

The Influence of Sowing Time on Dry Matter Partitioning in Spring Wheat*

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Received January 30, 1992

Abstract : To evaluate the response of sowing time on partitionings to leaf blade, ear and grain in spring wheat, the regression formulas for these partitionings against days after emergence and developmental index were calculated in four growth phases. Data was from a field experiment with three sowing times at two week intervals for three varieties.

In growth phase I, from emergence to double ridge stage, the partitioning to leaf blades, Y_l , was evaluated by the regression formulas, $Y_{l1} = b_1X + c_1$ against days after emergence (X) and $Y_{l1} = B_1X + C_1$ against developmental index (X). The coefficient b_1 was higher with later sowing time. Shortening of this phase duration with later sowing did not cause this increase of b_1 , because the coefficient B_1 was also higher with later sowing. In growth phase II, from double ridge stage to flag leaf emergence, the partitioning to leaf blades, Y_l , was evaluated by regression formulas, $Y_{l2} = -b_2X + c_2$ against days after emergence and $Y_{l2} = -B_2X + C_2$ against developmental index. The coefficient b_2 was lowest with early sowing for all varieties. Long duration of this phase with early sowing resulted low b_2 value, because the coefficient B_2 showed a different tendency with b_2 . In growth phase III, from flag leaf emergence to anthesis, the partitioning to ear, Y_e , was evaluated by regression formulas, $Y_e = -a_3(X - b_3)^2 + c_3$ against days after emergence and $Y_e = -A_3(X - B_3)^2 + C_3$ against developmental index. As sowing time was later, the shape of the regression curve was narrower and more acute because of secondary coefficient a_3 and higher constant c_3 . This difference in shape of the regression curve was not due to a difference in phase duration, because the coefficient A_3 and the constant C_3 were highest with late sowing, in contrast to a_3 and c_3 . In growth phase IV, from anthesis to milk ripe stage, the partitioning to grains, Y_g , was evaluated by a regression formula against days after emergence, $Y_g = b_4X - c_4$. However this regression did not fit this relation, because the correlation coefficients were low. The results indicated that grain has a fixed growth rate, while the increase rate of culm reserved material altered depending on the influence of radiation.

Key words : Developmental index, Dry matter partitioning, Growth phase, Regression formula, Sowing time, Spring wheat.

播種期の違いが春播コムギの乾物分配率に及ぼす影響 : 高橋 肇・中世古公男 (北海道大学農学部)

要 旨 : 春播コムギ 3 品種を 2 週間間隔で 3 回播種し、主要生育ステージを転換点とする 4 つの生育相について、播種期の違いによる葉身、穂および子実への乾物分配率の動向の変化を出芽後日数および発育指数に対する回帰式によって評価した。

生育相 I (出芽期～幼穂分化期) では、葉身への分配率 (Y_l) を出芽後日数 (X) に対する回帰式 $Y_{l1} = b_1X + c_1$ と発育指数 (X) に対する回帰式 $Y_{l1} = B_1X + C_1$ で示した。播種期の遅れにともない、係数 b_1 は増加し、係数 B_1 も同様に増加することから係数 b_1 の増加が生育相の期間の短縮に原因しないことが明らかとなった。生育相 II (幼穂分化期～止葉出葉期) では、葉身への分配率を出芽後日数に対する回帰式 $Y_{l2} = -b_2X + c_2$ と発育指数に対する回帰式 $Y_{l2} = -B_2X + C_2$ で示した。係数 b_2 は 3 品種とも早播区で最も低い値を示したが、係数 B_2 は播種期による変動の傾向が係数 b_2 と異なり、早播区で生育相の期間が長かったことに起因するものと考えられた。一方、生育相 III (止葉出葉期～開花期) では、穂への分配率 (Y_e) を出芽後日数に対する回帰式 $Y_e = -a_3(X - b_3)^2 + c_3$ と発育指数に対する回帰式 $Y_e = -A_3(X - B_3)^2 + C_3$ で示した。播種期の遅れにともない係数 a_3 と定数項 c_3 が増加し、回帰曲線が細く尖った形を示した。係数 A_3 と定数項 C_3 は晩播区で最も高く、形の変化が生育相の期間の差に起因しないことが明らかとなった。生育相 IV (開花期～乳熟期) では、子実への分配率 (Y_g) を出芽後日数に対する回帰式 $Y_g = b_4X - c_4$ で示したが、相関関係が低く、回帰式が適合しないことが明らかとなった。この原因として、子実が常時一定の生長を示すのに対し、稈の貯蔵養分は日射量の変化にともない増減することが明らかとなった。

