春播コムギの登熟機構の解明(3)

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Grain Filling Mechanisms in Spring Wheat*

III. Effects of shadings on dry matter accumulation in grain and culm

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Abstract: To determine the effects of assimilate shortage to grain filling mechanisms in spring wheat canopy (cv. Haruyutaka), we examined the accumulation and translocation of dry matter in grain, along with water soluble sugar content (WSC) and structural material in culm under shading conditions during grain filling phases. Shading treatments were conducted using 95% shading cloth from −2 to 7 days after anthesis (DAA) (initial shading), 7 to 14 DAA (early shading) and 14 to 21 DAA (late shading). These shadings prevented the wheat canopy from producing any assimilate. However rates of increase in grain dry weights for all the shadings were 50-60% of the control (no shading), while the WSC in culm was used for the grain growth. During the initial grain filling phase, the WSC in culm for the initial shading decreased (−15 mg $pl^{-1}day^{-1}$), whereas that for the control increased (20 mg $pl^{-1}day^{-1}$). The grain dry weight showed a high rate of increase (11 mg $pl^{-1}day^{-1}$) for the initial shading, being about 50% of the control (19 mg $pl^{-1}day^{-1}$). During the early phase, the WSC in culm for the early shading decreased (−15 mg $pl^{-1}day^{-1}$), although that for the control increased (12 mg $pl^{-1}day^{-1}$). The rate of grain weight increase for the early shading (24 mg $pl^{-1}day^{-1}$). During the late phase, the WSC in culm for the late shading decreased (−33 mg $pl^{-1}day^{-1}$) five times as much as the control (−7 mg $pl^{-1}day^{-1}$). The rate of grain weight increase for the late shading (34 mg $pl^{-1}day^{-1}$) was 60% of that for the control (55 mg $pl^{-1}day^{-1}$). Although the culm lengths at harvest were no different between the initial shading and the control, the dry weight of culm structural material for the initial shading was lower than that for the control. The difference between the cases in which the partitioning rate to grain did or did not increase is discussed herein.
Key words: Dry matter accumulation rate, Dry matter partitioning, Grain filling phase, Regression analysis, Shading, Source activity, Spring wheat, Water soluble sugar content.

春播コムギの登熟機構の解明　第3報　遮光処理が子実および稈の乾物蓄積に及ぼす影響：高橋　肇・土橋直之・高久俊宏・中世古公男（北海道大学農学部）

要　旨：春播コムギ（品種ハルユタカ）の登熟機構に対する同化産物の不足の影響を解析することを目的として，コムギの登熟初期（開花2日前～開花7日後），登熟前期（開花7日後～14日後）および登熟後期（開花14日後～21日後）にそれぞれ95%遮光布による遮光処理を行い，子実および稈の可溶性糖分（WSC）と構造物質の乾物蓄積および転流の動向を調査した．95%遮光処理は，処理中の同化産物の生産をほぼ停止した．しかしながら，子実乾物重は処理中においても対照区の50～60%の高い増加速度を維持し，不足分の同化産物を稈のWSCの転流により補っていた．登熟初期では，WSCは対照区で増加したものの（20 mg pl^{-1}），初期処理区では減少し（−15 mg pl^{-1}），子実乾物重は対照区で19 mg pl^{-1}の増加速度を示したのに対して，初期遮光区では11 mg pl^{-1}とそのおよそ50%の増加速度を維持した．登熟前期でも，WSCは対照区で増加（12 mg pl^{-1}），前期遮光区で減少（−15 mg pl^{-1}）し，子実乾物重は対照区で38 mg pl^{-1}の増加速度を示したのに対して，前期遮光区で24 mg pl^{-1}とそのおよそ60%の増加速度を維持した．また，登熟後期では，WSCは対照区で−7 mg pl^{-1}の速度で減少し，後期遮光区ではその5倍の−33 mg pl^{-1}で減少した．このため子実乾物重は対照区で55 mg pl^{-1}の増加速度を示したのに対して後期遮光区では34 mg pl^{-1}とおよそ60%の増加速度を維持した．一方，登熟初期では，初期遮光区でも対照区と同様の稈長を示したが，稈の構造物質重は遮光区で増加しなかった．これらの生理的機構から遮光処理により子実への分配が高まる場合と高まらない場合との違いについて論議した．
キーワード：回帰分析，可溶性糖含有量，乾物増加速度，乾物分配率，遮光，ソース能力，登熟相，春播コムギ．

