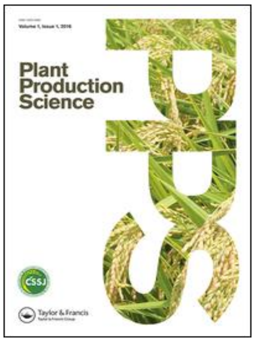

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Variation and Association of the Traits Related to Grain Filling in Several Extra-Heavy Panicle Type Rice under Different Environments

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Abstract: Raising the degree of grain filling is an important issue for the genetic improvement of extra-heavy panicle type rice which does not always realize the high yield potential due to low degree of grain filling. The objective of this study was to analyze the variation and association of the traits related to grain filling in four cultivars, three extra-heavy panicle types and one non-extra-heavy panicle type as a control, under seven environments. The results showed wide variation among cultivars and among growing environments in most of the traits examined. In addition, significant interactions between cultivar and environment were detected. From the analyses of joint regression and genetic and environmental correlations, an extra-heavy panicle type cultivar, Milyang 23, showed a higher degree of grain filling and higher rate of grain filling (grain weight/cumulative temperature), in response to several environments with a higher temperature and longer sunshine hours under which a large amount of photoassimilates would be available to grains. On the contrary, another extra-heavy panicle type cultivar, Akenohoshi, showed a lower rate of grain filling, even under the favorable environments mentioned above, resulting in a lower degree of grain filling. The difference in the rate of grain filling between Milyang 23 and Akenohoshi might be due to the difference in the growth of individual endosperm cells, not in the number of cells, because these two cultivars had similar grain sizes. This study obviously emphasized the importance of high grain sink activity in the genetic improvement of grain filling in extra-heavy panicle type rice.

Key words: Environmental correlation, Extra-heavy panicle type, Genetic correlation, Genotype-by-environment interaction, Grain filling, Rate of grain filling, Rice.

The degree of grain filling is an important factor in grain crops as one of the components of grain yield, and also as a critical element affecting grain quality. Particularly rice (*Oryza sativa* L.) cultivars with numerous spikelets in a panicle (extra-heavy panicle type) often have a low degree of grain filling. This is because their spikelet number per panicle has been increased through mainly increasing the spikelets on the secondary rachis-branches which are generally “inferior” spikelets for grain filling. Therefore, the low degree of grain filling restricted the high yield potential of extra-heavy panicle types, e. g., New Plant Types of the International Rice Research Institute and hybrid rice cultivars (Peng et al., 1999; Yan et al., 2002; Peng and Khush, 2003). On the other hand, several extra-heavy panicle types showed relatively higher degree of grain filling, even in inferior spikelets (Yamamoto et al., 1991; Kato and Tamaki, 1999; Peng et al., 1999; Shiotsu et al., 2006; Kato et al., 2007). Such genetic variation in the grain filling among extra-heavy panicle types should be an indispensable genetic resource for the improvement of grain filling in these cultivars.

The degree of grain filling is highly affected by various factors, not only genetic, but also environmental factors. Tsukaguchi et al. (1996) examined the degree of grain filling (measured as percentage of filled grain and other parameters) in an extra-heavy panicle type rice, Milyang 23, under a number of cultivation conditions with different years and nitrogen application levels. They demonstrated large environmental variation for the degree of grain filling which was associated with the amount of non-structural carbohydrates available to grains during the initial phase of grain filling process. The interaction

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Abbreviations: DAH, days after heading; FG%, proportion of filled grain; HG% proportion of high-density grain; FGW, final grain weight; RGF, rate of grain filling; GDD, growing degree days; PB, primary rachis-branch; SB, secondary rachis-branch; r_g, genetic correlation coefficient; r_e, environmental correlation coefficient; Ak, Akenohoshi; Ml, Milyang 23; Nk, Nakateshinsenbon; Tk, Takanari.

Table 1. Cultivation practices in seven growing environments in this experiment.