キーワード : 回帰式, 乾物分配率, 生育相, 播種期, 発育指数, 春播コムギ。

We divided the growth of spring wheat into five main phases, based on the pattern of dry

matter partitioning. In growth phase I (emergence to flag leaf initiation), dry matter produced is main partitioned to the leaf blades; in growth phase II (initiation to emer-

* This work was presented at the 188th (October, 1989) meeting of the Crop Science Society of Japan.

gence of flag leaf), the partitioning to leaf blades decreases while that to culm increases. In growth phase III (flag leaf emergence to anthesis), dry matter is mainly partitioned to the ear; in growth phase IV (anthesis to milk-ripe stage), partitioning to grains increases; and in growth phase V (milk-ripe stage to maturity), all of the dry matter goes to grains¹². We also present a linear or a curvilinear regression against the days after emergence to the partitioning to one of the three plant organs in each growth phase. We evaluated the proportions of partitioning for three spring wheat varieties, which differ in phenological and morphological characters, using coefficients and constants of their regression formulas¹³.

Many researchers have studied the phenology of wheat and have attempted to predict the main growth stage^{3,6,17}. Shifting the growth stage changes the duration and regression formulas in these growth phases. Generally, developmental rate increases under high temperature and long daylength conditions. Porter et al.⁷ and Flood and Halloran² reported how these conditions affected duration of growth phase, while Baker et al.¹¹ and Wright and Hughes¹⁸ reported the effect on leaf appearance. There are few papers on quantitative growth, although Kirby⁵ reported the relation of thermal time to leaf, ear and

culm internode lengths. We have not previously known the relation between these environmental factors and dry matter partitioning.

In this experiment three spring wheat varieties were sown at two week intervals to provide a change of environmental conditions. Our objective was to investigate the influence of this environmental change on proportions of partitionings for these varieties.

Materials and Methods

Three spring wheat varieties, Haruyutaka and Selpek, were sown in 1988 on April 11th (early sowing), April 25th (middle sowing) and May 10th (late sowing) at the Experimental Farm of Hokkaido University. Early tall Haruhikari and early semi-dwarf Haruyutaka are raised in Hokkaido, and late tall Selpek is raised in Germany. Seeds were set up to seeder tapes (Nihon Plant Seeder) at 5 cm intervals. The seed tapes were planted 2 cm deep. Two tapes were set in each row and thinned to a single plant when two to three leaves expanded. The final density was an equi-distant square pattern with 400 plants m^{-2} . The plot size was 2 m by 9 m with 23 sampling areas (50 cm \times 50 cm). Sample locations were laid out with two replications. Fertilizer was applied just before sowing: N 90 kg hectare⁻¹, P₂O₅ 150 kg and K₂O₅ 75 kg. Fungicide and insecticide were applied a few times to prevent powdery mildew, rust, fly, army worm and plant louse. Haruhikari was prevented from lodging by supporting the plants with poles and strings after anthesis.

Fifty uniform plants were removed from each sampling area 23 times during the growing season. They were washed, root and tillers removed and separated into leaves, culms including leaf sheath, ears (chaff and rachis) and grains. The plant parts were dried for 48 hours at 80°C and weighed. The partitioning to each part was determined by dividing the weight increased of each part by that of the total above ground ($\Delta P \Delta W^{-1}$, %).

To evaluate the proportion, we used regression formulas against days after emergence (X) as follows (Fig. 1): in growth phase I and II, $Y_{\ell 1} = b_1 X + c_1$ and $Y_{\ell 2} = -b_2 X + c_2$ were used: Y_{ℓ} being the partitioning to leaf blade, b_1 and b_2 the increase and decrease rates of the partitioning. In growth phase III, $Y_e = -a_3(X - b_3)^2 + c_3$ was used: Y_e being

