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The Rate of Leaf Emergence and Its Heritability in Wheat*

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Abstract : Using two varieties of wheat with genetically differing leaf lengths, several parameters concerning leaf growth were examined under controlled environmental conditions. Heritabilities for the parameters of leaf growth were calculated based on measurements of F_2 generation of the hybrid between these two varieties. The rate of leaf emergence (i. e., the speed of leaf emergence per unit time or per unit length) was almost the same between the two parent varieties, although the average length of leaf and average number of days required for the emergence of one leaf were different due to the difference in leaf length. Heritabilities for the average length of leaf and for the days required for the emergence of one leaf were 77.7 and 85.2%, respectively. In F_2 generation, however, no correlation was detected between the two characteristics (r=0.152). The heritabilities for the speed of leaf emergence per unit time and unit length were 55.5 and 45.2%, respectively, suggesting that the leaf growth rate (speed of leaf growth per unit time and per unit length) can be changed by selection.
Key words : Heritability, Leaf emergence, Wheat.

コムギにおける葉展開速度とその遺伝力：菅　洋・高橋秀幸・武田和義**，(東北大学遺伝生態研究センター，**岡山大学資源生物科学研究所)

要　旨：葉長が遺伝的に異なるコムギ２品種を用いて，葉の生長に関するいくつかのパラメーターについて制御環境下において研究した．葉の生長についてのパラメーターの遺伝力を，それら２品種間の雑種第２代の測定値にもとづいて計算した．葉の展開速度すなわち，単位時間または単位葉長当たりの葉展開速度は両親品種で同じであったが，平均葉長と平均１葉展開必要日数は葉長の差に依存して両親品種で異なった．平均葉長と平均１葉展開必要日数の遺伝力はそれぞれ，77.7%と85.2%であった．雑種第２代においては，しかしながら，それらの２つの形質間には相関は認められなかった (r=0.152)．単位時間または単位葉長当たりの展開速度の遺伝力はそれぞれ，55.5%と45.2%であった．このことより，葉の展開速度（単位時間または単位葉長当たり）は，選抜によって可変な形質であると推定された．
キーワード：遺伝力，コムギ，葉展開速度．

Length, width and area of leaf, as well as shape contribute to high yield capacity in crop plants, of which genetic backgrounds have also been studied by several workers[4,6,9,11,15,16]. Little attention, however, has been paid to leaf growth rate. It is not known whether crop varieties differ in their speed of leaf growth, although the rate itself has been found to change greatly under different environmental conditions[2,3,8,14,18]. Usually, rice varieties grown in the north-eastern part of Japan head much earlier than those grown in south-western Japan. This has been explained to occur because the latter have a greater number of leaves[21]. In this case also, the rate of leaf emergence has been disregarded. Varieties having longer leaf blades, especially in monocotyledonous cereal crops, are often said to take longer for the emergene of leaves than the varieties that have much shorter leaf blades. However, it is not known whether this depends simply on the difference of the leaf length or if it involves the rate of leaf growth. Thus, information on genetic backgrounds of crop plants is hardly available.

Using two wheat varieties that evidently differ from one another in leaf length, therefore, we examined the genetic background of leaf growth rate.

Materials and Methods

Two wheat varieties, a Chinese cultivar, Hong Mang Mai (Kobo-mugi), regarded as drought tolerant[17], and a Japanese cultivar, Norin 63, were used. Hong Mang Mai, found in the Loess plateau of China has been used by farmers for deep-seeding because soil moisture content is extremely low in the district and because it is difficult to obtain good stands when seeds are sown shallowly. Hong Mang Mai has longer leaves compared to

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those of Norin 63, but both varieties have no requirement of low temperature for the formation of inflorescences. Seeds were soaked in water at room temperature for 24 h and planted with 5×5 cm spacing in plastic boxes (64.0×37.5×23.0 cm) filled with commercial soil, Kureha Engei Baido (Kureha Chemicals, Tokyo), containing 0.5g N, 1.5 g P and 0.5 g K per kg of soil. They were then grown in a growth cabinet (Koito KG type, Koito Kogyo, Tokyo) and subjected to a 24-h photoperiod at 25°C. The light source consisted of 22 80-W fluorescent lamps (Toshiba, Tokyo), 9 400-W extra high-pressure mercury lamps (metal-haloid, Yoko, Toshiba) and 12 200-W refractor lamps (Toshiba), providing about 232 $\mu mol\ m^{-2}\ s^{-1}$ (400−700 mm) at the top of the plastic box.

