

Plant Production Science

ISSN: 1343-943X (Print) 1349-1008 (Online) Journal homepage: https://www.tandfonline.com/loi/tpps20

Grain Filling Mechanisms in Two Wheat Cultivars, Haruyutaka and Daichinominori, grown in Western Japan and in Hokkaido

Md. Alamgir Hossain, Tadashi Takahashi, Hironobu Jinno, Kazuma Senju, Yasuhiro Kawata, Li Zhan & Hideki Araki

To cite this article: Md. Alamgir Hossain, Tadashi Takahashi, Hironobu Jinno, Kazuma Senju, Yasuhiro Kawata, Li Zhan & Hideki Araki (2010) Grain Filling Mechanisms in Two Wheat Cultivars, Haruyutaka and Daichinominori, grown in Western Japan and in Hokkaido, Plant Production Science, 13:2, 156-163, DOI: 10.1626/pps.13.156

To link to this article: https://doi.org/10.1626/pps.13.156

© 2010 Crop Science Society of Japan

1	ſ	•	1	1
I				

Published online: 03 Dec 2015.

	_
r	
	074
~	_

Submit your article to this journal 🗹

Article views: 164



💽 View related articles 🗹

Citing articles: 1 View citing articles 🗹

Grain Filling Mechanisms in Two Wheat Cultivars, Haruyutaka and Daichinominori, grown in Western Japan and in Hokkaido

Md. Alamgir Hossain¹, Tadashi Takahashi², Hironobu Jinno³, Kazuma Senju², Yasuhiro Kawata², Li Zhang¹ and Hideki Araki²

> (¹The United Graduate School of Agricultural Sciences, Tottori University, Tottori 680-8553, Japan; ²Faculty of Agriculture, Yamaguchi University, Yamaguchi 753-8515, Japan; ³Hokkaido Central Agricultural Experiment Station, Naganuma 069-1395, Japan)

Abstract: Wheat cultivar Haruyutaka, bred in Hokkaido, as a cultivar with improved genetic traits for production in western Japan, had a lower grain yield when grown in Yamaguchi in western Japan than Daichinominori, native to Yamaguchi. We examined the yield and grain growth of these two cultivars in the two areas in 2005/2006, 2006/2007 and 2007/2008 to elucidate their grain filling mechanisms under the two environments. When grown in Yamaguchi, Haruyutaka had a lower grain yield due to smaller grains than Daichinominori and when grown in Hokkaido, Daichinominori had a lower grain yield due to smaller grains than Haruyutaka. The slower grain growth, especially, at the later period of grain filling was considered to be the major cause of smaller grain in both cultivars, but it was more pronounced in Haruyutaka grown in Yamaguchi. Haruyutaka and Daichinominori ceased total dry mass production earlier when grown in the nonnative area, Yamaguchi and Hokkaido, respectively, resulting in less supply of current assimilation products to grain growth. When grown in Yamaguchi, the amount of post-anthesis culm reserves, water soluble carbohydrate (WSC), was smaller in Haruyutaka than in Daichinominori, while they accumulated a similar amount of WSC in Hokkaido. The pattern of remobilization of WSC to grains was similar in both areas. However, the grain filling period was significantly shorter in the non-native area. These results suggested that in the non-native environment, the grain size is decreased due to slower grain growth, mainly due to less current assimilation, and shorter grain filling period.

Key words: Culm WSC, Current assimilation, Daichinominori, Grain filling mechanisms, Haruyutaka, Remobilization, Wheat.

Wheat cultivars grown in western Japan have been developed mostly from the crossings between cultivars in Kyushu, central and southwestern part of Honshu and Shikoku regions, under similar growing conditions; that is, much precipitation, with a humid and hot summer. In these regions, spring wheat is sown in fall due to mild coldness. Foreign cultivars have not been used for breeding because of susceptibility to Fusarium head blight or pre-harvest sprouting in these regions (Fujita and Ujihara, 1993). Daichinominori is a spring wheat cultivar bred in Kyushu from a cross between Kanto 85 (bred in central part of Honshu from a cross between Ushiokomugi (bred in Chugoku in Honshu) and Norin 11 (bred in Shikoku)) and Asakaze-komugi (bred in Kyushu from a cross between Hiyoku-komugi (bred in Kyushu) and Shirogane-komugi (bred in Kyushu)) (Ujihara et al., 1991). However, introduction of foreign genetic resources should be valuable for developing new cultivars with a higher yield and better quality of product.