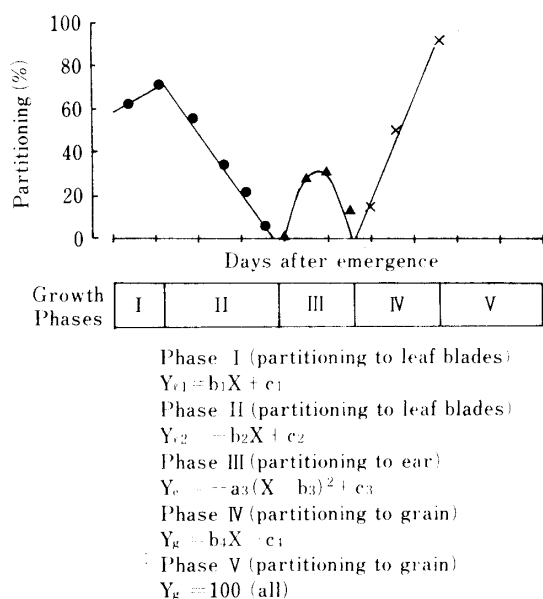


Fig. 1. Relationships between days after emergence (X) and dry matter partitioning to each organ (Y) (●: leaf blades, ▲: ear, grain, Takahashi et al. 1989.).

the partitioning to ear, a_3 and c_3 indicating the intensity of the partitioning. In growth phase IV, $Y_g = b_4 X - c_4$ was used, with b_4 meaning the increase rate of the partitioning. Regression formulas against the developmental index, DVI (X) reported by us previously¹⁵⁾, were also used to account for the influence of environmental change, excluding phenological effects. These formulas are shown in the same manner as those for days after emergence: in growth phase I and II, $Y_{t1} = B_1 X + C_1$ and $Y_{t2} = -B_2 X + C_2$, and in growth phase III, $Y_e = -A_3 (X - B_3)^2 + C_3$.

In growth phase IV, after anthesis, we found that the change in culm reserve materials closely reflected the change in culm dry weight¹⁴⁾. Therefore, to evaluate the partitioning to grain with the culm reserve materials, the culm was milled and cellular contents analyzed by near infrared reflectance spectroscopy (NIRS). NIRS data were measured using a Pacific Scientific Neotec Model 51A Scanning Reflectance Monochromator. For NIRS calibration, eighty-four subsamples were assayed by the neutral-detergent method¹⁰⁾.

In this experiment we defined growth phase I as that from emergence to double ridge stage, and growth phase II that from double ridge stage to flag leaf emergence. The double ridge stage is observed a few days after flag leaf initiation, and is generally and more usefully applied in determination of stage.

Results

1. Evaluation of the regression formula against days after emergence

Table 1 shows the regression formulas, their correlation coefficients and degree of freedom ($n-2$) for the three varieties and three sowing times in each of the four growth phases. In growth phase I, these regressions reflected the relation between the partitioning to leaf blades and days after emergence well, because the correlation coefficients were high at more than 0.9 for most varieties and sowing times, except middle sowing Haruhikari and early sowing Haruyutaka. The coefficient b_1 rose with later sowing time, more notably in Haruyutaka and Selpek. The constant c_1 was lower with later sowing, and increased the coefficient b_1 . In growth phase II, these regressions reflected the relationship well too, because correlation coefficients showed a level of significance above

0.1% for all varieties and sowing times. However, we were unable to recognize any distinct relationship between the coefficient or constant of regression and the difference in sowing times, although the coefficient b_2 was lowest at early sowing for all three varieties. In growth phase III, these regressions fitted well to the partitionings to ear against days after emergence, because the correlation coefficients showed more than 1% level of significance for most varieties and sowing times, but a 5% level of significance for most varieties and sowing times, but a 5% level of significance only for middle sown Selpek. Because the secondary coefficient a_3 was the highest and the duration of this phase was the shortest at late sowing for each variety, the shape of the regression curve was narrow and sharp. Further, the maximum value of the partitioning to ear was the highest at late sowing, because the constant c_3 was highest at late sowing for all three varieties. For these reasons, the partitioning to ear was intense within a short period at late sowing. The coefficient b_3 decreased with later sowing, thus the partitioning to ear was earlier. In growth phase IV, the correlation coefficients were not significant for two varieties and sowing times despite five or six degrees of freedom, were especially low in late sowing Haruhikari, $r=0.336$, and middle sowing Selpek, $r=0.245$. These regressions thus did not reflect the relations between the partitioning to grain and days after emergence, and the partitioning to grain did not increase linearly from anthesis until the milk ripe stage.