Shading decreases the amount of radiation incident on crop canopy, resulting in an artificial condition in which the source activity is inhibited and the assimilate is short. Many studies on shading treatment have been reported, but the shading time and duration differ

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from study to study. The effects of assimilate shortage on the grain growth are neither simple nor can they be understood systematically.

As a first step in studying the physiological and morphological mechanisms of grain filling in spring wheat, we divided the grain filling period into four phases as follows : (1) **Initial grain filling phase** from anthesis to cessation of culm elongation ; (2) **Early grain filling phase** from cessation of culm elongation to the milk ripe stage ; (3) **Late grain filling phase** from the milk ripe stage to cessation of photosynthesis ; and, (4) **Final grain filling phase** from cessation of photosynthesis to maturity[9]. In addition, we quantitatively assessed the growth of plant organs with regressions against DAA during these four phases[10]. Information of the artificial condition of assimilate shortage might enable a more detailed understanding of the grain filling mechanisms.

Our objective in this paper is to determine the effects of an assimilate shortage (source inhibition) on the grain filling mechanisms, and to assess the growth, accumulation and translocation of grain and culm characters under shading conditions during each grain filling phase.

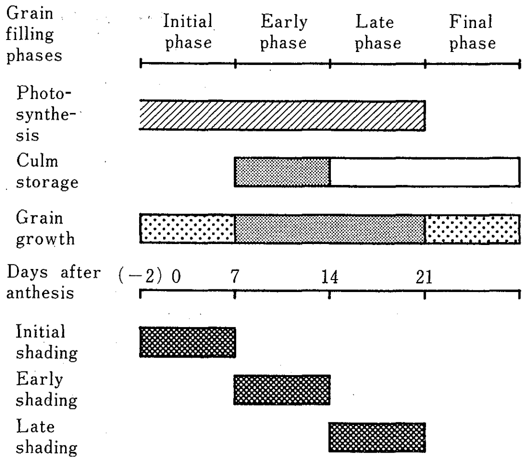

Fig. 1. Three periods of shading treatment in relation to four grain filling periods as defined by patterns in grain growth, culm storage and photosynthetic activities. ////: activity, ▒: increase, ░: slight increase, □ : decrease and ▓: shading period.

Materials and Methods

Crops

The spring wheat variety, Haruyutaka, was planted on 11 April 1992 at the Experimental Farm of Hokkaido University. Seeds were set on seeder tapes (Nihon Plant Seeder) every 5 cm and the tapes were planted 2 cm deep. Two tapes were placed in each row and thinned to a single plant after two or three leaves expanded. The final density was an equidistant square pattern with 400 plants m^{-2}. Fertilizer was applied prior to sowing : N, 90 kg $hectare^{-1}$; P_2O_5, 150 kg ; and K_20 75 kg. Fungicides and insecticides were applied a few times to control powdery mildew, rust, flies, army worms and aphids.

Shading treatment

Shading treatment was conducted using 95% shading cloth for each of the initial, early and late grain filling phases, as determined previously[9], to inhibit source activity and result in failure to assimilation (Figure 1). The initial grain filling phase is from anthesis until cessation of culm elongation ; the early phase is from cessation of culm elongation until milk ripe stage ; and the late phase is from milk ripe stage until cessation of photosynthesis. However, since it is practically impossible to determine the exact dates of these stages in a plant growing situation, we designated the shading period from two days before anthesis until seven after anthesis as the initial shading ; the one from seven days until 14 days after anthesis as the early shading ; and the one from 14 days until 21 days after anthesis as the late shading. The shading cloth was positioned 30 cm above the top of the canopy.