Haruyutaka, a cultivar bred in Hokkaido which has less precipitation, and a dry and cool summer, produces high protein grains suitable for bread. It was developed from Siete Ceros and Tob 8156(R) bred in Mexico, Pal 1 bred in Colombia, and Haruhikari bred in Hokkaido from a cross between foreign cultivars (Ozeki et al., 1988). The excellent and distinct genetic background of Haruyutaka should be valuable for developing new cultivars for production in western Japan.

Haruyutaka had lower grain yield with smaller grains than Daichinominori under nine cultivation conditions in four growing seasons in Yamaguchi of western Japan (Takahashi et al., 2002b). It had a lower crop growth rate

Received 25 August 2009. Accepted 10 November 2009. Corresponding author: T. Takahashi (tadashit@yamaguchi-u.ac.jp, fax +81-83-933-5840).

(CGR) during grain filling period because of lower net assimilation rate (NAR) caused by lower photosynthetic rate of the leaf blades especially during the late grain filling period (Takahashi et al., 2002a). In Haruyutaka, photosynthate is highly competitive among grains and vegetative organs showing over-luxuriant growth since removal of lower leaves increased grain weight with increased NAR and CGR during grain filling period (Takahashi et al., 2004). In addition, reserve materials, water soluble carbohydrate (WSC), were not accumulated in the culm during the grain filling period to support grain growth (Takahashi et al., 2002b). However, the grain weight is not simply regulated by WSC. Increased WSC contents in culm induced by the treatment of Ethephon, a growth regulator restricting elongation of culms, had no effect on grain weight and yield in Haruyutaka (Takahashi, 2002).

The F_1 grains derived from the reciprocal crossings between the two cultivars have also been studied in Yamaguchi (Takahashi et al., 2006). Haruyutaka contains a dominant gene which controls the grain size in the F_1 generation. The gene in Haruyutaka restricts the grain growth in Yamaguchi. However, the same gene accelerates the grain growth of Haruyutaka grown in Hokkaido since the grains are usually much larger in Hokkaido. Therefore, the genotype controlling grain filling interacts with environmental factors.

The difference in grain filling of the two cultivars was examined only in the area native to Daichinominori. We, therefore, compared the two cultivars in both of their native areas, Yamaguchi in western Japan and Hokkaido to understand their original characters regulating the grain filling. The data on grain yield and its components, the changes in dry matter production and its partitioning, and WSC content of the culm during the grain filling period in the two regions were analyzed in this study.

Materials and Methods

1. Experimentation

The experiments were conducted at Experimental Farm, Faculty of Agriculture, Yamaguchi University, Yamaguchi (34°09.6'N, 131°27.2'E and 18m) and Hokkaido Central Agricultural Experiment Station, Hokkaido (43°03.5'N, 141°19.7'E and 8m) in Japan in three successive growing seasons 2005/2006, 2006/2007, and 2007/2008. The seeds of 2 wheat cultivars, Haruyutaka and Daichinominori, were sown on 25, 22, and 21 November in Yamaguchi and on April 18, 17, and 18 in Hokkaido in the season 2005/2006, 2006/2007 and 2007/2008, respectively. Spacing between the lines was 20cm, the seeding rate was 300 and 340 seeds m⁻² in Yamaguchi and Hokkaido, respectively. Fertilizer was applied as basal dressing at a rate of N:P₂O₅:K₂O=16:10:8 and 10:18:12 g m⁻² in Yamaguchi and Hokkaido,

respectively. The experiments were arranged in a randomized complete block design with 3 replicates.

2. Sampling and Data Collection

Thirty effective tillers were sampled twice a week during grain filling period for both cultivars grown in both locations in three growing seasons. The grain filling period was defined as the duration from anthesis to physiological maturity. The date of anthesis was the day when the anthers extruded in 50% of the spikes in the field and the date of physiological maturity was the day when the grain attained its maximum weight. The days to anthesis was calculated as the duration from sowing to anthesis. Out of 30 tillers sampled, 5 largest and 5 smallest tillers were discarded, to obtain 20 tillers for analysis. The tillers were separated into culm with sheaths, leaves, and spikes, then heated for 30 min at 110°C and dried for 48 hr at 70°C, and finally weighed. The grains were separated from the spikes with tweezers and weighed. The culm was milled for water soluble carbohydrate (WSC) by the anthrone method. The weight of structural materials in the culm was determined by subtracting WSC from the culm dry weight.

