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Geographical variation in heading characters among wheat landraces, *Triticum aestivum* L., and its implication for their adaptability

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Summary. Heading time and its constituent traits, photoperiodic response, narrow-sense earliness and vernalization requirement, were surveyed for 158 wheat landraces. Wide varietal variation was observed in each character. Nearly half of the variation for each character was explained by a geographical difference in origin. Based on these data and the growing environments in each locality, we analyzed "adaptation strategy", seen as the adjustment of heading time in terms of differences in the constituent traits, both individually and combined. The difference among localities indicated that wheat landraces had been selected for early heading as an adaptation strategy to water stress and/or high temperature in early summer. This change was caused by a reduction in photoperiodic response and narrow-sense earliness. The vernalization requirement was also reduced for adaptation to relatively mild winters. Adaptation strategy deduced from the variation within each locality was also different amongst localities. In the central region of wheat evolution, where wide variations existed in both photoperiodic response and narrow-sense earliness, the late-heading trait was achieved by either one of these traits individually or both of them combined. On the contrary, in the eastern and the western regions, wide variation in heading time was achieved by the unique combination of photoperiodic response and narrow-sense earliness. A sampling strategy for wheat germ plasm is also discussed.

Key words: Heading characters – Geographical variation – Adaptation strategy – Genetic resource – *Triticum aestivum*

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Introduction

Landraces are regarded as an important gene pool for crop improvement. To utilize these efficiently, primary information on their agronomic traits is a prerequisite. In cultivated wheat, extensive surveys have concentrated on several traits, such as morphological and metrical characters (Witcombe and Rao 1976; Bekele 1984; Ehdaie and Waines 1989). Less attention has so far been paid to developmental characters, even though the adaptability of wheat varieties is largely affected by such characters.

As one of the primary developmental characters, heading time has been surveyed in both hexaploid wheat (Jaradat 1991) and tetraploid wheat (Qualset and Puri 1974), and shows wide variation among landraces and areas of their origin. However, heading time is evaluated in the field and thus varies depending on the growing environment. However, the constituent traits, that is, photoperiodic response, narrow-sense earliness and vernalization requirement, are intrinsic characters of each landrace and can be evaluated under controlled environments. According to Kato and Yamashita (1991) about 85% of the varietal variation in heading time of fall-sown wheat in the south-western part of Japan could be explained by differences in photoperiodic response and narrow-sense earliness, which suggests that once the relationship between heading time and its constituent traits is established for each area, heading time can be roughly estimated on the basis of the three traits. In addition, breeding for heading time becomes more efficient when individual traits rather than the combined product, namely heading time itself, is selected for (Yoshida et al. 1983). For efficient utilization of wheat landraces, therefore, each trait should be surveyed as well as heading time itself. Additionally, geographical aspects of variation patterns must be revealed in order to collect wheat germ plasm efficiently (Murphy and Witcombe 1981).

By an analysis of the geographical diversity in heading characters, the adaptation strategy to diverse growing environments through the adjustment of heading time should be explainable in terms of a combination of the three traits. This relationship has been analyzed for many improved varieties (Hoogendoorn 1985). However, these may have lost the genes that adapted them to local environments, through outbreeding with foreign varieties. On the contrary, characteristic, adapted genotypes of each area should be found in landrace collections. Accordingly, a study of landraces should lead to the understanding of adaptation strategy to each growing environment.

Variability in adaptive characters is related to environmental heterogeneity (Murphy and Witcombe 1981), although the center of diversity in qualitative characters corresponds to the center of crop evolution. In the study presented here, therefore, heading time and its constituent traits were surveyed for wheat landraces not only in the center of wheat evolution but also in neighboring areas. The adaptation strategy in each area is discussed in relation to the prevailing environment.

Materials and methods

To cover a wide range of variation in the combination of the three heading traits as well as in each trait itself, 158 wheat landraces, *Triticum aestivum* L., collected from various countries were examined. Seeds of these varieties were supplied by the Plant Germplasm Institute, Kyoto University, Japan. Landraces were grouped into 13 localities (Fig. 1, Table 1) according to area of origin and growing environment. These localities were again grouped into four regions (Table 1) on the basis of geographical distance and similarity in growing environments. The collection sites of each landrace have been described in full by Tanaka (1983).

