Effects of Ear Removal on Dry Matter Production and Its Partitioning in Wheat and Barley*

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Abstract : In order to clarify the response of crop to sink restriction, we examined the effect of ear removal on dry matter production, its partitioning into various organs and nonstructural carbohydrate content of the flag leaf during grain filling in wheat and barley with different inflorescences. In both crops, there was no significant difference in the total dry weights of the control and no-ear plants from ear removal treatment to the harvesting stage. The weights of leaf blade, leaf sheath, roots, stem and late tillers that developed after ear removal increased after ear removal. Although the weight of stem plus leaf sheath did not decrease until the maturation stage in the no-ear wheat, the weight in the no-ear barley decreased to the same extent as in the control plants. The increase in the late tillers in barley was larger than in wheat. The increase in weights of leaf blade and leaf sheath was larger at the upper leaf position in wheat, but was the same among the leaves at different positions in barley. The increase in the weight of the flag leaf after ear removal was mainly due to the increase in sucrose in both crops. The increase in sucrose was larger in wheat than in barley, while the increase in glucose and fructose began earlier and was larger in barley than in wheat.

Key words : Barley, Carbohydrate content, Dry matter partitioning, Dry matter production, Ear removal, Sink-source relationship, Wheat.

穂切除がコムギとオオムギの乾物の生産と分配に及ぼす影響 : 小出可能・石原 邦 (東京農工大学農学部)

要 旨 : シンクが制限された時に示す作物の反応を明かにするために、穂切除が登熟期間中の乾物生産と乾物分配、および止葉中の非構造性炭水化物含量の変化に及ぼす影響を花序が異なるコムギとオオムギについて調べた。穂切除処理後から収穫期まで、両作物とも対照区と穂切除区の間全乾物重に違いはなかった。しかし、乾物分配には大きな違いがあり、穂切除によって老化に伴う根重の減少が小さくなり、葉身、葉鞘、稈と遅発生分げつ重が増加した。穂切除区の稈+葉鞘重はコムギでは登熟後期まで減少しなかったのに対して、オオムギでは対照区と同様に減少した。遅発生分げつ重の増加はコムギに比べてオオムギの方が大きかった。葉身や葉鞘の乾物重の増加はコムギでは上位葉でより大きかったがオオムギではこうした葉位間差はなかった。穂切除による止葉の乾物重の増加は両種とも主としてシュクロース含量の増加によるもので、コムギの方がオオムギよりも大きかった。一方、グルコースやフルクトースの増加はオオムギの方がコムギよりも大きくその開始も早かった。

キーワード : オオムギ, 乾物生産, 乾物分配, コムギ, シンク-ソース, 炭水化物含量, 穂切除。

The idea of dividing a plant into two parts, where photosynthate are either stored or utilized in growth (i.e. 'sink') and where photosynthesis occurs (i.e. 'source') has prevailed for some time. Since the main sink is usually the harvestable portion in crop plants, high yielding varieties have been bred for an increase in the sink capacity. However, high yield has been accomplished by an increase not only in sink size but also in supply of photosynthetic products to the sink. Therefore, the sink capacity increased with increase in source

capacity as a result of much effort to improve crop yield. On the basis of the concept that sink capacity interrelates closely with source activity, there is an idea that the increase in source capacity has been accomplished by an increase in the sink capacity improved throughout breeding. However, the mechanism of how sink capacity directly affects the source activity has not been elucidated yet. To clarify the sink-source relationship, many investigators have studied the effects of the sink restriction on source activity^{7,11,13}). For example, King et al.¹¹) examined the ear removal effect on flag leaf photosynthesis in wheat which was cut back to leave only the intact main culm and two no-ear tillers. However, sink restriction affects not only leaf

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photosynthesis, but also partitioning of carbohydrate and nitrogen compounds as well as growth and development patterns. There have been few studies for clarifying the relationship between the various effects of the sink restriction on the processes of the plant.

Initially in a series of our studies on sink-source relationship using ear removal as the sink restriction, we examined the effects of ear removal on the dry matter production and its partitioning into various organs, including late tillers which developed after ear removal in wheat and barley with different inflorescences and discussed the difference in the effect of the ear removal between wheat and barley from a physiological and ecological point of view. In addition, the effects of ear removal on the nonstructural carbohydrate contents in flag leaf were examined.