In addition, the plants in 1.0 m² (1.0 m×1.0 m) area were sampled at maturity for yield and yield components. The spikes were counted and all the plants were dried for 48 hr at 80°C and weighed to determine the biomass yield. All spikes were hand-threshed and weighed for grain yield. A thousand grains were counted and weighed for 1000-grain weight. The harvest index was calculated as the grain yield divided by total dry mass. The number of grains per spike was calculated as the grain yield divided by spike number and 1000-grain weight. The data on monthly total precipitation (mm) and monthly average air temperature (°C) of Yamaguchi and Sapporo (Hokkaido) during the growing period of wheat in 2005/2006, 2006/2007 and 2007/2008 were collected from the web page of Japan Meteorological Agency (http://www.data.jma.go.jp/obd/ stats/data/en/smp/index.html).

3. Estimation of WSC in culm

The milled culm was weighed and extracted once with 80% ethanol at 60°C for 15 min followed by two successive extractions with distilled water at 80°C for 30 min each. The extracts were combined and evaporated to dryness. The dried carbohydrates were resolved in 1 mL distilled water and centrifuged at 5,000 rpm for 5 min followed by the addition of charcoal to make clear solution. Twenty µL of the clear solution were added to 10 mL anthrone reagent (Yemm and Willis, 1954) and heated for 10 min in a boiling water bath and then cooled with ice water. The WSC of the reacted solution was measured using a spectrophotometer at 620 nm wave length.

Growing season	Location	Cultivar	Grain yield $(g m^{-2})$	Biomass yield (g m ⁻²)	Harvest index (%)	Spike m ⁻²	Grain spike ⁻¹	1000- grain weight (g)
2005/2006	Yamaguchi	Haruyutaka	363	1282	28.2	646	24.4	23.0
		Daichinominori	464	1136	40.6	519	27.0	32.8
	Hokkaido	Haruyutaka	413	1147	36.0	485	21.7	39.3
		Daichinominori	330	1030	32.0	438	21.7	35.4
2006/2007	Yamaguchi	Haruyutaka	348	1177	29.5	525	23.4	28.2
		Daichinominori	480	1257	38.3	542	23.8	37.5
	Hokkaido	Haruyutaka	477	1198	39.8	488	21.7	45.2
		Daichinominori	440	1062	41.4	475	21.9	42.5
2007/2008	Yamaguchi	Haruyutaka	357	1397	25.7	519	24.1	30.2
		Daichinominori	577	1490	39.0	500	33.2	34.7
	Hokkaido	Haruyutaka	485	1238	39.2	548	22.8	38.9
		Daichinominori	409	1077	38.0	492	24.3	34.3
	Significance							
	Culti	war (C)	NS	NS	***	NS	NS	*
	Location (L) Season (S)		NS	**	***	*	**	***
			NS	NS	**	NS	NS	***
	$C \times L$		***	NS	***	NS	NS	***
	L×S		NS	NS	***	NS	NS	**
	$\mathbf{C} \times \mathbf{S}$		NS	NS	NS	NS	NS	NS
	$C \times L$	L×S	NS	NS	*	NS	NS	NS

Table 1. Grain yield, biomass yield, harvest index and yield components in wheat cvs. Haruyutaka and Daichinominori grown in Yamaguchi and Hokkaido in growing seasons 2005/2006, 2006/2007, and 2007/2008.

*, ** and ***, significant at 5%, 1%, 0.1% level of significance, respectively. NS, non significant.

4. Statistical Analysis

All data on yield and yield components were subjected to three factor (cultivar, location, and season) analysis of variance in randomized completely block design (RCBD). Data on phenological characters were subjected to 2 factor (cultivar and location) analysis of variance considering 3 seasons as 3 replicates.

Results

1. Yield and its components

Table 1 shows the grain yield, biomass yield, harvest index and yield components of wheat cultivars Haruyutaka and Daichinominori grown in Yamaguchi and Hokkaido in the growing seasons 2005/2006, 2006/2007, and 2007/2008. There were no significant differences in grain yield between the cultivars, between the growing locations and also among the growing seasons. However, the interaction of cultivar and location was highly significant (P<0.001) which indicates that Daichinominori had a significantly higher yield than Haruyutaka in Yamaguchi while Haruyutaka had a higher yield than Daichinominori in Hokkaido. The biomass yield did not show significant difference between the cultivars, and also between the growing seasons. However, it showed significant (P<0.01) difference between the growing locations. It was significantly higher in Yamaguchi than in Hokkaido. None of the interactions were significant.