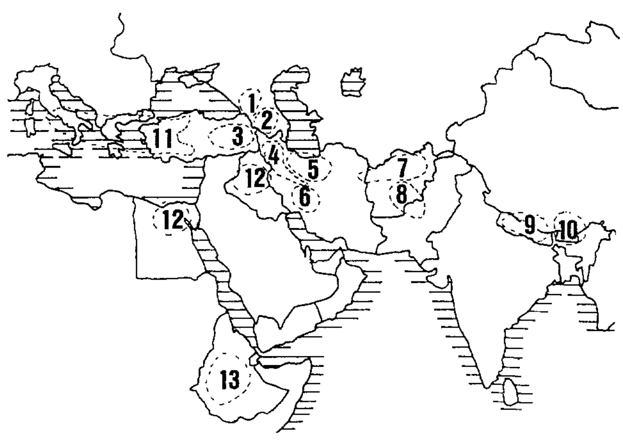

Fig. 1. Geographical distribution of localities where wheat landraces were collected. *Numbers* represent locality number shown in Table 1

For the evaluation of vernalization requirement, sprouted seeds were vernalized for various periods ranging from 0 to 80 days at intervals of 10 days. They were then grown in a glasshouse under a 24-h daylength regime. The vernalization requirement was evaluated on the basis of the difference in Dof (the number of days from forced sprouting to flag leaf unfolding) among vernalization treatment durations. The details of the evaluation method are described in Kato and Yamagata (1988), where the vernalization requirement was referred to as "chilling requirement" to distinguish it from the "vernalization requirement" measured by another method (Gotoh 1976). For each landrace, six plants were allotted to each treatment.

For the evaluation of narrow-sense earliness and photoperiodic response, sprouted seeds of winter and spring wheat varieties were fully vernalized by low temperature treatment for 70 and 40 days, respectively. These were then grown at 20 °C in growth chambers under 12-h and 24-h daylength regimes. Narrow-sense earliness was measured as Dof under a 24-h daylength regime. Photoperiodic response was measured as the ratio of Dof between daylength regimes, as proposed by Kato and Yamashita (1991). For each landrace, four plants were allotted to each treatment.

Heading time was recorded on a single plant basis as the days from the 1st of April, using plants sown in the experimental field of Kochi University (33°32′N, 133°41′E, 7 m above sea level) on the 15th of November in 1983. Ten plants were grown for each variety. The methods of cultivation and calculation are fully described for each character in Kato and Yamashita (1991).

The frequency distribution, mean and variance were calculated for each character for each region or locality. Differences in the mean and variance among regions or localities were tested for significance by using *F*-tests. By an analysis of variance the total variance of each character was divided into components due to differences among regions, among localities within regions and among landraces within localities. Simple correlation coefficients were calculated between heading time and its constituent traits for each locality.

Climatic data was taken from Hatakeyama (1964) and "Climatic Table for the World" published by the Japanese Meteorological Agency.

Results

Frequency distributions for each character are shown for each region in Fig. 2A–D. Estimation of the variance components revealed that more than 50% of the total variance for all characters was ascribable to varietal differences within localities; the second most important variance component was that due to differences among regions (Table 2). Variance components due to differences among localities within regions were the least important among the three components for all characters, which justifies the adequacy of grouping of localities into regions.

The mean and standard deviation of each character is shown for each region in Table 3. Differences in mean value among regions were statistically significant for each character ($P < 0.01$). Landraces in the central region generally exhibited the largest values for the three heading traits, and thus became late in heading time. Conversely, landraces from the other regions showed rela-

Table 1. Number of landraces examined and mean heading time and three heading traits in each region