Environment		Seeding	Trans-planting	Basal dressing[1]	1st top dressing	2nd top dressing	3rd top dressing
Hiroshima	1997	24 April	30 May	5:8:8	2:0:0 (12)	3:2:2 (27)	2:0:0 (45)
	1998	30 April	4 June	5:8:8	2:0:0 (14)	3:2:2 (35)	Not done
	2000	29 April	2 June	5:8:8	2:0:0 (22)	3:2:2 (43)	Not done
	2001	4 May	7 June	5:8:8	2:0:0 (20)	3:2:2 (39)	2:0:0 (48)
Wakayama	2002	10 May	13 June	6:6:6	3:0:0 (18)	3:4:4 (41)	Not done
	2003	9 May	10 June	6:6:6	3:0:0 (17)	3:4:4 (42)	Not done
	2004	12 May	15 June	6:6:6	3:0:0 (16)	3:4:4 (37)	Not done

[1] The ratio shows N:P:K (g m^{-2}). Values in parentheses are the application days after transplanting.

between genotype and environment for the degree of grain filling, however, has not fully been examined.

The process of grain filling after anthesis, which eventually determines the final degree of grain filling, also varies with the genetic and environmental factors. Kato (1999) examined the rate and duration of grain filling and final grain weight using ten rice cultivars with various final grain weights under three environments of different years and locations. The results showed highly significant variations among cultivars and environments for the rate and duration of grain filling and final grain weight. Environmental variation in the final grain weight, however, was not wide as compared with the variations in the rate and duration of filling. This result was explained as a negatively correlated change of the rate with the duration of grain filling, which led to the stability in the final grain weight (=rate × duration).

The objective of the present study is to examine the variation in the traits related to the degree and process of grain filling among three extra-heavy panicle types grown in seven environments of different years and locations, and to analyze the genotype-by-environmental interaction for these traits. Additionally, genetic and environmental correlations among traits were elucidated from these multi-trial experiments. The results for variation and correlation of grain filling in extra-heavy panicle types in different environments should provide some implements to the breeding for the improvement of grain filling of these genotypes.

Materials and Methods

1. Plant materials

Three rice cultivars of extra-heavy panicle types, Akenohoshi (Ak), Takanari (Tk), and Milyang 23 (Ml), were used. As a control of these extra-heavy panicle types, a cultivar with small panicles (a panicle-number type cultivar), Nakateshinsenbon (Nk), was also used. Ak and Nk are *japonica*-type cultivars and Tk and Ml are *indica*-types. Ak (derived from a cross between Chugoku 55 and KC 89) and Tk (Milyang 42 and Milyang 25) were developed in Japan in 1980s as a course of rice breeding project aiming at super-high yield. Ml was derived from a cross between Suwon 232 and IR24 in Korea.

These four cultivars were grown in paddy fields at the School of Bioresources, Hiroshima Prefectural University, Shobara-shi, Hiroshima, Japan (34º40′N, 132º58′E, 295 m above sea level) in 1997, 1998, 2000, and 2001, and at the Faculty of Biology-Oriented Science and Technology, Kinki University, Kinokawa-shi, Wakayama, Japan (34º17′N, 135º20′E, 97 m above sea level) in 2002, 2003, and 2004. Seeds of the four cultivars were sown in nursery boxes, and grown in a vinyl house or a greenhouse. Table 1 shows the profile of cultivation and fertilizer application in each environment. Other cultivation practices, pest management, irrigation, etc., were followed to standard ways in the respective locations. In all environments, the four cultivars were arranged in paddy fields according to a completely randomized design with two replicates at the density of 15 cm inter-hill and 30 cm inter-row. A plot of each cultivar/replicate consisted of five rows and 40 hills with three plants per hill in Hiroshima, and five rows and 25 hills with a single plant per hill in Wakayama.