In the harvest index (HI), a significant difference (P<0.01) was observed between the cultivars, between the locations and also among the growing seasons. It also showed highly significant (P<0.001) interaction between cultivar and location which indicates significantly higher HI in Daichinominori than in Haruyutaka when grown in Yamaguchi. There was, however, no or little difference in HI between the cultivars when grown in Hokkaido. HI was significantly lower in the season 2005/2006 than in 2006/2007 and 2007/2008 in Hokkaido. However, there was no or little difference in HI among the seasons in Yamaguchi as the interaction between the location and season was highly significant.

The number of spikes per square meter and the number of grains per spike did not vary with the cultivars and also with the growing seasons. However, they significantly varied with the growing location; higher in Yamaguchi than in Hokkaido. These interactions were insignificant.

In the thousand grain weight a significant difference was observed between the cultivars, with the location and also with the season. It also showed highly significant interactions of cultivar and location, and also of location

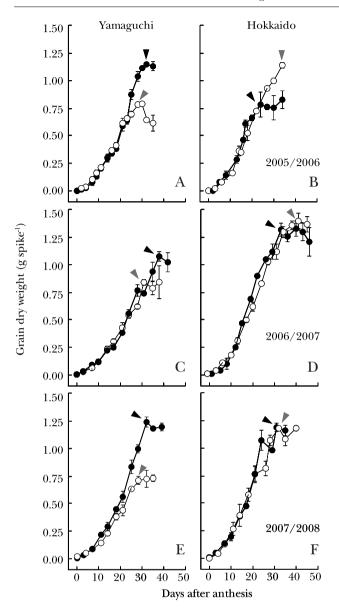


Fig. 1. Changes in grain dry weight during grain filling period in wheat cvs. Haruyutaka (open circles and standard lines) and Daichinominori (closed circles and bold lines) grown in Yamaguchi (A, C, E) and Hokkaido (B, D, F) in the growing seasons 2005/2006 (A, B), 2006/2007 (C, D) and 2007/2008 (E, F). Vertical bars indicate the standard errors of the means (n=3). Arrows show the physiological maturity.

and season. The grain was significantly heavier in Daichinominori than in Haruyutaka when grown in Yamaguchi while it was heavier in Haruyutaka than in Daichinominori when grown in Hokkaido. It was significantly heavier in Hokkaido than in Yamaguchi. It was heavier in 2006/2007 than in 2005/2006 and 2007/2008 in Hokkaido while it was heavier in 2006/2007 and 2007/2008 than in 2005/2006 in Yamaguchi.

2. Grain growth

Figure 1 shows the changes in grain dry weight during

Table 2. Phenological characters, days to anthesis (from sowing) and grain filling period in wheat cvs. Haruyutaka and Daichinominori grown in Yamaguchi and Hokkaido in 2005/2006, 2006/2007 and 2007/2008.

			Duration (days)	
Sseason	Location	Cultivar	Days to anthesis	Grain filling
2005/2006	Yamaguchi	Haruyutaka	171	28
		Daichinominori	157	32
	Hokkaido	Haruyutaka	73	34
		Daichinominori	71	24
2006/2007	Yamaguchi	Haruyutaka	166	31
		Daichinominori	152	38
	Hokkaido	Haruyutaka	67	41
		Daichinominori	65	33
2007/2008	Yamaguchi	Haruyutaka	169	28
		Daichinominori	155	32
	Hokkaido	Haruyutaka	69	32
		Daichinominori	66	31
	Significance	Cultivar (C)	**	NS
		Location (L)	***	NS
		C×L interaction	**	*

*, ** and ***, significant at 5%, 1%, 0.1% level of significance, respectively. NS, non significant.

the grain filling period. The grain dry weight increased very slowly during the initial days of grain filling followed by a rapid increase until physiological maturity (PM) in all cases. However, the increasing patterns varied with the cultivars in both locations especially at the later period of grain filling. The grain dry weight increased in a similar pattern from anthesis to around 25 d after anthesis (DAA) followed by a different pattern until PM in Haruyutaka and Daichinominori in Yamaguchi. The pattern was nearly consistent in every season studied. Haruyutaka showed slower grain growth with the cessation of growth earlier than Daichinominori leading to a lighter grain at maturity (around 0.75 g spike⁻¹). However, Daichinominori continued its sharp grain growth until PM leading to a heavier grain at maturity (around 1.2 g spike⁻¹) in Yamaguchi. By contrast, Haruyutaka in Hokkaido showed grain growth more or less similar to that in Daichinominori in Yamaguchi. However, Daichinominori ceased growth earlier leading to lighter grain at maturity compared to Haruyutaka in Hokkaido in all seasons except in 2007/2008 when showed similar pattern in grain growth until PM.