Materials and Methods

1. Plant materials

This study was carried out in 1988 and 1989. Wheat (*Triticum aestivum* L., cv. Aoba) and barley (*Hordeum vulgare* L., cv. Sekitori-sai 1) were grown in 1/2000 a Wagner pots, which contained a mixture of paddy and upland soils (1 : 1). Three young seedlings per hill were planted in three hills per pot early in November. They were thinned to one plant per hill at the internode elongation stage. Compound fertilizer (14, 14, 14) and superphosphate were applied to soil mixture at 2.4 g and 5.7 g per pot, respectively. Three grams of the compound fertilizer per pot was supplied as topdressing. The plants were irrigated every five days to keep sufficient moisture in the soil after internode elongation stage. In 1988, the plants were grown outdoors and anthesis was observed early in May. In 1989, they were grown outdoors until the beginning of December and thereafter in the glasshouse. Anthesis was observed one month earlier owing to higher temperature during daytime than in 1988.

2. Treatment of ear removal

At the time of anthesis, the pots were divided into two plots with one plot kept as the control and the other subjected to the ear removal treatment. Ears of the main culm and tillers were cut at their basal node of the ear about one week after the anthesis of the main

culm, when the linear phase of grain growth began. The dates of the treatments were May 13 (wheat) and May 3 (barley) in 1988 and April 12 (wheat) and April 9 (barley) in 1989. The cut ends of culms were coated with lanolin to prevent evaporation. The removed ears were dried at 90°C for two days and preserved. Ears of 'the late tillers' which developed after ear removal were not removed.

3. Sampling procedure

Each six control plants and no-ear plants were sampled every eight days after ear removal treatment to the maturation stage of the main culm and tillers. The shoot was divided into the tillers, including the main culm, and the late tillers. The tillers were further divided into leaf blades, leaf sheaths, ears, stems, and senescent parts. The leaf blades and sheaths were classified according to their positions on the stem. Leaf blade area of the main culm and tillers were measured with an automatic area meter (Hayashi Denko, AAM-8). The late tillers were divided into leaf blades and sheaths plus stems. The mud was removed from combined root of three plants per pot. All plant parts were dried at 90°C for 2 days and weighed.

4. Carbohydrate analysis

Carbohydrate analysis was conducted with plant material in 1989. Several flag leaf blades on the main culm and tillers of the control and no-ear plants were sampled between 3p.m. and 5p.m. The area of these leaves were measured and they were dried at 90°C for two days, weighed and stored. The dried leaves were ground to pass through an 0.3 mm screen with mortar and pestle. Part of this sample (50 mg) was extracted twice with 8 ml of 80% ethanol at 80°C for 20 min. After each extraction the samples were centrifuged at 5000 g for 15 min. The supernatants were combined, dried and then redissolved to 10 ml distilled water. Aliquot of this extract was analyzed for soluble carbohydrates.

Glucose, fructose and sucrose were determined enzymatically using sequential measurement method with hexokinase/glucose-6-phosphate dehydrogenase, phosphoglucose-isomerase and β -fructosidase¹⁷⁾. Each sugar was determined spectrophotometrically at a wavelength of 340 nm as the rate of formation

of reduced form of nicotinamide adenine dinucleotide phosphate (NADPH). Total soluble carbohydrate was determined by an anthrone method²²⁾ using glucose as a standard. Other soluble carbohydrates were determined by subtracting sucrose and hexose from total soluble carbohydrate.

For starch analysis, the residue of ethanol extraction was suspended in 1 ml water, and boiled for 10 min, and then solubilized in 1 ml of 0.2 M KOH at 100°C for 30 min. They were neutralized to pH 4–5 with 1M citric acid and filled up to 20 ml with water. One-tenth ml of these samples were incubated with 3 units amyloglucosidase with 0.2 ml of 20 mM citric acid buffer (pH 4.6) for 15 to 60 min at 55 to 60°C. Glucose released from enzymatic starch hydrolysis was determined according to the method as described above. The rate of recovery was found to be greater than 80%, which was determined by using wheat starch (Wako) as the standard.

The enzymes used for this experiment were from Boehringer Mannheim. Carbohydrate concentrations were expressed on an area basis.