2. Measurement of grain-filling traits

At 40 to 45 d after heading, six largest panicles per hill were harvested from the 20 hills at the center of each plot and air-dried. From five panicles out of the six per hill, spikelets including unfertilized and poor filled ones were collected from primary rachis-branches (PBs) and secondary rachis-branches (SBs). The spikelets were combined through 20 hills for each PB and SB, and the proportion of filled grain (specific gravity >1.06, FG%) and that of high-density grain [specific gravity >1.20, Venkateswarlu et al. (1986), HG%] were measured using NaCl solutions of the respective specific gravities. The data for these preparations were summarized as pooled values instead of simple means, and were converted according to arcsin transformation in data analysis. The remaining panicle in each hill was measured for the number of spikelets per panicle. Heading date, the number of panicles per hill, and culm length were also measured for the 20 hills.

In all environments, heading dates of individual panicles at the second and fourth rows of each plot were also recorded. Five panicles were sampled from each plot every fifth d from 5 d after heading (DAH) to 50 DAH. After drying at 80°C overnight, fertilized spikelets on PBs and SBs on these five panicles were collected. Single grain weight was measured for each sampling time and plot after another drying at 70°C for two d. The rate of grain filling process (RGF) and final grain weight (FGW) were estimated by fitting the data of single grain weight to a bi-linear regression model (Kato, 1989) which consists of increasing phase in the earlier period and plateau phase in the later period of grain growth. In this model, growing degree days (GDD, cumulative temperature from heading to sampling day without a cut-off value) were used as an independent variable. RGF was shown by grain weight/GDD. Meteorological data for the respective years and locations were cited from the website of the Japan Meteorological Agency (http://www.data.jma.go.jp/etrn/index.php). Accessed date was 30 September 2008.

3. Statistical analysis

An ANOVA of two-way classification with two replicates was conducted for every trait, in which both cultivar and environment were regarded as fixed effects. To elucidate the responses of cultivars to different environments, a linear regression analysis of data on environmental indices (the means across four cultivars in the respective environments) for each cultivar was conducted for each trait (Finley and Wilkinson, 1963; Eberhart and Russell, 1966), to obtain regression coefficients and residual means of squares from regression. Differences in regression coefficients among cultivars were evaluated by a joint regression analysis (Snedecor and Cochran, 1989). Genetic correlation coefficients between every trait combination were calculated as the ratios of genetic covariance components to the geometric averages of genetic variance components (Kato and Takeda, 1996). The same procedure was adopted to calculate environmental correlation coefficients. In this correlation analysis, only the data of three extra-heavy panicle types were used in order to obtain the trends within these extra-heavy panicle types. Significance test for the genetic and environmental correlations was not done, because sample distributions for these coefficients were not defined. Simple correlations between the environmental index of each trait and meteorological data were also calculated.

Results

1. Meteorological conditions and agronomic traits

In August and September of the seven growing environments, in which most of the materials were in the grain filling period, materials grown at Wakayama apparently experienced higher mean daily temperatures and longer monthly sunshine hours than those at Hiroshima, particularly in September (Table 2). Across these heterogeneous environments, three extra-heavy panicle types, Ak, Tk and Ml, had spikelets about two times more than those of a non-extra-heavy panicle type, Nk (Table 3). On the contrary, Nk had a significantly higher number of panicles per hill and longer days to heading than those of three extra-heavy panicle types. Within these extra-heavy panicle types, similar values for agronomic traits were obtained, though most of the differences were significant statistically.

2. Cultivar differences and environmental variation

Fig. 1 shows the changes in the traits related to grain filling in each spikelet position of four cultivars under seven growing environments. In all of these traits, spikelets on PBs showed higher values than spikelets on SBs in all

Table 2. Meteorological elements around grain filling period in seven growing environments.

Environment		Mean daily temperature (°C)		Monthly sunshine hours	
		August	September	August	September
Hiroshima	1997	24.5	19.4	177.6	129.3
	1998	24.9	21.8	131.7	135.4
	2000	24.9	20.5	178.0	146.7
	2001	24.4	19.6	178.0	140.6
Wakayama	2002	28.0	24.7	241.5	198.8
	2003	27.9	25.5	215.7	221.5
	2004	27.9	25.8	197.1	155.9

Table 3. Agronomic traits of four rice cultivars used in the present experiments.