Samplings

Twenty standard plants were sampled from three replication plots of four shading treatments at 5 am and 6 am every day during treatment periods. For control (no shading), sampling periods were every day from −2 to 35 days after anthesis (DAA), from 25 June to 1 August. For the initial shading, they were from −2 to 8, 14, 15, 21, 22, 28 and 29 DAA ; for the early shading, they were from 7 to 15, 21, 22, 28 and 29 DAA ; and for the late shading, they were from 14 to 22, 28 and 29 DAA. Tillers and roots were discarded and the main stems were separated into ears, culms including the leaf sheath, and leaf blades. These plant parts were initially heated for 30 minutes at 105 °C, then dried for 48 hours at 70 °C and finally desiccated and weighed. All of the grains were removed from the ears with tweezers and weighed. The culms were milled and their water soluble sugar content (WSC) was determined using the anthrone method[13]. The structural material weight in culm was calculated by substracting WSC from culm dry weight.

Calculation of rate of dry weight increase

Linear regressions ($Y=aX+b$) of dry weights (Y) in total biomass, grain, WSC and structural material in culm were calculated against DAA (X) for the initial, early, late and final grain filling phases. We added 0.5 point to morning DAA data to express evening DAA data (e.g., 5 DAA + 0.5=5.5 DAA for evening data). The coefficients of these regressions were determined as the increasing rate. Least significant differences (LSD) among the shading treatments and those among the grain filling phases were calculated using the adjusted value of $(Y-b)/X$.

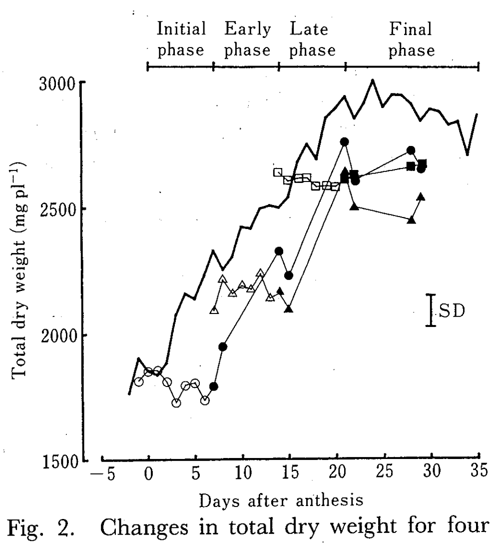

Fig. 2. Changes in total dry weight for four shading treatments in spring wheat canopy (cv. Haruyutaka).
——: control (no shading); ○—●: shading during initial grain filling phase;
△—▲: shading during early phase;
□—■: shading during late phase.
Open symbols indicate data during treatment and solid ones those after treatment.
Vertical bar: mean standard deviations (SD) at all measurement points.

Results

1. Changes in dry weights of total biomass, grain, WSC and structural material in culm

The dry weight in total biomass increased during initial, early and late grain filling phases, but not during each shading period (Figure 2). For the control, the total biomass weight increased linearly until 21 DAA, then slightly decreased. Thus, the final grain filling phase begins at 21 DAA. For the initial shading, the total biomass weight did not increase during the first week after anthesis (i.e., during the shading period), then increased until 21 DAA, during which time the rate of increase was similar to that for control. For the early shading, once again the total biomass weight did not increase from 7 to 14 DAA, but then increased until 21 DAA, as did the control. Likewise, for the late shading, the total biomass weight did not increase from 14 DAA, during the shading period. It is therefore clear that the wheat canopy ceased to photosynthesize, failing to produce any assimilate because of the severe shading used in this experiment. The total biomass weights for all three shadings did not increase from 21 DAA, during the final phase, as was also true for the control.