2. Evaluation of the regression formula against developmental index, DVI

Duration of each growth phase is determined by developmental rate, and the regression formula is influenced by this duration. Difference in sowing time induced a difference in the phenology and developmental rate. In order to exclude the influence of developmental rate from the regression formula and evaluate the difference of partitionings without this influence, partitionings to leaf blade or ear were evaluated by regression formulas against DVI in growth phases I, II and III for Haruyutaka and Selpek (Table 2). In these three phases, the regressions against the days after emergence were significant and well fitting. In growth phase I, the coefficient B_1 was the highest at late sowing; middle sowing was almost the same as early sowing in Haruyuta-

ka, and the coefficient b_1 of regression formula against days after emergence was also higher with later sowing time. These findings indicate that increase of the coefficient b_1 with later sowing was influenced not only by shortening of phase duration, but also by other factors. On the contrary, in growth phase II, the coefficient B_2 was lower with later sowing in Haruyutaka, but was almost the same in each of the three sowing times in Selpek. Because this tendency of the coefficient B_2 was different from the coefficient b_2 of the regression

against days after emergence, the lowest value of coefficient b_2 at early sowing was due to long duration of this phase. In growth phase III, the secondary coefficient A_3 was highest at late sowing in both varieties, and the constant C_3 was lowest at middle sowing in Haruyutaka and highest at late sowing in Selpek. Because this tendency of the coefficient A_3 and constant C_3 was similar to that of coefficient a_3 and constant c_3 , differences in sowing time on the latter factors were not due to development or duration of this phase. Contrary to this, the

Table 1. Formula and correlation coefficients of the regression of partitioning for days after emergence.

	Phase I (emergence to double ridge stage)				Phase II (double ridge stage to flag leaf emergence)					
	b_1	c_1	n-2	r	b_2	c_2	n-2	r		
Haruhikari										
Early	$Y=0.76X+60.2$		3	.998***	$Y=-2.31X+116$		8	.980***		
Middle	$Y=0.93X+62.7$		3	.616	$Y=-2.61X+115$		8	.987***		
Late	$Y=1.17X+60.6$		3	.934*	$Y=-2.34X+98$		8	.980***		
Haruyutaka										
Early	$Y=0.15X+67.0$		3	.461	$Y=-2.14X+110$		8	.976***		
Middle	$Y=0.43X+65.2$		3	.997***	$Y=-2.62X+114$		8	.974***		
Late	$Y=1.73X+56.4$		3	.927*	$Y=-2.46X+106$		8	.894***		
Selpek										
Early	$Y=0.35X+67.6$		3	.867	$Y=-1.52X+94$		8	.896***		
Middle	$Y=0.87X+63.3$		3	.973**	$Y=-2.00X+105$		8	.964***		
Late	$Y=1.75X+58.4$		3	.977**	$Y=-2.16X+102$		8	.978***		
	Phase III (flag leaf emergence to anthesis)					Phase IV (anthesis to milk ripe stage)				
	a_3	b_3	c_3	n-2	r	b_4	c_4	n-2	r	
Haruhikari										
Early	$Y=-0.17(X-53.6)^2+24.4$				8	.957***	$Y=3.25X-191$		6	.800*
Middle	$Y=-0.19(X-46.9)^2+24.5$				8	.899***	$Y=4.49X-245$		6	.785*
Late	$Y=-0.32(X-41.7)^2+29.1$				8	.844**	$Y=1.60X-50$		6	.336
Haruyutaka										
Early	$Y=-0.26(X-54.0)^2+43.2$				8	.797**	$Y=5.00X-303$		6	.863**
Middle	$Y=-0.20(X-44.9)^2+32.5$				8	.930***	$Y=3.41X-157$		6	.609
Late	$Y=-0.32(X-39.8)^2+37.4$				8	.809**	$Y=3.13X-129$		6	.806*
Selpek										
Early	$Y=-0.18(X-61.3)^2+24.0$				8	.780**	$Y=4.23X-280$		6	.977***
Middle	$Y=-0.16(X-55.7)^2+23.5$				8	.641*	$Y=1.59X-62$		5	.245
Late	$Y=-0.37(X-49.3)^2+36.2$				8	.814**	$Y=2.27X-114$		6	.683

*, **, ***: 5%, 1%, 0.1% level of significance.

decrease of the coefficient b_3 with later sowing was clearly due to shortening of phase duration, because coefficient B_3 was near 0.5 at all sowing times for both varieties.