Cultivar	Days to heading	Panicles hill^{-1}	Culm length (cm)	Spikelets panicle^{-1}
Nakateshinsenbon	113.5^{a}	21.5^{a}	71.2^{b}	86.3^{c}
Akenohoshi	109.5^{b}	13.0^{b}	74.8^{a}	190.0^{a}
Takanari	106.3^{c}	13.3^{b}	66.5^{c}	189.3^{a}
Milyang 23	104.9^{d}	13.9^{b}	72.0^{ab}	165.6^{b}

Means for each cultivar do not include the data in 1998 because of data missing. Means without a common letter differed significantly to each other (df=24, $P<0.05$), according to F-protected Fisher's LSD.

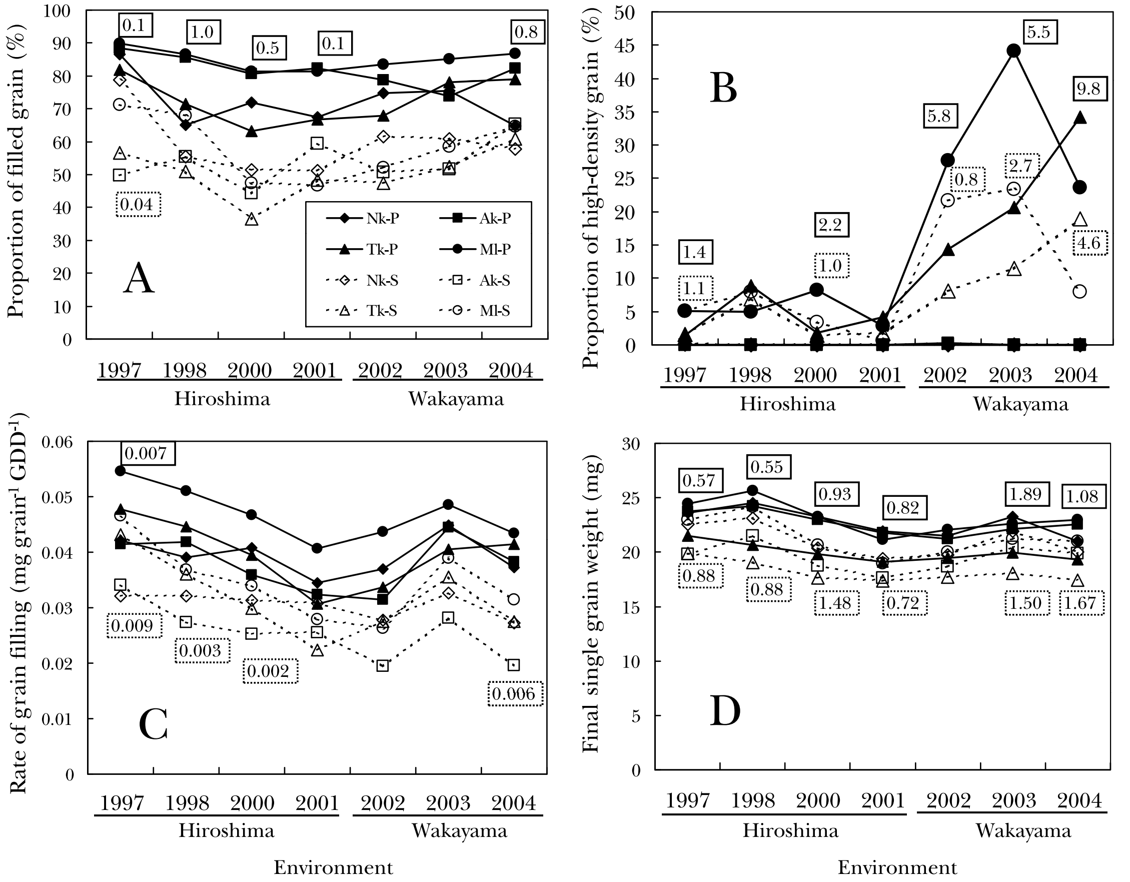

Fig. 1. Differences among cultivars and environmental variation of the traits related to grain filling in four rice cultivars grown in seven environments. A, proportion of filled grains; B, proportion of high-density grains; C, rate of grain filling; D, final grain weight. Ak, Ml, Nk, and Tk mean Akenohoshi, Milyang 23, Nakateshinsenbon and Takanari, respectively. A value in a square is F-protected Fisher's LSD (df=4, $P<0.05$) for cultivar difference in the respective environments. LSD in a solid square and that in a broken square are for spikelets on PBs and on SBs, respectively. No significant difference was detected in a preliminary ANOVA when no LSD was attached.

Table 4. Variance components in the analysis of variance for the traits related to grain filling of four rice cultivars grown in seven environments.

	Proportion of filled grain		Proportion of high-density grain		Rate of grain filling ($\times 10^{-5}$)[1]		Final grain weight	
Source	P[2]	S[2]	P	S	P	S	P	S
Cultivar	19.41**	5.12**	104.17**	47.55**	1.50**	1.31**	2.10**	2.09**
Environment	8.70**	13.35**	20.84**	6.91**	1.70**	2.33**	1.15**	1.62**
Cult. × Env.	8.20**	9.60**	29.91**	11.72**	−0.35	0.40	0.22**	0.25*
Residual	3.85	10.48	23.67	9.92	1.91	1.10	0.24	0.31

* and ** mean significant differences at the 0.05 and 0.01 probability levels, respectively. Data for the proportions of filled and high-density grains are those after arcsin transformation.

[1] Actual values are $\times 10^{-5}$ of the presented values. [2] P and S mean the spikelets on PBs and on SBs, respectively.