Figure 3 shows the changes in dry weight of grain. For the control, the grain weight slowly

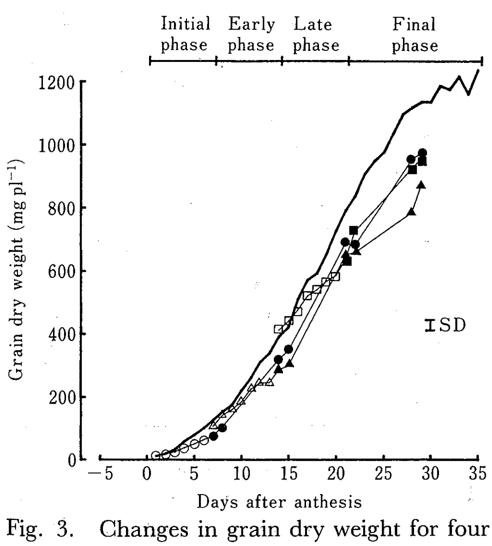

Fig. 3. Changes in grain dry weight for four shading treatments in spring wheat canopy (cv. Haruyutaka).
See Fig. 2 for symbols, etc.

increased during initial phase, then rapidly increased until 27 DAA. From 27 DAA to maturity its rate of increase slowed again. So this indicates that the rate of increase for the first week was different from that for the second week over the two weeks of the final grain filling phase. For the initial shading, the grain weight increased substantially during the first week after anthesis, in spite of shading period, although the rate of increase was lower than for the control. Then it increased rapidly until 28 DAA, similar to the control. For the early shading, the grain weight also increased from 7 to 14 DAA, irrespective of the shading period. Again, the rate of increase was lower than the control, then increased until 28 DAA, as did the control. Likewise, with the late shading, the grain weight substantially increased during the shading period.

WSC in culm is known to complement the grain growth as an assimilate buffer[9]. For the control, the WSC increased until two weeks after anthesis, then decreased until maturity with some fluctuation (Figure 4). For the initial shading, the WSC decreased until 7 DAA, during the shading period, in spite of the increase in grain weight. Then it increased until 14 DAA similar to the control. For the early shading, the WSC decreased from 7 to 14 DAA, in spite of the increase in grain weight.

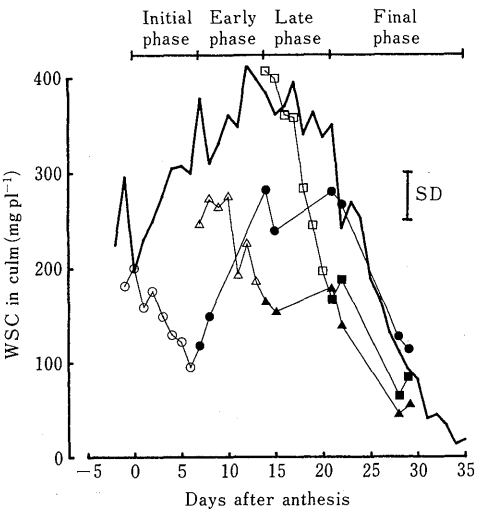

Fig. 4. Changes in water soluble sugar content (WSC) in culm for four shading treatments in spring wheat canopy (cv. Haruyutaka).
See Fig. 2 for symbols, etc.

These WSC at milk ripe stage were 60% of the control level for the initial shading and 50% of the control level for the early shading. With late shading, the WSC decreased more rapidly than the control after milk ripe stage.

The structural material weight in culm for the control increased linearly during the first week after anthesis, then decreased slightly (Figure 5). In the initial shading, it did not increase during the shading period and continued to be lower the control until maturity. Thus the shading also inhibited the increase in structural material weight of culm. However, the culm lengths at harvest were not significantly different between the control (93.1 cm) and the initial shading (93.8 cm). The culm for the initial shading elongated during the initial phase, in spite of the heavy shading.