Results

The results in 1988 and 1989 were similar; we mainly discuss the latter results.

1. Effects of ear removal on dry matter production and its partitioning into shoots and roots

Fig. 1 shows the changes in the total dry weight, including roots, root weight, and the shoot-root ratio (S/R ratio). There was no significant difference in the total dry weight of the control and the no-ear plants though the total dry weight of the no-ear plants was slightly smaller than the control until the 24th day and 16th day after ear removal in wheat and barley, respectively.

On the other hand, the root weights of wheat and barley obviously differed between the control and no-ear plants. In wheat, the root weight of the control began to decrease gradually on the 8th day after ear removal, while the weight of the no-ear plants did not decrease during 32 days. As a result, the S/R ratio of the control plants increased earlier than the no-ear plants. At the last sampling

Fig. 1. Effects of ear removal on total dry weight, root weight and shoot-root ratio in wheat (left) and barley (right).

○—○: control plants, ●—●: no-ear plants. (These symbols are the similar for Fig. 2–5). Each point of total dry weight is the mean of six plants and vertical bars represent the range of standard error. Each point of root weight is the mean of two pots calculated per plant and vertical bars represent the range of two values.

(on the 48th day after ear removal), the S/R ratio of the no-ear plants was half as much as that of the control plants. In barley, the differences in the root weights and the S/R ratios between the control and no-ear plants were recognized late, as compared with the case of wheat.

2. Effects of ear removal on the partitioning of dry matter into various organs

Fig. 2 shows the changes in the dry weight of various organs. In wheat, the ear weight of the control increased until the 24th day after ear removal. The weight of stem plus leaf sheath in the control plants began to decrease on the 8th day, while the weight in the no-ear plants remained practically constant. The weight of the rest of the organs, i.e. the leaf

blades of the main culm and tillers, and the ears, stem plus leaf sheaths and the leaf blades of the late tillers were always greater in the no-ear plants than in the control from the 8th day after ear removal. The leaf area of the late tillers was small enough to ignore as compared with that of the main culm and tillers in two crops.

The results on the dry matter partition into various organs in barley were similar to those in wheat except for the following results. Firstly, the weight of the stem plus leaf sheath in no-ear barley began to decrease on the 24th day. Secondly, the ear weight of the late tillers in no-ear barley increased remarkably compared with the control, and the difference of the weight between the control and no-ear plants was much larger compared with wheat.

Fig. 2. Effects of ear removal on dry matter partitioning into various organs in wheat (left) and barley (right).

Ear weights in no-ear plants are values at the time of ear removal. Each point is the mean of six plants and vertical bars represent the range of standard error, which is similar for Fig. 3-4.

Fig. 3. Effects of ear removal on leaf blade weight on an area basis at the different leaf positions in wheat (left) and barley (right). Roman numerals indicate the leaf positions (e.g. I: the flag leaf), which is similar for Fig. 4.

Fig. 4. Effects of ear removal on leaf sheath weight per culm at the different leaf positions in wheat (left) and barley (right).

Fig. 5. Effects of ear removal on nonstructural carbohydrate content of flag leaf in wheat (left) and barley (right).

Each point is the mean of two plants and vertical bars represent the range of two values.

3. Increase in the weight of leaf blade and sheath by ear removal

Fig 3 and 4 show changes in the leaf blade weight on an area basis and in the leaf sheath weight per culm at different leaf positions, respectively. In the case of wheat, the weights of the leaf blade and sheath at every leaf position of the no-ear plants were greater than those of the control plants from the 16th day after ear removal up to maturation*. The difference in weights between the control and no-ear plants was the largest in the flag leaf.

Similar results were also obtained in barley.

* In 1988, the weight in the no-ear plants were greater significantly than those in the control plants from the 7th day and the 11th day after ear removal in wheat and barley, respectively (data not shown).

However, the degree of increase in their weight was not different among leaves on the different positions in barley.

4. Increase in the weight and carbohydrates content of flag leaf blade by ear removal

Fig. 5 shows the changes of the leaf blade weight and nonstructural carbohydrate contents after ear removal. In both crops, the leaf blade weight of the control plants was practically constant until the 20th day, while the weight of no-ear plants began to increase on the 6th day after ear removal. Then the weight of the control and the no-ear plants declined at the end of grain filling. The difference in leaf weight of control and no-ear plants was

due to increase in nonstructural carbohydrates, mainly sucrose by ear removal. In barley, an increase in these substances were smaller than that in wheat.