cultivars. These traits showed highly significant differences among cultivars and environments, and also demonstrated significant cultivar-by-environment interactions, except for RGF (Table 4). Though the interactions were mostly significant, Ml showed the highest HG% and RGF at both spikelets positions in most of the seven growing environments (Fig. 1B, C). On the other hand, Ak showed almost no high-density grains and the lowest RGF among the three extra-heavy panicle types. Tk showed about the middle values between Ml and Ak for these two traits. These differences were statistically significant within the individual environment in many cases. FG% in the

Table 5. Joint regression analysis of the traits related to grain filling in four rice cultivars grown in seven environments.

	Spikelet on primary branches				Spikelet on secondary branches			
Item[1]	Nk[2]	Ak[2]	Tk[2]	Ml[2]	Nk	Ak	Tk	Ml
Proportion of filled grain (%)								
Pooled value	72.5	81.7	73.2	85.2	59.6	53.8	51.4	58.7
Regression coef.	1.30	0.69	1.25	0.76	1.08^{ab}	0.46^{b}	1.10^{ab}	1.36^{a}
Regression MS	186.41**	52.26*	172.94**	63.25**	205.78*	37.76	209.62**	327.25**
Residual MS	14.83	8.75	11.06	1.88	26.95	16.29	10.50	8.85
Proportion of high-density grain (%)								
Pooled value	0.01	0.04	10.96	13.97	0.02	0.01	5.59	6.30
Regression coef.	-0.01^{b}	0.05^{b}	1.88^{a}	2.08^{a}	-0.03^{b}	0.07^{b}	1.86^{a}	2.10^{a}
Regression MS	0.06	0.75	1010.18**	1237.88**	0.07	0.54	336.88**	429.66**
Residual MS	0.16	1.25	41.29	45.53	0.63	0.39	25.14	15.67
Rate of grain filling (mg grain^{-1}GDD^{-1})								
Mean	3.94	3.80	3.97	4.70	3.05	2.56	3.17	3.46
Regression coef.	0.67	1.04	1.27	1.02	0.34^{b}	0.95^{a}	1.33^{a}	1.38^{a}
Regression MS	10.50**	24.99**	37.49**	24.28**	3.50	26.96**	52.14**	56.28**
Residual MS	1.42	0.63	2.17	1.71	0.97	0.59	1.26	0.93
Final single grain weight (mg)								
Mean	22.7	22.7	20.0	23.2	21.0	19.5	18.2	21.3
Regression coef.	1.04^{ab}	0.94^{ab}	0.70^{b}	1.33^{a}	1.13^{ab}	0.90^{b}	0.63^{b}	1.34^{a}
Regression MS	15.14**	12.54**	6.85**	24.76**	25.29**	16.06**	8.01**	36.01**
Residual MS	0.48	0.26	0.23	0.36	0.35	0.43	0.44	0.25