3. Phenological characters

Table 2 shows the phenological characters of Haruyutaka and Daichinominori grown in Yamaguchi and Hokkaido in 3 seasons. The days to anthesis significantly

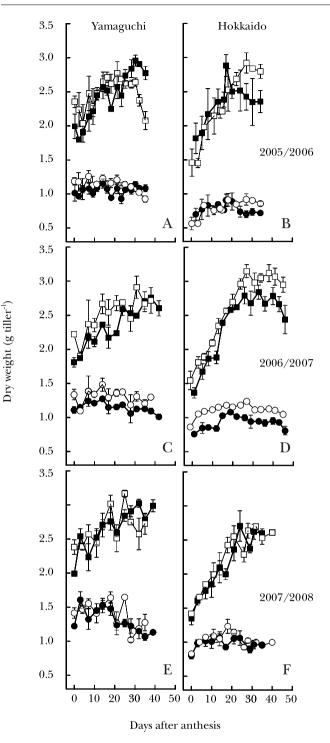


Fig. 2. Changes in total dry mass (rectangles) and culm structural materials (circles) in wheat cvs. Haruyutaka (open symbols with narrow lines) and Daichinominori (closed symbols with bold lines) grown in Yamaguchi (A, C, E) and Hokkaido (B, D, F) in the growing seasons 2005/2006 (A, B), 2006/2007 (C, D) and 2007/2008 (E, F). Vertical bars indicate the standard errors of the means (n=3).

varied with the cultivar and also with the location. It was much longer (about 2.5 times) in Yamaguchi than in Hokkaido because of different sowing times, and it was significantly longer (about 2 wk) in Haruyutaka than in

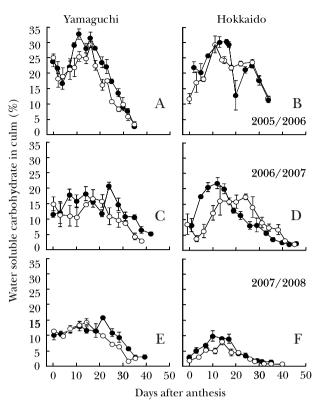


Fig. 3. Changes in water soluble carbohydrate (WSC) in culm during grain filling period in wheat cvs. Haruyutaka (open circles and normal lines) and Daichinominori (closed circles and bold lines) grown in Yamaguchi (A, C, E) and Hokkaido (B, D, F) in the growing seasons 2005/2006 (A, B), 2006/2007 (C, D) and 2007/2008 (E, F). Vertical bars indicate the standard errors of the means (n=3).

Daichinominori in Yamaguchi. However, there was no significant difference in days to anthesis between the two cultivars in Hokkaido resulting in a significant cultivar/location interaction. The grain filling period (GFP) did not vary with the cultivar or location. It showed a significant interaction between cultivar and location which indicates longer GFP in Daichinominori than in Haruyutaka in Yamaguchi and vice-versa in Hokkaido.

4. Changes in TDM and CSM

Figure 2 shows the changes in total dry mass (TDM) and dry weight of culm structural materials (CSM) during the grain filling period. TDM at anthesis was much heavier in both cultivars in Yamaguchi (about 2.0 g tiller⁻¹) than that in Hokkaido (about 1.5 g tiller⁻¹). However, it increased more sharply in Hokkaido while it increased less sharply in Yamaguchi. Haruyutaka showed a higher TDM production at anthesis than Daichinominori in Yamaguchi in all seasons studied. The TDM continued to increase until around 20 DAA and remained more or less unchanged towards maturity in Haruyutaka while it continued to increase until around 30 DAA in Daichinominori in Yamaguchi. In Hokkaido, they showed a similar pattern in

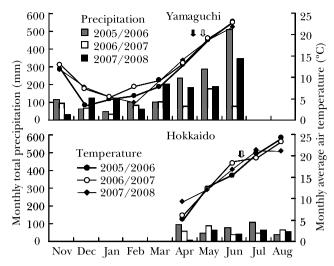


Fig. 4. Monthly total precipitation (bars) and monthly average air temperature (lines) in the study areas during the cropping seasons (sowing to harvest) in 2005/2006, 2006/2007, and 2007/2008. Arrows indicate the time of anthesis (open arrow for wheat cv. Haruyutaka and closed arrow for wheat cv. Daichinominori).