No.	Locality	Number of landraces	Heading time	Vernalization requirement (days)	Photo-periodic response	Narrow-sense earliness (days)
	Central region					
1	Georgia (CIS)	10	36.7	58.0	2.18	40.1
2	Armenia (CIS)	9	38.3	27.8	2.21	38.1
3	Turkey (east)	8	40.9	52.5	2.26	40.5
4	Iran (north)	13	40.5	51.5	2.71	43.3
5	Iran (east)	5	37.4	60.0	2.43	38.6
6	Iran (south)	9	32.5	37.8	1.88	38.0
	Eastern region					
7	Afghanistan (north)	17	33.3	37.7	2.09	36.2
8	Afghanistan (south), Pakistan	15	28.1	34.3	1.89	34.8
9	Nepal	13	29.4	35.4	1.83	34.9
10	Bhutan	10	26.6	33.3	1.74	33.3
	Western region					
11	Turkey (west), Italy and Greece	16	29.5	30.6	1.79	35.2
	Southern region					
12	Egypt, Iraq	10	23.1	7.0	1.72	33.3
13	Ethiopia	23	25.2	14.4	1.71	34.0
LSD ($P<0.01$)		–	1.88	5.32	0.12	1.08

Table 2. Variance components (% phenotypic variance) due to regional effect, local effect and differences among landraces within localities

Character	Among regions (%)	Among localities within regions (%)	Within localities (%)	Total (%)
Heading time	42.0	5.9	52.1	100
Vernalization requirement	36.1	7.7	56.2	100
Photoperiodic response	23.9	13.7	62.4	100
Narrow-sense earliness	37.2	6.7	56.1	100

tively early heading, being earliest in the southern region. Two types of clinal patterns in geographical difference are clearly demonstrated in Fig. 2. In heading time and narrow-sense earliness, landraces were concentrated in the medium or late classes in the central region, while the frequency of late types decreased and early types, which were absent in the central region, appeared in the other regions, especially in the eastern (Nepal and Bhutan) and southern regions (Fig. 2A, D). With respect to the vernalization requirement and photoperiodic response, a whole range of varietal variation was covered by landraces from the central region (Fig. 2B, C). Relative to the relative frequency of sensitive and insensitive types in

Table 3. Mean and standard deviation of heading time and three heading traits for wheat landraces for each region

Region	Number of landraces	Heading time	Vernalization requirement (days)	Photoperiodic response	Narrow-sense earliness (days)
Central region	54	37.8±5.26	47.4±22.2	2.31±0.513	40.1±4.25
Eastern region	55	29.8±8.13	35.5±15.6	1.91±0.401	35.0±3.85
Western region	16	29.5±6.97	30.6±19.5	1.79±0.459	35.2±3.13
Southern region	33	24.6±5.29	12.1±16.5	1.71±0.267	33.8±3.03
Total	158	31.4±8.23	34.2±22.6	1.99±0.485	36.5±4.58
LSD ($P<0.01$)		1.95	5.54	0.13	1.12
Difference in variance		**	*	**	*

*, ** Significant at 5% and 1%, respectively

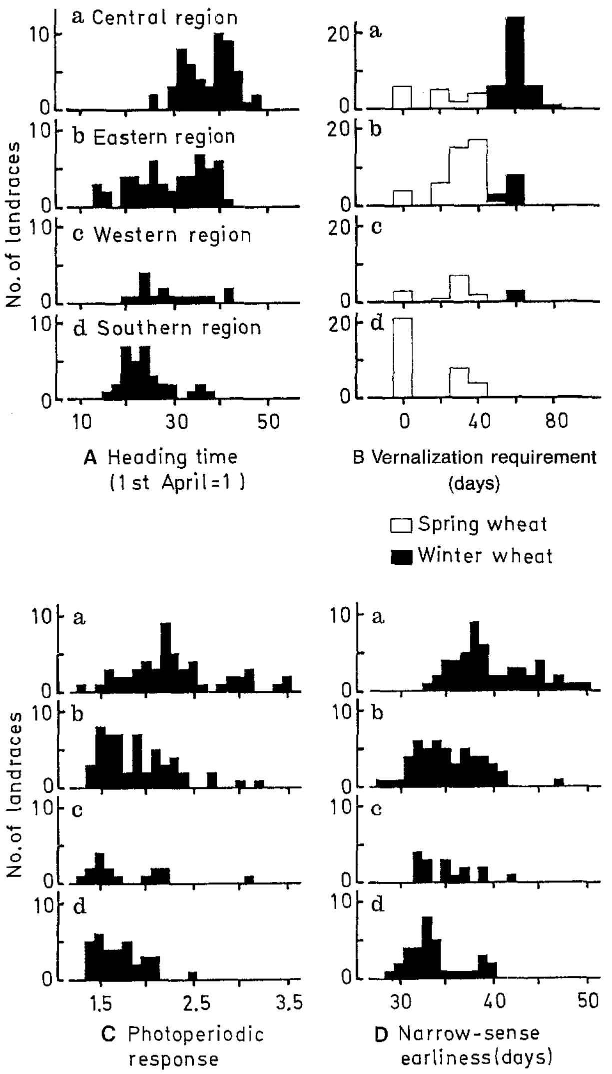

Fig. 2A–D. Frequency distribution of heading time and three heading traits for wheat landraces from each region