The number of days from sowing to flag-leaf emergene (appearance of whole leaf blade of the leaf) and the lengths of all leaves on the main stem were recorded. No plants produced tillers under the outlined experimental conditions. The average number of days required for emergence of one leaf was calculated by dividing the number of days until the emergence of the flag leaf by the number of leaves on the main stem. Several parameters indicating the rate of leaf emergence were calculated as follows. To obtain the length of leaf emergence per day, the average length of the leaf was divided by the average number of days required for the emergence of one leaf. The number of days required for 1 cm of leaf emergene was obtained by dividing the average number of days required for the emergence of one leaf by the average length of the leaf. Ten F_1 seeds were obtained by single crossing between Norin 63 and Hong Mang Mai. Norin 63, a maternal parent, was emasculated before fertilization by Hong Mang Mai. Heritability in a broad sense was calculated using the formula $(V_T - V_E)/V_T$, in which V_T and V_E indicate total variance of F_2 and environmental variance, respectively. Environmental variance was estimated using the average of variances of the two parental varieties and calculated according to the formula $(Vp_1 + Vp_2)/2$, in which Vp_1 and Vp_2 indicate variances of one parent (Norin 63) and the other parent (Hong Mang Mai), respectively. Twenty-nine plants of Norin 63, 27 plants of Hong Mang Mai and 246 F_2 plants were used for the experiment.

Results

1. Parameters of leaf emergence in parents

Several parameters for the rate of leaf emergence in the parent varieties are shown in Table 1. Mean leaf length of Hong Mang Mai was 4 cm longer than that of Norin 63. The number of days required for the emergence of one leaf was also greater by about 1 day in Hong Mang Mai than in Norin 63. Hong Mang Mai produced more leaves until emergence of the flag leaf than did Norin 63, although the rate of leaf emergence per day or the number of days required for 1 cm of leaf emergence was almost the same for both varieties. Thus, no difference was detected in the rate of (or speed of) leaf emergence between the two cultivars, Norin 63 and Hong Mang Mai.

2. Parameters of leaf emergence in F_2

The difference in the length of the first leaf between the two varieties and the feature of segregation in the F_2 generation are shown in Fig. 1. The difference in length of the first leaf between the two varieties was much greater

Table 1. Several parameters for leaf growth in two wheat varieties, Norin 63 and Hong Mang Mai.

Parameter	Norin 63 (n=29)	Hong Mang Mai (n=27)
Average length of leaves (cm) (A)	23.670±1.284	27.910±1.465*
Average number of days for the emergence of one leaf (day) (B)	5.840±0.156	6.930±0.391*
Average length of leaf emergence per day (cm) (C)	4.033±0.266	4.043±0.365
Average number of days required for 1 cm leaf emergence (day) (D)	0.249±0.017	0.249±0.023

Values are the mean±standard deviation.
* Significantly different from that of Norin 63 at 1% level.

than the value indicated in Table 1, because the difference has a tendency to decrease in leaves at higher node positions on the main stem. Patterns of segregation in the number of days required for the emergence of one leaf and in the length of leaves in the F_2 generation are shown in Figs. 2 and 3, respectively. Distribution of segregants in the F_2 generation showed a single-peak curve for both characteristics. Most F_2 segregants were within the total range of the two parent varieties, although small transgressive segregants appeared on both sides, transgressive towards longer and shorter sides as well as towards earlier and later sides.