TDM production until 20 DAA followed by a continued sharp increase in Haruyutaka while almost ceased growth in Daichinominori in all seasons except in 2007/2008 when they showed almost similar patterns until around maturity.

CSM during grain filling hardly changed or decreased toward maturity in Yamaguchi. In Hokkaido, however, it increased markedly during the initial days of grain filling followed by an unchanged pattern towards maturity.

5. Changes in WSC in culm

Figure 3 shows the change in the water soluble carbohydrate (WSC) content of culm. The WSC in culm was similar in both cultivars at anthesis when grown in Yamaguchi in all seasons studied. However, Daichinominori showed a sharp increase in WSC from anthesis until around 15 DAA while Haruyutaka showed only a slight increase in WSC in all seasons except for 2007/2008 when they showed a similar patterns. Haruyutaka showed earlier remobilization of WSC to grains than Daichinominori under Yamaguchi environment in all seasons. However, the same amount of WSC remained in culm at maturity in both cultivars. In Hokkaido, the patterns of accumulation and remobilization of culm WSC were similar in both cultivars in all seasons except in 2006/2007 when Daichinominori showed earlier accumulation and remobilization than Haruyutaka.

6. Climatic patterns

Figure 4 shows the monthly total precipitation (mm) and monthly average air temperature in all experiments. Total precipitation during the cropping season was about 4

times higher in Yamaguchi (1123 mm, three-year average) than that in Hokkaido (295 mm, three-year average). The total monthly precipitation was similar in all months during the cropping season in Hokkaido (60 mm) while it was much higher (230 mm) around the reproductive phase (April-June) than vegetative phase (87 mm, Nov-Mar) in Yamaguchi. However, there was much variation in monthly total precipitation in different growing seasons during the grain filling period in Yamaguchi.

The temperature continued to increase from sowing to harvest in Hokkaido while it continued to increase from about 3 mo after sowing toward harvest in Yamaguchi. Though the temperature during pre-anthesis period varied with the location there was very little difference, if any, in temperature during the post anthesis period.

In Yamaguchi, the precipitation during the post-anthesis period was less in 2006/2007 than in the other seasons. In Hokkaido, the temperature during the post-anthesis period was lower in 2006/2007 than in the other seasons.

Discussion

Wheat cultivar Haruyutaka, bred in Hokkaido, had lower grain yield in Yamaguchi while Daichinominori, bred in Kyushu, had lower grain yield in Hokkaido (Table 1). Grain yield in wheat is determined by 3 yield components; number of spikes per square meter, number of grains per spike and 1000-grain weight. The former two components in the two cultivars did not vary with the location (Table 1). However, the 1000-grain weight was the main factor contributor for the yield difference between the two cultivars in this study. The grain was lighter in Haruyutaka than in Daichinominori when grown in Yamaguchi and vice-versa in Hokkaido (Table 1). This result suggests that the grain filling mechanism is interfered by the environment of western Japan in wheat cultivar Haruyutaka bred in Hokkaido, and by the environment of Hokkaido in wheat cultivar Daichinominori bred in Kyushu.

The grain filling starts with the increase in the number of endosperm cells followed by the increase in cell volume through accumulation of photosynthate (Austin et al., 1980; Singh and Jenner, 1984; Schnyder, 1993). In this study, the grain filling patterns were similar in the two cultivars in both locations from anthesis until about 25 d after anthesis (DAA) followed by the variant patterns until maturity (Fig. 1). Haruyutaka showed much slower grain growth at the later period of grain filling than Daichinominori producing lighter grains at maturity in Yamaguchi in all seasons studied. On the contrary, Daichinominori showed slower grain growth at the later period of grain filling resulting in smaller grains at maturity in Hokkaido in at least two seasons, 2005/2006 and 2006/2007 (Fig. 1). The difference in grain filling between the cultivars could be accounted for by the

difference in post-anthesis carbon assimilation and culm reserves remobilized to grains (Takahashi et al., 1993; Hossain et al., 2009) and also by the difference in the duration of grain filling (Sharma, 1994).

In the cultivar Haruyutaka, TDM production was increased only slightly during the grain filling period with earlier cessation than in Daichinominori in Yamaguchi (Fig. 2). This result reveals the less contribution of current assimilation to grain growth in Haruyutaka in Yamaguchi. Moreover, Haruyutaka produced a relatively larger amount of TDM than Daichinominori at anthesis indicating overluxuriant growth in Yamaguchi as was reported by Takahashi et al. (2004). The lower NAR in the over-luxuriant Haruyutaka may not be able to meet the demand of grains for assimilates during grain filling. Daichinominori showed a similar trend in TDM production, but with early cessation compared to Haruyutaka in Hokkaido. It also indicates less contribution of current assimilates to grain growth in Daichinominori especially at the later grain filling period under a non-native environment.