3. The relation between the partitioning to grains and the reserve material of culm in growth phase IV

Since the partitioning to grains did not increase linearly from anthesis until milk ripe stage, we investigated this by the relationship between grain growth and amount reserved in culm. Figure 2 shows two relations, that between daily radiation and grain increase rate, and that between daily radiation and culm reserve material increase rate. There was a positive linear relation between the daily radiation and the increase rate of culm reserved material, while there was no significant relation between the daily relation and the grain growth rate. This result suggests that under a high radiation condition, such as a

clear day, the partitioning to culm increase, and under a low radiation condition, like a cloudy or rainy day, the partitioning to grain increase. This is assumed to be the cause for the partitioning to grain not increasing linearly.

Discussion

We found several relationships in this experiment among the coefficient and constant of regression formulas and difference of sowing times which are common to the three wheat varieties. In growth phase I, the coefficient b_1 increased with later sowing times. Similarly, the coefficient B_1 of regression against developmental index increased with later sowing time. This influence of the difference in sowing time on the partitioning was thus due to the change in phase duration. Contrary to this, in growth phase II, although the coefficient b_2 of regression of the partitioning to leaf

Table 2. Formula and correlation coefficients of the regression of partitioning for development index (DVI)

	Phase I (emergence to double ridge stage)				Phase II (double ridge stage to flag leaf emergence)			
	B_1	C_1	n-2	r	B_2	C_2	n-2	r
Haruyutaka								
Early	$Y = 5.73X + 66.1$	5	5	.814*	$Y = -48.6X + 69.3$	7	7	.978***
Middle	$Y = 4.10X + 66.7$	5	5	.856*	$Y = -53.3X + 69.6$	7	7	.982***
Late	$Y = 23.30X + 57.3$	5	5	.786*	$Y = -41.8X + 74.0$	8	8	.894***
Selpek								
Early	$Y = 2.57X + 69.8$	4	4	.383	$Y = -41.5X + 57.9$	5	5	.953***
Middle	$Y = 14.79X + 65.0$	4	4	.948**	$Y = -42.3X + 58.3$	6	6	.926***
Late	$Y = 39.23X + 57.5$	3	3	.988**	$Y = -43.5X + 61.1$	6	6	.961***
Phase III (flag leaf emergence to anthesis)								
	A_3	B_3	C_3	n-2	r			
Haruyutaka								
Early	$Y = -99(X - 0.452)^2 + 41.8$	8	8	8	.771**			
Middle	$Y = -71(X - 0.498)^2 + 31.3$	8	8	8	.914***			
Late	$Y = -108(X - 0.521)^2 + 39.4$	8	8	8	.848**			
Selpek								
Early	$Y = -70(X - 0.586)^2 + 25.2$	8	8	8	.830**			
Middle	$Y = -55(X - 0.602)^2 + 24.7$	8	8	8	.675*			
Late	$Y = -110(X - 0.536)^2 + 35.9$	8	8	8	.804**			

*, **, ***: 5%, 1%, 0.1% level of significance.

blades against days after emergence was lowest in early sowing for all three varieties, the coefficient B_2 of regression against developmental index show a different tendency from coefficient b_2 . The trend of coefficient b_2 with the difference of sowing time was therefore due to the change of this phase duration. We previously reported that the developmental rate of wheat changes with the influence of temperature and photoperiod¹⁵. Although we found that the difference in phase duration under this influence changes the inclination of regression, other factors also changed this inclination in growth phase I. It is assumed that the partitioning to leaf blades was increased with later sowing time due to these other factors rather than the shortening of phase duration, because at the cross point of regressions in growth phases I and II, the partitioning of leaf blades was higher as sowing time was later, except at late sowing in Haruhikari (Table 3). In growth phases I and II, the mean temperature and photoperiod increased with later sowing; thus we believe that this other factor is temperature or photoperiod. On the other hand, in growth phase III the secondary coefficient A_3 and the constant C_3 of regression against developmental index had a similar trend for difference of sowing time to secondary coefficient a_3 and constant c_3 of regression against days after

emergence. Other factors than developmental rate therefore influence the difference in the shape of the regression curve. In particular, in this phase, we assume that temperature influences coefficient a_3 and constant c_3 , because temperature increase as sowing time was later.