2. Rates of dry weight increase determined by regressions

Table 1 shows the rates of dry weight increase for total biomass, grain, WSC and structural material in culm for the control, initial, early and late shadings during five grain filling phases. These rates were determined as coefficients of regressions of dry weights against days after anthesis. The final grain filling phase was divided into two phases in terms of the difference in grain growth rates (see Figure 3) ; the final phase (I) was regarded as the first week, and the final phase (II) as the second week during the two weeks of

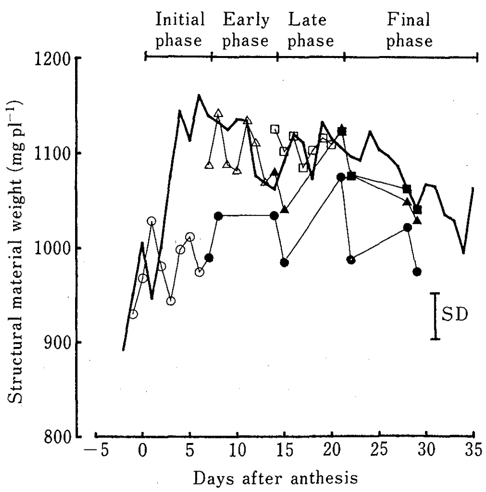

Fig. 5. Changes in structural material weight in culm for four shading treatments in spring wheat canopy (cv. Haruyutaka).
See Fig. 2 for symbols, etc.

Table 1. Dry matter accumulation rate (mg $pl^{-1}day^{-1}$) in total biomass, grain and water soluble suger (WSC) and structural material in culm for five grain filling phases.

	Intial phase	Early phase	Late phase	Final (I)	Final (II)	LSD# (0.01)
Control (no shading)						
Total biomass	54.6	45.1	52.7	8.2	− 7.7	40.1
Grain	19.1	38.4	54.5	48.2	18.2	1.5
WSC in culm	10.8	12.2	− 6.7	−30.5	−13.7	19.7
Struct. in culm	25.4	− 7.5	2.0	− 0.9	− 2.8	NS
Initial shading						
Total biomass	−14.2	55.0	54.3	4.5	—	
Grain	10.5	34.3	49.4	41.4	—	
WSC in culm	−15.3	17.3	1.5	−22.5	—	
Struct. in culm	2.8	− 0.8	1.7	− 3.2	—	
Early shading						
Total biomass	—	4.7	48.4	4.1	—	
Grain	—	23.9	48.2	32.9	—	
WSC in culm	—	−14.5	− 2.2	−14.7	—	
Struct. in culm	—	− 0.9	1.9	− 5.2	—	
Late shading						
Total biomass	—	—	2.2	13.4	—	
Grain	—	—	33.5	39.5	—	
WSC in culm	—	—	−33.1	−13.5	—	
Struct. in culm	—	—	1.9	− 5.3	—	
LSD (0.01) among shading treatments						
Total biomass	NS	5.6	4.3	3.5		
Grain	**	2.8	1.2	1.4		
WSC in culm	NS	2.9	2.0	0.9		
Struct. in culm	NS	3.2	NS	1.5		

Final phase is divided into two periods, final (I) and final (II), for grain growth rates.
LSD (0.01) among five grain filling phases for control.
** : 1% level of significance. NS : not significant.

the final phase. We did not measure dry weights in the final phase (II) for the initial, early and late shadings.

The rates in total biomass were high in the initial, early and late phases for the control (averaging 50 mg $pl^{-1}day^{-1}$), but much lower in the final phases. The rates in grain increased from the initial to late phase (19 to 55 mg $pl^{-1}day^{-1}$) for the control. The rate remained high in the final phase (I) (48 mg $pl^{-1}day^{-1}$) but declined to 18 mg $pl^{-1}day^{-1}$ in the final phase (II). The rates in the WSC were positive in the initial and early phases for the control and negative in the late and two final phases. The rates in the structural material were high only in the initial phase, corroborating our recent findings[10].