* and ** indicate significant differences at the 0.05 and 0.01 probability levels, respectively. Data for the proportions of filled and high-density grains are those after arcsine transformation, except for pooled values.

Regression coefficients without a common letter differed significantly to each other (df=24, $P<0.05$) in a joint regression analysis. No significant difference in the joint regression analysis was detected for the data without any letters.

[1] 'Regression coef.', 'Regression MS' and 'Residual MS' mean the regression coefficient of the respective cultivar data on environmental indices, the mean of squares for the regression (df=1) and that for residual (df=12), respectively. The last two parameters were derived from the ANOVA for regression analysis. For the rate of grain filling, actual values for mean and for MS are $\times 10^{-2}$ and $\times 10^{-5}$, respectively, of the presented values. GDD means growing degree days.

[2] Ak, Ml, Nk and Tk mean Akenohoshi, Milyang 23, Nakateshinsenbon and Takanari, respectively.

spikelets on PBs was also higher in Ml but Ak also showed similarly high values, which exceeded the FG% of Nk, particularly in Hiroshima (Fig. 1A). In Hiroshima, Tk showed significantly lower FG% than other two extra-heavy panicle types. There was no consistent and a few significant differences in FG% on SBs. In most of the environments, FGW on both PBs and SBs was the lightest in Tk, but was similar in other cultivars (Fig. 1D). Means and pooled values of the grain-filling traits in each cultivar under seven environments are also shown in Table 5.

3. Regression analysis of the cultivar responses to environmental variation

In most cases the means of squares for regression of data on environmental indices were highly significant against those for residual means of squares (Table 5). This indicates that cultivars used generally showed linear responses to a range of growing environments. Residual means of squares, which correspond to the variances not explained by the regression, were not so much different among cultivars, indicating that the contribution of the regression to overall variation might be similar among cultivars in most traits (Table 5). The extremely low regression coefficients (b) and residual means of squares found in Ak ($b=0.05$ to 0.07) and Nk ($b=-0.03$ to -0.01) for HG% were apparently due to nearly null values in these two cultivars in all environments for this trait. Ml showed the highest regression coefficients ($b=1.33$ to 2.10), except for FG% and RGF in the spikelets on PBs. On the contrary, Ak showed the lowest coefficients ($b=0.05$ to 0.95) among these three extra-heavy panicle types, except for RGF in the spikelets on PBs. The regression coefficients of Ak were significantly lower than those of Ml in several cases. Tk showed the middle values between Ml and Ak in many cases.

Simple correlation coefficients (r) of environmental

Table 6. Genetic and environmental correlations among the traits related to grain filling in three extra-heavy panicle type rice cultivars grown in seven environments, and simple correlations with the environmental indices and meteorological data.