On the contrary, in growth phase IV, the correlation coefficient of regression was low, so that regression formulas obviously did not fit the relation between the partitioning to grains and days after emergence. When the growth rate of cellular contents changed with radiation compensating for grain growth, the growth rate of grain was not related to radiation. This is the reason for the lack of fit of the regression formula. Although it was reported that an extreme low intensity (17.5% of daylight) reduced dry weight accumulation in both the stem and ear¹⁶, Spiertz¹¹) provided evidence for a more positive effect on grain growth by an increase of light intensity under low intensity conditions (from 92 to 147 cal $\text{cm}^{-2} \text{day}^{-1}$) than by that under high intensity conditions (from 147 to 175 cal $\text{cm}^{-2} \text{day}^{-1}$). Jenner and Rathjen⁴) suggested that the magnitude of photosynthesis is adequate to maintain a maximum flow of sucrose into the grain, but this flow is limited by the capacity of the process transporting the sugar into the grain. Rawson and Evans⁸) suggested that mobilization increased when photosynthesis

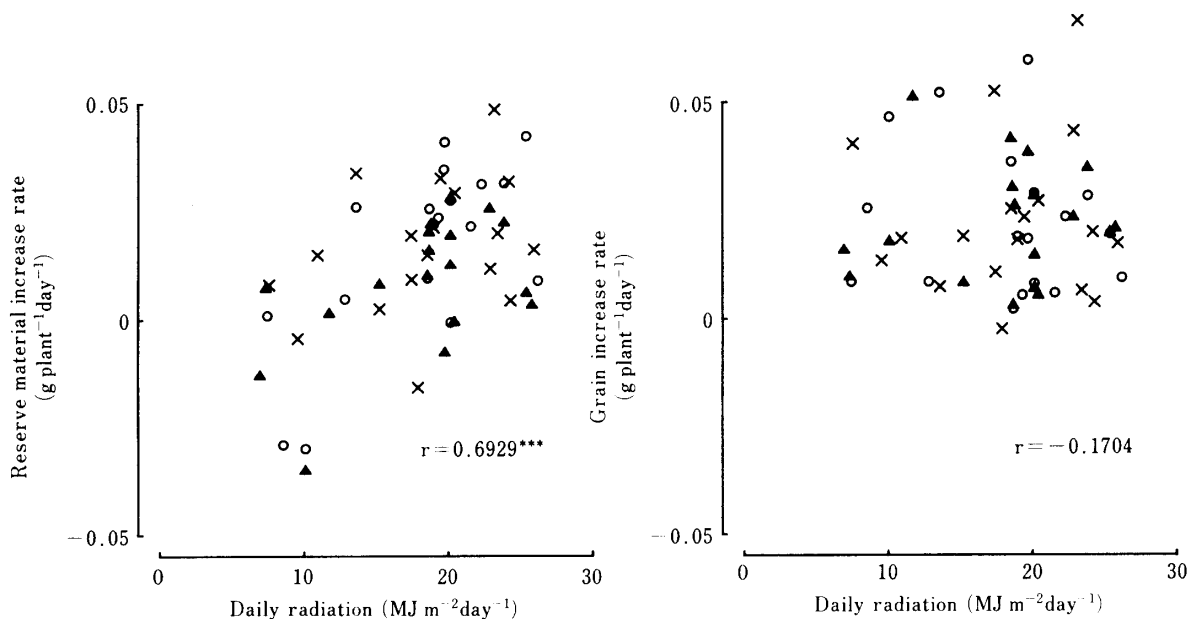


Fig. 2. Relationships between daily radiation and reserve material increase rate, and between daily radiation and grain increase rate during growth phase IV.

○ : Haruhikari, ▲ : Haruyutaka, × : Selpek.

*** : 0.1% level of significance.

Table 3. The values (partitioning to leaf blade) of cross points between regression lines of phase I and II.

	Haruhikari	Haruyutaka	Selpek
Early	73.9	69.8	72.5
Middle	76.4	72.0	75.8
Late	73.1	76.9	77.7

was reduced, which indicated that grain yields were not limited by lack of assimilate. Thus, we concluded that there is no systematic relationship between the partitioning rate to grain and the days after emergence in phase IV.

In future, a model of the response of partitioning depending on the environment will be needed, and we must elucidate the physiological mechanisms acting in the relation between grain growth and culm cellular contents as reserve material.

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