Figures 4 and 5 show segregation patterns of two parameters that indicate the rate of leaf emergence. Again, these two parameters showed segregation patterns with single peak in the F_2 generation, but segregants of which leaves emerged more rapidly than those of parent varieties appeared. A relationship between the average length of one leaf and the average number of days required for the emergence of one leaf is illustrated in Fig. 6. The correlation coefficient of these two leaf characteristics was only 0.152, indicating virtually no correlation between those characteristics in F_2 populations. In other words, plants with longer leaves did not always manifest a delay in the emergence of leaves, and leaf emergence in plants with shorter leaves was not always faster. Heritabilities of the average length of leaf and of the average number of

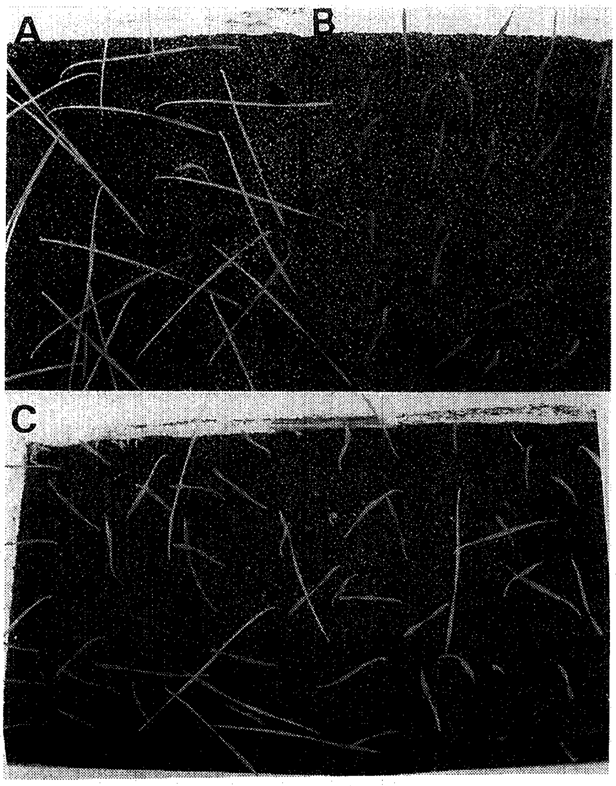

Fig. 1. Photographs showing the difference in the length of the first leaf between the two parent cultivars used (A ; Hong Mang Mai, B ; Norin 63) and the feature of segregation in the F_2 generation (C).

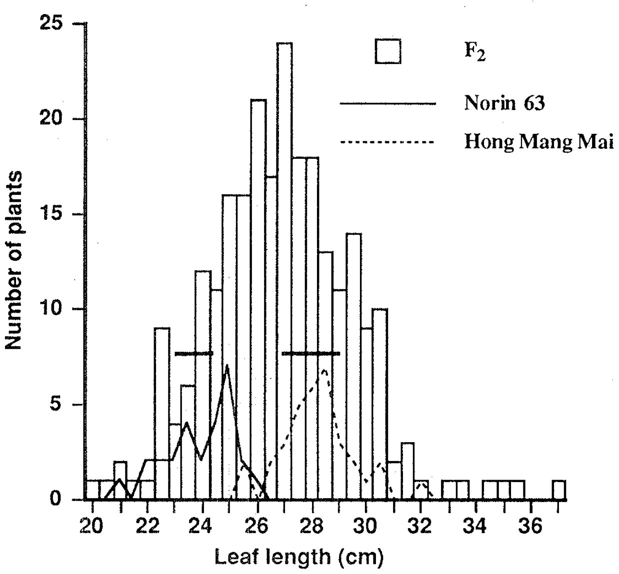

Fig. 2. Distribution of average length of leaf in F_2 segregants. Horizontal bars indicate 99% confidence intervals by *t*-test for two parent varieties.