Trait[1]	A	B	C	D	E	F	G	H
A. FG% for P		0.822	−0.081	0.156	0.844	0.773	0.707	0.732
B. FG% for S	0.961		0.338	0.475	0.541	0.345	0.386	0.566
C. HG% for P	−0.103	0.295		0.964	0.046	−0.250	−0.346	−0.020
D. HG% for S	−0.210	0.182	0.996		0.343	0.022	−0.074	0.272
E. RGF for P	0.606	0.921	0.800	0.723		0.957	0.940	0.992
F. RGF for S	0.082	0.488	1.019	0.992	0.872		0.813	0.799
G. FGW for P	1.001	0.932	−0.231	−0.334	0.477	−0.065		0.934
H. FGW for S	0.961	1.065	0.213	0.107	0.827	0.378	0.904	
Temperature	−0.125	0.244	0.989**	0.902**	−0.060	−0.384	−0.425	−0.122
Sunshine hour	−0.173	−0.081	0.794*	0.699	−0.223	−0.328	−0.620	−0.394

Coefficients above and below the diagonal mean environmental and genetic correlation coefficients, respectively. Coefficients below the broken line mean simple correlation coefficients. * and ** mean significantly different at the 0.05 and 0.01 probability levels, respectively (df=5).

[1] FG%, HG%, RFG, FGW, P and S mean proportion of filled grain, proportion of high-density grain, rate of grain filling, final grain weight, spikelets on PBs and spikelets on SBs, respectively.

Temperature and Sunshine hour mean the mean daily temperature and total sunshine hours, respectively, of August and September.

indices with mean daily temperature and monthly sunshine hours were calculated for every trait (the last two rows of Table 6). Only the index for HG% showed positive significant correlations with daily temperature (r=0.902 to 0.989) and sunshine hours (r=0.699 to 0.794).

4. Genetic and environmental correlation among the traits related to grain filling

For both genetic and environmental correlations (r_g and r_e, respectively), very high positive coefficients were observed between the spikelets on PBs and SBs (r_g=0.872 to 0.996, r_e=0.822 to 0.964, Table 6). This indicated that r_g and r_e tended to be the same on either PBs or SBs, though the values appeared to differ.

The correlation coefficient between FG% and HG% on both PBs and SBs was low in both genetic (r_g=−0.103 to 0.182) and environmental correlations (r_e=−0.081 to 0.475). FG% showed moderate positive coefficients with RGF in genetic (r_g=0.488 to 0.606) and environmental correlations (r_e=0.345 to 0.844), and also with FGW in the environmental correlation (r_e=0.566 to 0.707). However, it showed extremely high genetic correlations with FGW (r_g=1.001 to 1.065). HG% showed high positive coefficients with RGF in genetic correlation (r_g=0.800 to 0.992), while very low coefficients in environmental correlation (r_e=0.022 to 0.046). Correlation coefficients between RGF and FGW were moderate in genetic correlation (r_g=0.378 to 0.477), but high in environmental correlation (r_e=0.799 to 0.940).

Discussion

In this study, wide variation among rice cultivars including extra-heavy panicle types and also among growing environments was demonstrated for the traits related to grain filling, which confirms the previous results (Yamamoto et al., 1991; Tsukaguchi et al., 1996; Kato, 1999; Kato and Tamaki, 1999; Peng et al., 1999; Shiotsu, et al., 2006; Kato et al., 2007). In addition, significant cultivar-by-environment interactions were obtained in most of the traits; the most typical interaction in HG% at both PBs and SBs (Fig. 1B). In Hiroshima, where the mean daily temperature and monthly sunshine hours were lower and shorter, respectively, than in Wakayama, Ml and Tk showed relatively lower HG%. On the other hand, in Wakayama, HG% in Ml and Tk were greatly higher compared with Al and Nk. These clear responses of HG% to favorable conditions for grain filling in Ml and Tk were reflected in the high correlation coefficients of the environmental index for HG% and daily temperature and sunshine hours (Table 6). However, HG% in Ak and Nk were consistently low irrespective of the difference in environment conditions. Osada et al. (1973) showed that several *indica* cultivars had grains with higher density compared with *japonica* cultivars.