The culm reserves play a vital role in buffering grain yield when canopy photosynthesis is restricted by senescence (Austine et al., 1980; Gaunt and Wright, 1992; Takahashi and Kanazawa, 1996; Tahir and Nakata, 2005; Ehdaie et al., 2006). The culm elongates and stores water soluble carbohydrate (WSC) mainly during initial and early period of grain filling (from anthesis to milk ripe, at around 15 DAA) and it is remobilized to grains during the late and final period (from milk ripe to maturity) (Takahashi et al., 1993). The increase in culm structural materials (CSM) indicates the elongation of culm for increasing the storage pool. The CSM in both cultivars hardly increased during the initial period of grain filling in Yamaguchi while it showed intensive growth in Hokkaido during the same period (Fig. 2). The WSC content of culm hardly increased during the initial period of grain filling in Haruyutaka grown in Yamaguchi at least in 2 seasons, 2005/2006 and 2006/2007 (Fig. 3). However, Daichinominori showed an increase in culm WSC under the same environment. On the contrary, both of the cultivars showed more or less similar pattern in the changes of WSC in the Hokkaido environment. These results suggest that Haruyutaka has a problem in accumulation of culm reserves during the initial period of grain filling only in Yamaguchi. The over-luxuriant canopy may interfere with post-anthesis culm reserves resulting in poor grain filling leading to smaller grain at maturity. However, the two cultivars showed similar trend in the remobilization of the culm reserves under both environments (Fig. 3).

Grain filling period (GFP) is a major factor in determining the grain size at maturity (Sharma, 1994). The shorter GFP in Haruyutaka compared with Daichinominori under Yamaguchi might also account for the lighter grain of the former (Table 2). On the contrary, the shorter GFP in Daichinominori might also account for lighter grains in Hokkaido. The shorter GFP was due to the early maturing tendency, which was possibly mediated by the early cessation of carbon assimilation in non-native area. Western Japan experiences a humid environment receiving much precipitation during the cropping season especially around the reproductive phase (Fig. 4) which may induce waterlogging stress and reduces the carbon assimilation due to reduced root activity (Drew, 1991). Haruyutaka is well adapted to a dry environment and may be susceptible to waterlogging around the reproductive phase. Daichinominori is well adapted to the humid environment of western Japan and may have tolerance to waterlogging. However, further studies are needed to evaluate their tolerance to waterlogging.

In Hokkaido, the temperature during the post-anthesis period was lower in 2006/2007 than in the other seasons (Fig. 4). The two cultivars showed heavier 1000-grain weight in 2006/2007 than in the other seasons (Table 1). Daichinominori showed earlier accumulation and remobilization of WSC in culm in 2006/2007 than in the other seasons while Haruyutaka especially showed longer GFP in 2006/2007 (Fig. 3, Table 2). Daichinominori might have been selected as an early maturing type, same as other cultivars bred in Kyushu, western Japan. Early maturing cultivars have been required to avoid rainy damage in western Japan (Taya, 1993). The early cessation of carbon assimilation and early maturity of Daichinominori in Hokkaido may be caused by the breeding policy in western Japan. However, further investigation in needed to elucidate the physiological mechanisms of the early maturing phenomena in both cultivars under the environment of a non-native area.

References

- Austine, R.B., Ford, M.A. and Blackwell, R.D. 1980. Contributions to grain yield from pre-anthesis assimilation in tall and dwarf barley phenotypes in two contrasting seasons. *Ann. Bot.* 45: 309-319.
- Drew, M.C. 1991. Oxygen deficiency in the root environment and plant mineral nutrition. *In* Jackson, M.B., Davies, D.D. and Lambers, H. eds., Plant life under oxygen deprivation. Academic Publishing, The Hague. 301-316.
- Ehdaie, B., Alloush, G.A., Madore, M.A. and Waines, J.G. 2006.Genotypic variation for stem reserves and mobilization in wheat:II. Postanthesis changes in internode water-soluble carbohydrates.*Crop Sci.* 46: 2093-2103.
- Fujita, M. and Ujihara, K. 1993. Some traits correlated with high yielding ability in south-western area of Japan. *Bull. Kyushu Natl. Agric. Exp. Stn.* 28: 29-43**.
- Gaunt, R.E. and Wright, A.C. 1992. Disease-yield relationship in barley. II. Contribution of stored stem reserves to grain to grain filling. *Plant Pathol.* 41: 688-701.
- Hossain, M.A., Takahashi, T., Zhang, L., Nakatsukasa, M., Kimura, K., Kurashige, H., Hirata, T. and Ariyoshi, M. 2009. Physiological mechanisms of poor grain growth in abnormally early ripening

wheat grown in west Japan. Plant Prod. Sci. 12: 278-284.