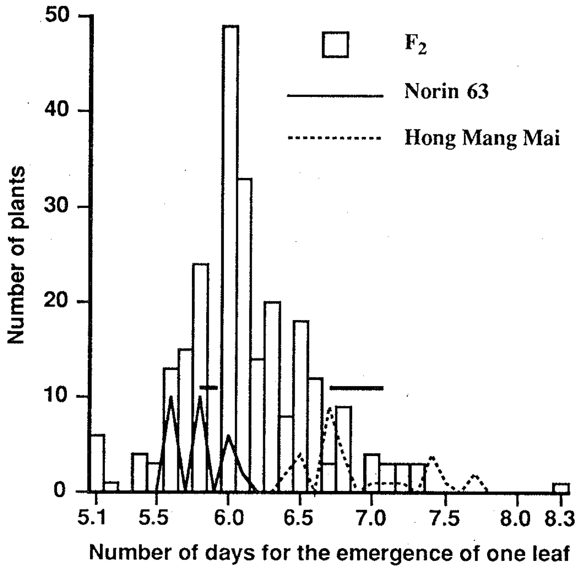

Fig. 3. Distribution of average number of days required for the emergence of one leaf in F_2 segregants. Horizontal bars indicate 99% confidence intervals by *t*-test for two parent varieties.

days required for the emergence of one leaf were 77.7% and 85.5%, respectively (Table 2). Heritabilities for the two parameters showing the rate of leaf emergence are also shown in Table 2. Two parameters of the rate of leaf emergence were calculated from different points of view: the length of the leaf that emerged per day and the time required for 1 cm of leaf emergence. Heritabilities for these two parameters were 55.5% and 45.2% for the former and the latter, respectively.

Discussion

As the characteristics of leaves greatly affect the production of dry matter through the capacity for light capture for photosynthesis, many workers have focused their attention on improvement of leaf characteristics. It is known that rice plants grown in the northern part of Japan require less time for heading than those grown in the southern part. This difference in heading time has been explained to occur mainly due to the difference in the final number of leaves on the main stem[21]. It is widely believed that no unequivocal difference in the rate (speed) of leaf emergence exists among rice varieties under the same growing conditions or in the same developmental stages, although leaf development itself is greatly influenced by environmental conditions such as temperature[10]. Under constant light and temperature conditions, Friend et al.[8] obtained a maximum rate of leaf primodium initiation and maximum rate of leaf emergence at 25°C when they tested the effects of temperatures in the range from 10 to 30°C in wheat. Our experiment was conducted at 25°C, presumably the optimum condition for leaf expansion of wheat plants. The temperature for obtaining maximum leaf width

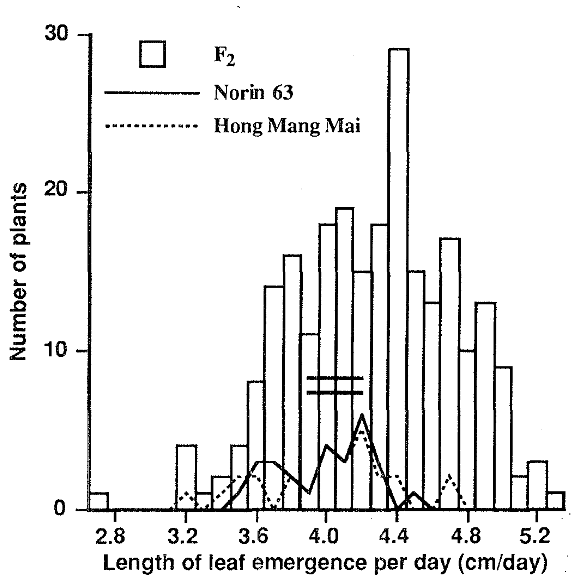

Fig. 4. Distribution of average length of leaf emergence per day in F_2 segregants. Horizontal bars indicate 99% confidence intervals by *t*-test for two parent varieties.

