exetnt by lowering of temperature.

In contrast, a predominant influence of the photoperiodic sensitivity on both time of heading and leaf number is distinctly recognizable under short day conditions, and the effect of this internal factor becomes very marked with the rise of temperature. The last mentioned fact has been confirmed also by Riddle and Gries (1958) in an experiment with wheats which were reared under the controlled conditions of light and temperature.

As stated briefly in the introductory remarks, Enomoto (1929) and also Kakizaki and Suzuki (1944) are of the opinion that wheat and barley varieties differ from each others in "thermic" as well as photoperiodic sensitivity: a typical spring barley is extremely sensitive to either high temperature or long photoperiod or it is moderately sensitive to both high temperature and long photoperiod. According to these authors, however, the "thermic" sensitivity of a variety is determined by comparing heading time of the plants of the variety which have been grown from late fall under natural (short) day, subjecting to high temperature in a heated green house in one hand, and to low temperature outdoors, on the other. Furthermore, they considered that earlier heading at high temperature than at low temperature might be wholly attributable to the sensitivity of the variety to temperature. However, just as above stated, under short photoperiod heading time is strongly affected by its photoperiodic sensitivity, though it is also considerably modified by temperature. So, it is necessary for estimating "thermic" sensitivity to adjust photoperiodic condition so as to be similarly favorable to all the varieties to be tested.

The effect of temperature on the photoperiodic response has been studied in various kinds of plants. Roberts and Struckmeyer (1939) have concluded from his extensive studies that photoperiod may be the primary factor for a certain range of temperature, but with many plants it is a contributing and not a controlling factor in the formation of flowers. One of the exceptional cases observed by them is the behavior of Maryland Mammoth tobacco, which has generally been known to be a strictly short day plant: The plants of this variety given short days at a very warm temperature remained vegetative, while they were capable of setting fruits in long, cool days. Quite a similar observation was reported by Muraoka *et al.* (1953) in several varieties of tobacco. According to Knott (1939), spinach plants growing under 15 hour photoperiod begin to elongate seedstalks at medium temperature sooner than at somewhat higher or lower temperatures. Garner and Allard (1930) have concluded from their experiments conducted outdoors and in the greenhouse that under field conditions variations from year to year in date of flowering of both early and late varieties of soybeans, when planted on any particular date, are due chiefly to differences in temperature, while length of day is the primary external factor responsible for the fact that one variety is always relatively early and another late in attaining the reproductive stage. This conclusion was re-affirmed by Steinberg and Garner (1936) by their experiment with the same materials grown under artificially controlled conditions of photoperiod and temperaure.

The last mentioned statement by Garner and Allard regarding the influences of temperature and photoperiod on soybeans seems to be wholly applicable to the cases with spring barleys. It is certain that earliness of barley varieties depends chiefly upon temperature, provided that they are insensitive to photoperiod, or they are subjected to continuous illumination. Further, however, as seen in Table 6, where changes of time to flag under natural conditions are shown, there is a general tendency that the day-neutral variety is always earlier than the light sensitive varieties when sown simultaneously on a particular date. This is probably because that in nature it prevails more or less short photoperiod below 14 hour days in Kurashiki, and day length still acts as the principal external factor responsible for relative earliness of different varieties, though temperature modifies considerably the effect of photoperiod.

It may be adequate to note that photoperiodic sensitivity has an intimate bearing on the earliness of fall-sown barleys including varieties of winter as well as spring growth habits. The relation was studied in the following way: first, average of the retardation rate at 15 to 11 hour days for each of the spring and winter barleys listed in Table 1 was calculated from the data in Table 2 and 3 in order to show the grade of sensitivity to short photoperiod of each variety. Then, correlation between this and heading date of the plants, sown in fall as is usually practised in our locality, was investigated separately for spring and winter barleys. The estimates of correlation coefficients were + 0.899 and + 0.994 for spring and winter barleys, respectively. In view of the importance of this fact for breeding of early variety of barley, a detailed study was made further, the result of which will be published in another paper.

SUMMARY

A study was made of varietal differences in responses to photoperiod and temperature in barley. Fifteen varieties of either spring or winter growth habit were used as the materials. The winter barleys were all fully vernalized before planting so as to respond readily to photoperiod and temperature. The results obtained may be summarized as follows:

1. Plants of the highly spring varieties behaved almost similarly under 24 hour day, but under short day conditions flag-leaf emergence was retarded and leaf number was increased in varying degree with variety. Thus, some varieties behaved as day-neutral ones, and some did as strictly long day plants, and others manifested more or less intermediate responses to short photoperiods. This was found to be true of the vernalized winter barleys.

2. The photoperiodic sensitivity is affected very much by temperature. In consequence, varietal differences in time of heading and leaf number to be exhibited under short photoperiod become by far more markedly at high temperature than at low temperature.

3. Under continuous illumination, heading time and growth rate of leaves of a variety are almost indifferent of its photoperiodic sensitivity, and leaf growth, and heading as well, is accelerated with the rise of temperature. No significant difference was recognized with respect to the temperature coefficients of these varieties or acceleration rates by the rise of temperature. These relations are consistent within a certain range of temperature, but varietal sensitivity to an extremely high temperature seems to be somewhat different. Furthermore, a light sensitive variety tends to develop more leaves on its main stem than does a light insensitive variety, with the fall of temperature.

4. Plants of a day-neutral variety develop almost the same number of leaves on their main stems, irrespectively of markedly varied conditions of temperature and day length to which they have been subjected, whereas on the leaf number light sensitive variety is strongly modified by the combined effects of photoperiod and temperature.

5. Although temperature markedly influences photoperiodic sensitivity, day length seems to act as the principal external factor in the sense that a day-neutral variety is always earlier than the light sensitive ones which have been sown on the same date, as in nature it prevails more or less short photoperiod.

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PLATE 1.

Plants of three spring barleys, Kinai No. 5 (top), Natsudaikon-mugi (middle) and Mensury C (bottom), which had been subjected to the following photoperiods: 11, 12, 13, 14, and 24 hour days from left to right. Photos taken 60 days after sowing.