The shadings made the rates in total biomass zero or negative during the respective shading periods. In the initial phase, the rate in grain for the initial shading (11 mg $pl^{-1}day^{-1}$) was about 50% of the control (19 mg $pl^{-1}day^{-1}$), although that in total biomass for the initial shading was negative (−14 mg $pl^{-1}day^{-1}$). Thus, the rate in the WSC was negative (−15 mg $pl^{-1}day^{-1}$), while that in the structural material was lower (3 mg $pl^{-1}day^{-1}$) for the initial shading.

In the early phase, all of the rates for the initial shading were almost similar to the control. The rate in grain for the early shading (24 mg $pl^{-1}day^{-1}$) was 60% of the control (38 mg $pl^{-1}day^{-1}$), against 5 mg $pl^{-1}day^{-1}$ in total biomass. Thus, that in the WSC was negative (-15 mg $pl^{-1}day^{-1}$) for the early shading, but positive (12 mg $pl^{-1}day^{-1}$) for the control.

In the late shading, all of the rates for the initial and early shadings were similar to the control, although the rates in grain were slightly lower for both shadings. The rate in grain for the late shading (34 mg $pl^{-1}day^{-1}$) was 60% of the control (55 mg $pl^{-1}day^{-1}$), against 2 mg $pl^{-1}day^{-1}$ in total biomass for the late shading. The rate in the WSC for the late shading (-33 mg $pl^{-1}day^{-1}$) was negative and five times as high as the control (-7 mg $pl^{-1}day^{-1}$).

In the final phase (I), the rate in total biomass for the late shading was slightly higher than the others, and the rates in grain for the three shadings were slightly lower than the control.

Discussion

Shading reduced crop growth rate (CGR) in direct proportion to the radiation reduction[1,7,8,11]. Shading by 95% made the wheat canopy produce no assimilate (Figure 2). We previously concluded that WSC in culm is used for grain growth as an assimilate buffer[9]. In this experiment, we found that the shadings during the initial and early phases caused the translocation of culm WSC to grains, whereas WSC accumulated in culm with no shading. Moreover, shading during the late phase caused a five-fold increase in the reflux rate over the case with no shading (Table 1). In short, the grain growth rates were unexpectively high with shading. These results, therefore, suggest that if shading is too severe to allow production of any assimilate for canopy, grain growth slows, but not so much as to inhibit overall growth. Obviously, to encourage the grain growth was the WSC in the culm rather than photosynthesis under little irradiance like these shadings.

Fischer[1] suggested that culm WSC, a pool of assimilate, behaves as a low priority reserve, decreasing under shading presumably so as to buffer other sinks such as growing spikes against the reduced supply of assimilate. The results of the present experiment corroborated this theory. A number of reports indicated that partitioning rate to grain or spike with grains increased as crop growth was reduced by shading[1,5,11,12], whereas Stockman et al.[8] found no effect by shading. Further, Fischer and Stockman[2] and McMaster[6] et al. found that only the spike weight significantly decreased due to shading. As mentioned above, the WSC in culm or other vegetative organs is translocated to grain, so that partitioning rate to grain increases. The latter experiment, which reported the decrease in the spike weight only, shaded wheat plants prior to anthesis, and so the shading period was continuous and very prolonged. The WSC, therefore, might be extremely low, and perhaps could not play the role of an assimilate buffer during the grain filling period. In our experiment, WSC was continuously translocated to grain under the shading. Thus, the WSC in culm decreased from 200 mg pl^{-1} to 100 mg pl^{-1} for the initial shading (Figure 4). If the initial shading were prolonged two or three more weeks, the WSC might be nil, then grain growth might decrease extremely. So partitioning rate to grain might be low. McMaster et al.[6], on the other hand, showed that shaded plants were significantly taller. The culm lengths at harvest were no different between the control and the initial shading in our experiment, even though the dry weight in culm structural material for the initial shading was lower than for the control. Culm does not always elongate with the increase in dry weight. The shortage of assimilate for the initial shading caused the culm structural material to decrease in dry weight. This might also be the reason for the high partitioning rate to grain.