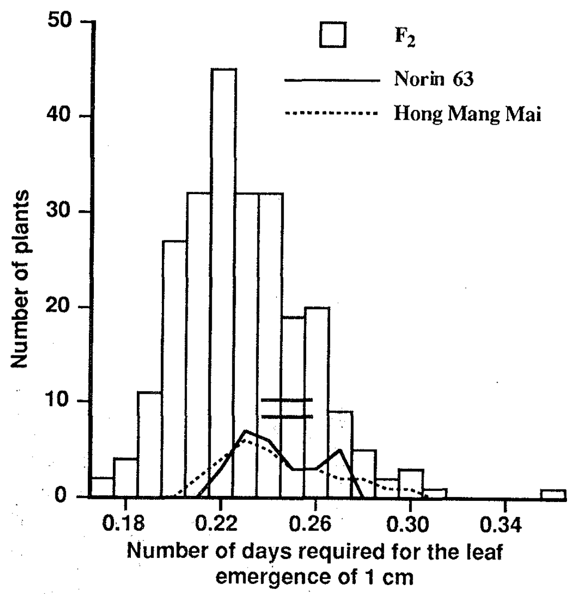

Fig. 5. Distribution of average of days required for the emergence of 1 cm leaf emergence in F_2 segregants. Horizontal bars indicate 99% confidence intervals by *t*-test for two parent varieties.

Table 2. Heritabilities for the parameters of leaf growth, estimated from parents and thier variance.

	(A)	(B)	(C)	(D)
Variance				
P_1 (Norin 63; n=29)	1.895	0.029	0.070	0.00027
P_2 (Hong Mang Mai; n=27)	2.939	0.020	0.133	0.00053
F_2 (Norin 63×Hong Mang Mai; n=246)	10.847	0.166	0.228	0.00073
Heritability (%)	77.7	85.2	55.5	45.2

Parameters indicated by the letters A, B, C and D are the same as those of Table 1.

was lower than for the maximum blade length[4]. The time interval between appearance of successive leaves on a culm was reportedly changed in wheat by low-temperature vernalization when the plant was grown under low temperature, although no change was found under conditions of high temperature[14].

Recent reports in the literature have described the phyllochron (simply defined as the time interval between appearance of successive leaves on a culm) concept to help elucidate development in grasses. In these reports, however, leaf length was not taken into consideration, and thus the speed of leaf emergence per unit leaf length was also neglected[7,12,20]. Varietal differences in the phyllochron interval were reported among different cultivars of wheat ; however, no information was contained in those studies as to whether the rate of leaf emergence per unit length of leaves was different among varieties[1].

The present results shown in Fig. 6 indicate that plants with longer leaves that grow faster and plants with shorter leaves that grow more slowly, existed within F_2 segregants of the cross Norin 63 × Hong Mang Mai, although the rate of leaf emergence was virtually the same as those of the parent varieties. As shown in Figs. 4 and 5, the patterns of distribution in the two parent varieties for those two parameters almost completely overlapped. In the F_2 population, many segregants showed an increased length of leaf emergence per day compared with those of the parent varieties (Fig. 4). This is also true, as shown in Fig. 5, when the parameter used is the number of days required for 1 cm of leaf emergence. The peak of F_2 segregants shifted toward a shorter time for the emergence of leaf in comparison