In wheat, the increase in glucose and fructose occurred on the 26th and 22nd day after ear removal, respectively. In barley, they increased on the 6th day after ear removal.

Starch was not detected in both crops by the method used here. Leaf powder was not stained with I_2/KI solution. When starch in the rice stem was analyzed as a check on our method, it was detected quantitatively and stained with I_2/KI solution.

Discussion

1. As evident from Fig. 1, there was no significant difference in the total dry weight of control and no-ear plants in both wheat and barley. This indicates that the dry matter production was not affected by the ear removal, though the ear of the photosynthetic organ^{2,12)} containing chlorophyll was removed. The leaf blade weight on an area basis at every leaf position was increased by the ear removal (Fig. 3). The increase of the weight in the flag leaf was mainly due to the accumulation of sucrose and other nonstructural carbohydrates, which should be translocated to the ear (Fig. 5). The effect of these carbohydrates on leaf photosynthesis may not be so much because the dry matter production was not affected by ear removal.

Removal of reproductive organs is well known to delay leaf senescence in wheat^{10,16)} and many plants^{14,20)}. If leaf photosynthesis in no-ear plants was maintained at a higher level due to the delay of senescence than in control plants, the dry weight in no-ear plants might have been larger than in control plants at the late maturation stage. However, significant differences between the control and no-ear plants of total dry weight could not be found, even at the harvesting stages (Fig. 1). It was reported that the decrease in total dry weight due to sink restriction was temporary and was not so large in wheat¹⁾, barley¹⁵⁾, and *Brassica campestris*⁵⁾, while sink restriction brought about the decrease in dry matter production in soybean³⁾, maize⁴⁾ and tomato¹⁹⁾. Thus the responses of dry matter production to sink restriction are different, depending on crops. Whether total dry matter production was

decreased by sink restriction or not might depend on the capacity of organ regeneration as an alternative sink after ear or fruit removal.

According to these facts the idea of source activity increasing due to increase in sink (panicle) size and/or activity could not be accepted.

2. The weight of the late tillers increased due to ear removal in wheat and barley (Fig. 2). The development and growth of the late tillers and the increase in the root weight (Fig. 1) was due to the changes in the translocation pattern of assimilation products from ear to the base of the stem. These changes in the translocation pattern were considered to be have been brought about by release from apical dominance due to the ear removal⁸⁾. However, considering that the weight of stem plus leaf sheath in the no-ear wheat remained practically constant and was larger than in the control (Fig. 2), assimilation products accumulated into these organs were not entirely consumed for the growth and development of the late tillers.

In no-ear barley, the weight of stem plus leaf sheath decreased to an almost similar extent as in control plants on the 32nd day after ear removal (Fig. 2). As a result, the increase in the weight of the late tillers by ear removal was considerably larger in barley than in wheat (Fig. 2). The reason why the weight of stem plus leaf sheath decreased more and the late tillers developed more vigorously in barley than in wheat is not known. One of the reasons may be related to different growth behavior based on the different inflorescence between barley and wheat. Barley has only one floret per spikelet and its ripening period is shorter in contrast to wheat, which has three-to-five florets per spikelet.

3. In both wheat and barley, the increase in weight of the flag leaf blade was mainly due to the increase in sucrose and other nonstructural carbohydrates. The content of glucose and fructose was low and increased at later grain filling stage. The increase in these substances in barley began earlier than in wheat (Fig. 5). The cause of the increase in these substances would be due to the hydrolysis of sucrose and fructans¹⁸⁾, decreasing remarkably at the late grain filling stage.

As mentioned above, the dry matter pro-

duction did not decreased due to ear removal (Fig. 1). It was assumed that leaf photosynthesis would not be affected by ear removal. However, the weight of the flag leaf increased most remarkably due to ear removal among all the leaves in wheat (Fig. 3 and 4). The increase in leaf blade weight was mainly due to the increase in sucrose (Fig. 5), which has been considered associated with feedback inhibition in photosynthetic activity^{6,9,21}). In the following studies, we will examine the effect of ear removal on photosynthesis of the flag leaf during grain filling in wheat.

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