Ml showed high regression coefficients for many traits, particularly for HG%. This cultivar, thus, could respond much more to the environmental variation for this trait and showed better performance in better environments and *vice versa*, in both PBs and SBs (Table 5). On the contrary, Ak showed low regression coefficients, indicating that this cultivar was the most insensitive to the environmental variation and showed relatively lower performance nearly in all environments. These contrasts between Ml and Ak were more evident in the inferior spikelets (spikelets on SBs). The same trends as in Ak were observed also in a non-extra-heavy panicle type, Nk, except for FGW. Such a positive correlation between mean performance and response to environments has already been reported [e.g., Matsuo et al. (1972) in rice].

Genotypic differences in the responses of the grain filling process to environmental conditions have also been demonstrated in several crops other than rice. Wych et al. (1981) reported a difference in the grain filling process and grain weight between two years in early and late cultivars of oats. Voltas et al. (1999) detected that two-rowed and six-rowed barley cultivars responded differently to 12 contrasting environments in several parameters of the grain filling process.

The present multi-trial study made it possible to elucidate genetic and environmental correlations among the traits related to grain filling (Table 6). Relatively low genetic and environmental correlation coefficients between FG% and HG% suggest that these two parameters might present different aspects of grain filling. It was suggested that FG% was affected by the degree of grain set as well as the early stage of grain growth, while HG% was mainly by the degree of filling efficiency of photoassimilates in the middle and later stages of grain filling. This weak association of FG% with HG% was also observed in a set of recombinant inbred lines derived from a cross between Nk and Ml (Kato, 2008). Such different aspects between FG% and HG% would appear in their genetic associations with FGW. Extremely high genetic correlation between FG% and FGW could be explained from the reduction of FGW due to early termination of grain growth.

The HG% showed high and positive genetic correlation coefficients with RGF (Table 6). Ml, which showed high HG% and high RGF, could express this high ability to accumulate photoassimilates extensively under favorable environments, and consequently could result in a much higher degree of grain filling. This might be reflected in the high regression coefficients of Ml as mentioned above (Table 5). On the contrary, Ak could not respond to such favorable environments due to low genetic ability for grain growth. Kato (2004) reported that Ak could not accumulate sufficient photoassimilates and deposited large amounts of non-structural carbohydrates in stems in later stages of grain filling. RGF, on the other hand, showed very low environmental correlations with HG%. This might be partly due to relatively weak responses of RGF to Wakayama's favorable environment (Fig. 1C), which reflected no correlations of the environmental index for RGF with meteorological data (Table 6).

The correlation coefficient between RGF and FGW was not high in genetic correlation (Table 6). This apparently showed a clear contrast with the results of previous experiments using cultivars with a wide variation in FGW, in which a high positive correlation was observed between these two traits (Kato, 1989; Kato, 1999). This high positive correlation between RGF and FGW was explained as the variation in the number of endosperm cells, each of which showed similar growth activity (Kato, 1995). In the present extra-heavy panicle types, thus, the genetic variation might be mainly due to the variation in the growth rate of individual cells. This variation in cell growth rate would be related to the variation in the activity of ADPglucose pyrophosphorylase in developing endosperm which was positively associated with HG% in the extra-heavy panicle-type rice that had a similar grain size (Kato et al., 2007).

In conclusion, the present study revealed clear differences in the degree of grain filling and the response to environmental variation among rice of extra-heavy panicle types, though only three cultivars were examined. This difference was most obvious in HG% and associated only genetically with RGF. High activity of developing grains to accumulate photoassimilates should underlie this high RGF, and should be a key factor in the genetic improvement of grain filling in extra-heavy panicle types, as well as the high ability to produce photoassimilates, e.g., high amount of non-structural carbohydrates in the initial stage of grain filling (Tsukaguchi et al., 1996). Probably, other extra-heavy panicle types with high degree of grain filling and high rate of grain filling, for example Nanjing 11 (Kato et al., 2007), would follow this scheme. Some appropriate bio-markers identifying this high grain sink activity should be explored in the course of breeding aiming at good grain filling.

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* In Japanese with English abstract.