the relative frequency of sensitive and insensitive types in the central region, the ratio of these types changed in the other regions, resulting in a weaker response both to low temperature and to photoperiod (Table 3). Such a clinal pattern was clearly demonstrated in vernalization requirement. In the central region, the whole range of variation from 0 days to 80 days was covered and the frequency of winter wheat was 67%. It decreased to about 20% in the eastern and western regions, and to 0% in the southern region. Furthermore, the frequency of highly spring type wheat increased to 63% in the southern region.

Differences in variance among regions were examined by the *F*-test, which was used to compare the minimum and the maximum variances. As shown in Table 3, difference among regions proved to be statistically significant for all characters. In heading time, variance was largest in the eastern region and least in the central region. On

Table 4. Correlation coefficients between three heading traits and heading time in the field

No.	Locality	Vernalization requirement	Photoperiodic response	Narrow-sense earliness
	Central region			
1	Georgia (CIS)	−0.049	0.927**	0.522
2	Armenia (CIS)	0.234	0.502	0.371
3	Turkey (east)	0.742	0.880**	0.756*
4	Iran (north)	0.433	0.283	0.522
5	Iran (east)	0.159	0.513	0.758
6	Iran (south)	0.550	0.578	0.439
	Eastern region			
7	Afghanistan (north)	0.216	0.686**	0.830**
8	Afghanistan (south), Pakistan	0.631*	0.665**	0.632*
9	Nepal	0.195	0.832**	0.833**
10	Bhutan	−0.268	0.977**	0.873**
11	Western region	0.435	0.737**	0.734**
	Southern region			
12	Egypt, Iraq	0.503	0.180	0.620
13	Ethiopia	−0.177	0.850**	0.518*

*, ** Significant at 5% and 1%, respectively

the contrary, for the three heading traits, it was largest in the central region.

Differences among localities for each character were also statistically significant ($P<0.01$), as shown in Table 1. Though the number of landraces in each locality was relatively small, differences were clearly demonstrated even among neighboring localities. Landraces from the southern part of Iran exhibited smaller values in the three traits and thus were earlier in heading time than the one from the northern part of Iran. Similar differences were observed between the northern and the southern parts of Afghanistan (plus Pakistan in Table 1).

Correlation coefficients between heading time and its constituent traits were calculated for each locality and are summarized in Table 4. Correlations with vernalization requirement were not statistically significant in all localities with one exception, indicating that the vernalization requirement did not influence the control of heading time. Photoperiodic response and narrow-sense earliness showed a similar trend with their relationship to heading time, being different among regions or localities. In the central region, the correlation coefficient was statistically insignificant in most localities. Figure 3 shows the relative contributions of these two traits to heading time for landraces from the northern part of Iran expressed as a multiple product of standardized data of each landrace and standardized partial regression coefficient of each trait on heading time. As clearly shown in this figure, the factor(s) causing late heading was different among landraces, being photoperiodic response or/

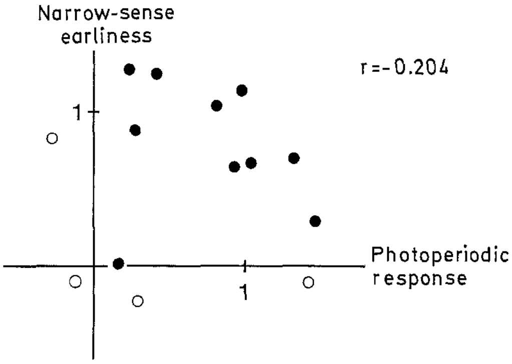

Fig. 3. Scatter diagram of landraces from the northern part of Iran for relative contribution of photoperiodic response and narrow-sense earliness to heading time. *Symbols* represent heading time of landraces (● late, ○ early). See text for calculation of relative contribution of each trait