- Ozeki, S., Sasaki, H., Amano, Y., Tsuchiya, T., Maeno, S. and Ueno, K. 1988. A new wheat variety "Haruyutaka". *Bull. Hokkaido Prefect. Agric. Exp. Stn.* 58: 41-54**.
- Schnyder, H. 1993. The role of carbohydrate storage and redistribution in the source-sink relations of wheat and barley during grain filling-a review. *New Phytol.* 123: 233-245.
- Sharma, R.C. 1994. Early generation selection for grain-filling period in wheat. *Crop Sci.* 34: 945-948.
- Singh, B.K. and Jenner, C.F. 1984. Factors controlling endosperm cell number and grain dry weight in wheat: Effects of shading on intact plants and of variation in nutritional supply to detached, cultured ears. *Aust. J. Plant Physiol.* 11: 151-163.
- Tahir, I.S.A. and Nakata, N. 2005. Remobilization of nitrogen and carbohydrate from stems of bread wheat in response to heat stress during grain filling. *J. Agron. Crop Sci.* 191: 106-115.
- Takahashi, T. 2002. Effect of Ethephon on the harvest index and grain weight of Hokkaido-bred wheat cultivar "Haruyutaka" grown in a warm area of western Japan. *Jpn. J. Crop Sci.* 71: 488-492*.
- Takahashi, T., Shimauchi, K., Nakagawa, Y., Shibata, K. and Iiyama, T. 2002a. Relationship between dry matter production and canopy structure in wheat cultivar "Haruyutaka" bred in Hokkaido when grown in warm area of western Japan. *Jpn. J. Crop Sci.* 71: 481-487*.
- Takahashi, T., Shimauchi, K., Nomiyama, A., Nakagawa, Y. and Shibata, K. 2002b. Harvest index and grain weight decline when wheat cultivar "Haruyutaka" bred in Hokkaido grows in the warm areas of western Japan. *Jpn. J. Crop Sci.* 71: 475-480*.
- Takahashi, T. and Kanazawa, T. 1996. Grain filling mechanisms in

spring wheat. IV. Effects of shading on number and size of spikes, grains, endosperm cells and starch granules in wheat. *Jpn. J. Crop Sci.* 65: 277-281.

- Takahashi, T., Tsuchihashi, N. and Nakaseko, K. 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.
- Takahashi, T., Yamaguchi, S., Zhang, L., Fujimoto, K. and Iiyama, T. 2006. Analysis of factors that decrease kernel weight of Hokkaido wheat cultivar "Haruyutaka" grown in the warm area of western Japan based on the weight of F₁ kernel derived from reciprocal crossing with a Kyushu cultivar. *Ipn. J. Crop Sci.* 75: 68-72*.
- Takahashi, T., Shimauchi, K., Nakagawa, Y., Shibata, K., Iiyama, T., Fujimoto, K., Yamaguchi, S. and Zhang, L. 2004. Influence of removal of lower leaves and detaching of tillers on kernel weight of Hokkaido-bred wheat cultivar "Haruyutaka" grown in a warm area of western Japan. *Jpn. J. Crop Sci.* 73: 276-281*.
- Taya, S. 1993. Breeding of early maturing wheat varieties with higher grain yield in southwestern regions of Japan. Bull. Kyushu Natl. Agric. Expt. Stn. 27: 333-398**.
- Ujihara, K., Nonaka, S., Yoshikawa, R., Taya, S., Fujita, M., Araki, H., Yamaguchi, A. and Shinmoto, E. 1991. A new wheat cultivar "Daichinominori". *Bull. Kyushu Natl. Agric. Exp. Stn.* 27: 81-90**.
- Yemm, E.W. and Willis, A.J. 1954. The estimation of carbohydrates in plant extracts by anthrone. *Biochem. J.* 57: 508-514.

* In Japanese with English abstract.

** In Japanese with English summary.