Therefore, shading increases partitioning rate to grain as long as it does not exhaust all of the WSC in vegetative organs. The decline in grain weight due to the initial shading is less than that induced by the early and late shading, because the initial shading affects the weight in culm structure as well. Grabau et al.[3] showed that mid-reproductive shading (14 to 19 DAA, 63%) reduced kernel growth rate more than did early-reproductive shading (1 to 6 DAA). In the present study, early shading caused a greater loss of grain weight than initial or late shading (Figure 3). Weather during the late phase was so overcast and rainy that the late shading might have affected the dry weight only slightly.

The rates of dry weight increase in plant organs were calculated from regressions against DAA, so that the effects of the shortage of radiation on grain filling mechanisms could be quantitatively evaluated for each grain filling phase. Since the variety, Haruyutaka, was also examined in previous studies[9,10], its developmental pattern was easy to estimate exactly. As a result the shadings could be conducted only during the initial, early and late phases. However, the timing and duration of these phases may differ among varieties. Jedel and Hunt[4], moreover, found a varietal difference in the effect of shading on dry matter production. Further studies must be conducted to determine differences in grain filling mechanisms among varieties and to elucidate these mechanisms.

References

1. Fischer, R.A. 1985. Number of kernels in wheat crops and the influence of solar radiation and temperature. J. Agric. Sci. Camb. 105 : 447—461.
2. ——— and Y.M. Stockman 1980. Kernel number per spike in wheat (*Triticum aestivum* L.) : Responses to pre-anthesis shading. Aust. J. Plant Physiol. 7 : 169—180.
3. Grabau, L.J., D.A. Van Sanford and Q.W. Meng 1990. Reproductive characteristics of winter wheat cultivars subjected to postanthesis shading. Crop Sci. 30 : 771—774.
4. Jedel, P.E. and L.A. Hunt 1990. Shading and thinning effects on multi —and standard— floret winter wheat. Crop Sci. 30 : 128—133.
5. Judel, G.K. and K. Mengel 1982. Effect of shading on nonstructural carbohydrates and their turnover in culms and leaves during the grain filling period of spring wheat. Crop Sci. 22 : 958—962.
6. McMaster, G.S., J.A. Morgan and W.O. Willis 1987. Effects of shading on winter wheat yield, spike characteristics, and carbohydrate allocation. Crop Sci. 27 : 967—973.
7. Puckridge, D.W. and D.A. Ratkowsky 1971. Photosynthesis of wheat field conditions IV. The influence of density and leaf area index on the response to radiation. Aust. J. Agric. Res. 22 : 11—20.
8. Stockman, Y.M., R.A. Fischer and E.G. Brittain 1983. Assimilate supply and floret development within the spike of wheat (*Triticum aestivum* L.). Aust. J. Plant Physiol. 10 : 585—594.
9. Takahashi, T, N. Tsuchihashi and K. Nakaseko 1993. Grain filling mechanisms in spring wheat. I. Grain filling phases according to the development of plant organs. Jpn. J. Crop Sci. 62 : 560—564.
10. ———, ——— and ——— 1994. Grain filling mechanisms in spring wheat. II. Growth, accumulation and translocatin in the daytime and at night during the four grain filling phases. Jpn. J. Crop Sci. 63 : 75—80.
11. Wang, P. and K. Nakaseko 1986. Effect of shading before and after heading time on growth and yield of spring wheat. Jpn. J. Crop Sci. 55 : 513—519*.
12. Willey, R.W. and R. Holliday 1971. Plant population, shading and thinning studies in wheat. J. Agric. Sci. Camb. 77 : 453—461.
13. Yemm, E.W. and A.J. Willis 1954. The estimation of carbohyrates in plant extracts by anthrone. Biochem. J. 57 : 508—514.

* In Japanese with English summary.