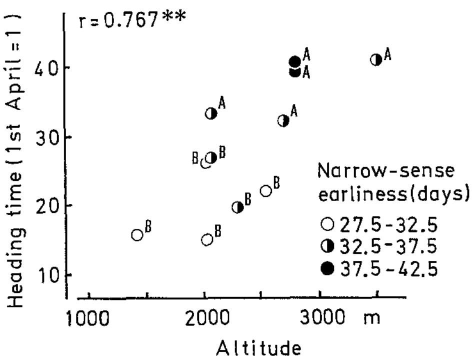

Fig. 4. Heading characters of Nepalese landraces collected at diverse altitudes. Photoperiodic response is represented by alphabetical characters: *A* more than 2.1, *B* less than 1.6. ** Significant at 1%

and narrow-sense earliness. On the other hand, the correlation coefficient was statistically significant in all localities in the eastern region ($P<0.01$). In Nepal, late-heading landraces exhibited large values both in photoperiodic response and in narrow-sense earliness, while early-heading ones exhibited small values in both traits (Fig. 4). This resulted in highly positive correlations between heading time and these two traits. A similarly close relationship was also observed in the western region and in Ethiopia (Table 4).

Discussion

The wheat landraces examined in the present study showed wide varietal variation in heading time (Fig. 2 A), and almost 50% of the variance was explained by differences in origin (Table 2). Since heading time is an adaptatively important character, the difference amongst localities can be regarded as the result of adaptation to different growing environments, as previously indicated by Murphy and Witcombe (1981). However, environmental factors limiting wheat adaptation must be different among localities, whether they be temperature, rainfall, photoperiod or others. This fact indicates that the adaptation strategy of a wheat landrace must be separately discussed for each factor or locality.

In the Near East, especially in the areas where annual rainfall is less than 500 mm, wheat cultivation is restricted to the period when sufficient water is available (Perrin de Brichambaut and Wallen 1963). In Iran and Afghanistan, for example, heading time and the beginning of dry season were both earlier in the southern part than in the respective northern part. Such a difference seems to be caused by selection to avoid the reduction of grain yield caused by a water deficit (Fischer and Maurer 1978; Worland et al. 1988). On the other hand, excessive rainfall is also disadvantageous for wheat adaptation. In Nepal, early-heading landraces seemed to have been selected for in order to avoid the damage of pre-harvest sprouting caused by the monsoonal rain in early summer. The existence of such a selection pressure was indicated by the fact that all of the Nepalese landraces were of a red kernel type (Kato, unpublished data), which is generally more resistant to pre-harvest sprouting than white kernel type.

In the areas where sufficient water is available, the adaptability of wheat is affected by temperature. A close negative correlation was observed between heading time and average daily temperature in May ($r=-0.879$, $P<0.01$) (Fig. 5). It is therefore quite clear that in wheat landraces early heading has been selected for as an adaptation to comparatively warm areas. Such a selection avoids the sterility caused by extreme high (Saini and Aspinall 1982) or low temperatures (Marcellos and Single 1984; Qian et al. 1986), and the reduction in kernel weight under high temperature conditions (Sofield et al. 1977). A small deviation from the relationship is observed in the western region (Fig. 5), indicating that heading can occur under relatively low temperatures as compared with the other localities. According to Kramer (1980), such differences may also be explained by adaptation to hot and dry summers, because it permits early growth to ensure completion of the life cycle before summer.

Using the local means shown in Table 1, correlation coefficients were calculated between heading time and its constituent traits. These were all positive and statistically significant ($P<0.01$, data was not shown). However, of the three traits, the vernalization requirement does not influence the control of heading time of fall-sown wheat, as stated by Worland et al. (1988) and Kato and Yamashita (1991) and also shown in Table 4. Thus it appears that photoperiodic response and narrow-sense earliness become so small as to hasten heading time and that