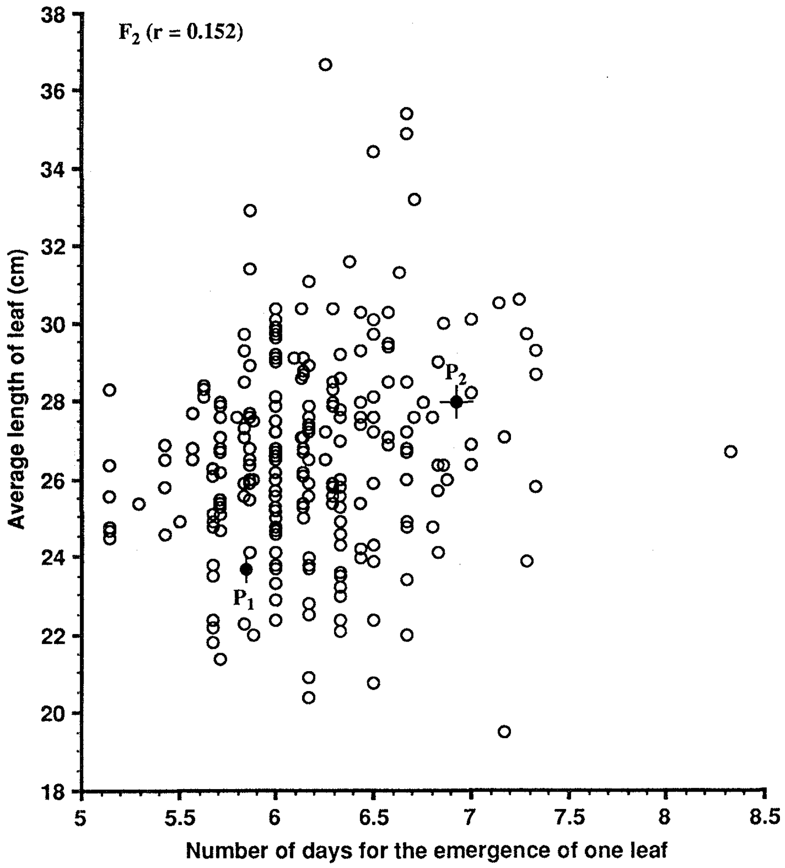

Fig. 6. Relationship between average number of days required for the emergence of one leaf and average length of one leaf in F_2 segregants. Closed circles with vertical and horizontal bars indicate average values of parent varieties. Bars indicate 95% confidence intervals. Horizontal bar for P_1 is smaller than the size of the symbol. Closed circles in the left (P_1) and in the right (P_2) indicate Norin 63 and Hong Mang Mai, respectively.

with that of parent varieties. The parameter indicated in Fig. 5 is the reciprocal of the parameter indicated in Fig. 4, and both of these parameters show the rate (speed) of leaf emergence. Heritabilities of these parameters are not extremely high, but may drop in the range of values useful for selection. The present results imply that breeding of wheat plants having different rates of leaf growth is possible.

The difference of leaf growth rate among different varieties may be attributed to the difference in the rate of cell division and cell elongation in leaf tissue[20,22]. The rates at which leaves form at the apical meristem, emerge and unfold, as well as the shape and size of the mature lamina, may change depending on the temperature, light intensity, daylength and nutritional status under which the plants are grown[2,3,6]. A recent study of sugar beet plants indicated that increased levels of transcripts for the small subunit of ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) and the cytosolic fructose-1,6-bisphosphatase caused accelerated leaf development[13]. Seneweera et al.[19] also found a relatively high correlation (r=0.65) between leaf blade elongation rate and sucrosephosphate synthase activity in rice. Thus, involvement of such enzyme activities in the growth rate of plant leaves will become a topic of future study. From the viewpoint of breeding, it should be clarified how the rate of leaf emergence results in an advantage to plants grown under stressful environmental conditions.

In rice plants, monomodal and transgressive segregations were reported in the F_2 generation of a hybrid between varieties with short broad leaves and long narrow ones for both length and width of leaves, indicating the existence of several polymeric genes for each of the characteristics[15]. Kikuchi et al.[11] also examined a hybrid between varieties with a broad and a narrow flag leaf. They showed that F_1 plants shifted towards the broad side from the mid-value and that F_2 segregants also shifted towards the broad side, resulting in more transgressive plants. These results indicate the partial dominance of the broad leaf and the existence of several polymeric genes. On the other hand, Murai et al.[16] stated that the narrow leaf was rather dominant in their diallel analysis using five varieties grown in Hokkaido, located in the northern part of Japan.

A high correlation (r=0.81−0.89) was found between the number of leaves and the duration of growth in rice plants[21]. Hosoi[10], using 44 rice cultivars from northern to southern Japan, examined the intervals of leaf emergence in days under controlled environmental conditions. The intervals required for the emergence of one leaf ranged from 6.3 to 8.5 days, but leaf length was not taken into consideration. Those studies, however, did not refer to the rate (speed) of leaf emergence. Thus, little information is available on the rate of leaf emergence although this factor may be important for evaluation of crop varieties as to the yield capacity and resistance to various environmental stresses. The present study, in that sense, may shed a new light on the role of leaf growth in evaluating varieties of crop plants.

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