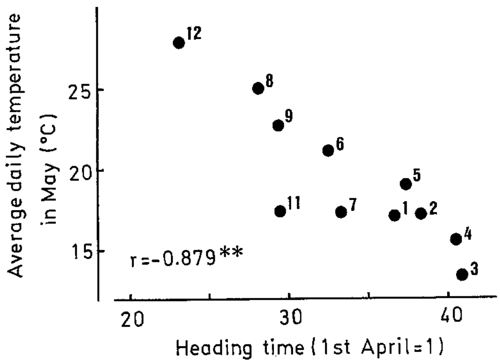

Fig. 5. Relationship between heading time and average daily temperature in May in 11 localities. Numbers represent locality number shown in Table 1. Bhutan and Ethiopia were excluded because of a lack of climatic data and of a completely different growing environment, respectively. ** Significant at 1%

this is the adaptation strategy to water stress and/or high temperature in early summer. Correlation coefficients between vernalization requirement and monthly average temperature were statistically insignificant from December to March ($r=0.32 \sim r=-0.54$), while they were statistically significant in November and in April ($r=-0.61$ and $r=-0.63$, $P<0.05$). Since the average temperature in the latter 2 months could be regarded as an indicator of the duration of winter coldness, the vernalization requirement may influence adaptation to winter coldness.

In the northern part of Iran, which is a part of the central region of wheat evolution, the summer is rather cool and the beginning of the dry season comes later than in the other areas of the Near East. Late-heading varieties would thus be able to adapt to such a condition, and actually existed frequently (Fig. 3) because of their long vegetative growth that was favorable to obtaining a better yield. On the contrary, it seems difficult for early-heading varieties to adapt to long winters (Fig. 5), a situation which causes the small variation in heading time. The key factor causing late heading proved to be different among the different landraces (Fig. 3), and correlation coefficients between heading time and its constituent traits were all statistically insignificant (Table 4). This result clearly indicates that the simple adaptation strategy of retarding heading time was achieved by various combinations of the three traits. Wide variation in each trait itself made it possible to keep such a diversity. The same phenomenon was also observed in the other localities in the central region (Table 4).

There must be a large diversity in growing environments in Nepal, as landraces were collected from diverse areas whose altitudes ranged from 1420 m to 3500 m. Heading time was delayed with increase in altitude (Fig. 4), resulting in wide varietal variation. Heading time correlated closely with both photoperiodic response and narrow-sense earliness (Table 4), though the variation in each trait was not necessarily large. These results indicate that the adaptation strategy dominating in this locality is to control heading time by the exquisite combination of photoperiodic response and narrow-sense earliness. This strategy is suitable for creating a wide variation in heading time based on the constituent traits with less variation. The same strategy was also adopted in the other localities of the eastern and the western regions (Table 4).

As heading time has been subjected to strong natural and/or artificial selection, only adapted variants would be selected in each area. Accordingly, environmental heterogeneity within each region should be necessary to keep wide varietal variation, even in the Vavilovian center of diversity, as indicated by Murphy and Witcombe (1981). This seems to be the reason why varietal variation was smaller in the central region than in the eastern region (Fig. 2A and Table 3). On the contrary, this situation was not true for its constituent traits, and variation was largest in the central region (Table 3). As to photoperiodic response and narrow-sense earliness, such a wide variation seemed to be maintained in the late-heading landraces, where insensitivity to photoperiod was accompanied by a large narrow-sense earliness and vice-versa (Fig. 3). The late initiation of spike primordium in these landraces should be advantageous in the avoidence of cold injury. Therefore, under such circumstances, even landraces without a vernalization requirement seem to be able to adapt to winter coldness, which results in the preservation of a wide variation in vernalization requirement. From another point of view, a whole range of variation existed in the central region in photoperiodic response and vernalization requirement, but not in narrow-sense earliness (Fig. 2). Such a discrepancy might be explained by the difference in their genetic systems, which are major genic in the former two traits (Pugsley 1972; Keim et al. 1973) and polygenic in the latter (Kato et al. 1989). In landrace populations, a new variant genotype does not appear in a major genic trait until spontaneous mutation occurs, but in a polygenic trait a new variant genotype can easily appear by recombination of minor genes through intra-specific hybridization. This seems to be the reason why genotypes with small narrow-sense earliness, which are absent from the central region, existed in the other regions. We suggest therefore that wide genetic variation in heading characters can be captured by collecting landraces from the Vavilovian center of diversity and that environmental heterogeneity should also be taken into account.

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