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Association of Duration and Rate of Grain Filling with Grain Yield in Temperate Japonica Rice (*Oryza sativa* L.)

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ABSTRACT Grain filling is a crucial factor that determines grain yield in crops since it is the final process directly associated with crops' yield performance. Grain filling process can be characterized by the interaction of rate and duration of grain filling. This study was conducted, using 16 temperate japonica rice genotypes, with aims to (1) seek variations in grain filling duration and rate on area basis, (2) compare the contribution of grain filling duration and rate to grain yield, and (3) examine the influence of temperature and solar radiation for effective grain filling on grain yield in relation to grain filling duration and rate. Grain filling rate and duration exhibited highly significant variations in the ranges of 20.7~46.3 g m^{-2} d^{-1} and 11.2~35.5 days, respectively, depending on rice genotypes. Grain yield on unit area basis was associated positively with grain filling duration but negatively with grain filling rate. Grain filling rate and duration were negatively correlated with each other. Final grain weight increased linearly with the rise in both cumulative mean temperature and cumulative solar radiation for effective grain filling. Higher cumulative mean temperature and cumulative solar radiation for effective grain filling were the results of longer grain filling duration, but not necessarily higher daily mean temperature and daily solar radiation for effective grain filling. Grain filling rate demonstrated an increasing tendency with the rise in daily mean temperature for effective grain filling but their relationship was not obviously clear. It was concluded that grain filling duration, which influenced cumulative mean temperature and cumulative solar radiation for effective grain filling, was the main factor that determined grain yield on unit area basis in temperate japonica rice.

Keywords : rice, grain yield, grain filling duration, grain filling rate, temperature, solar radiation

Seed filling process is one of the crucial factors that determine grain yield in cereal crops since it is the final process directly associated with crops' yield performance. Grain growth of field crops is initially slow, enters a linear phase where the growth rate is fast, and then slows down toward maturity (Yoshida, 1981). Cho *et al.* (1988) also divided rice grain filling duration into three phases: lag phase of five days from heading, linear increasing phase of 5-20 days after heading, and late filling period thereafter. Frequently, however, grain filling patterns demonstrate genotypic variations in many cereal crops.

It has been suggested that effective grain filling duration where grain growth is linear should be more important than the duration of ripening from the date of heading to the time when maximum grain weight is attained because most of dry grain weight is attained during the effective grain filling period (Yoshida, 1981). This approach conceptualized the interaction between effective grain filling duration and grain filling rate during the period, both of which contribute to grain yield in a multiplicative manner.

Frequently, source activity, represented by photosynthesis and related parameters in leaves, were explored with respect to grain filling process. Park & Lee (2003a) observed leaf photosynthetic rates positively related with chlorophyll meter values and leaf nitrogen concentration, and proposed that the stay-green characteristics of a rice variety, SNU-SG1, would contribute to increasing grain yield through improved photosynthesis during grain filling. They confirmed, in another study, that delayed senescence of upper leaves and rapid senescence of lower leaves were positively associated with grain yield increase in rice (Park & Lee, 2003b). Contradictory observations were reported in barley. Ryu & Lee (1994) stated that barley varieties, maintaining leaf

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greenness to the late phase of grain growth, were considerably advantageous to grain filling but Nam *et al.* (1991) mentioned that fast senescing barley varieties produced grain yield higher than slow senescing varieties. This opposed findings in barley make it difficult to impose more attention to either of photosynthetic activity of leaves or translocation of leaf nitrogen to grains for grain growth. Murchie *et al.* (2002) reported that the rate of grain filling in new plant type rice was not consistently related with light-saturated carbon assimilation rate and chlorophyll content, both of which remained mostly unchanged throughout active grain filling period and concluded that ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) accumulated to a level in excess of photosynthetic requirements, serving as a store of nitrogen for grain filling.

Since most in vivo biochemical reactions depend on temperature, effects of air temperature have been explored in association with grain filling process. Kim (1983) observed an optimum temperature for achieving maximum grain weight through carbohydrate accumulation in rice grains being as 26/18℃ (day/night) and further stated that grain filling period shortened as temperature rose in a range of 13~28℃. Similar temperature-response of ripening was reported in rice by Lee (1995). In sorghum, Muchow (1990) reported that grain growth rate increased linearly with temperature to 30℃, but not grain filling duration. But in wheat, average temperature of the grain filling period was associated with grain weight (Savin *et al.*, 1999). He & Rajaram (1993) reported that grain filling rate was temperature-sensitive more than duration of grain filling, when compared sixteen wheat cultivars. Solar radiation, along with temperature, is another important environmental factor that influences rice yield performance in a positive manner (Peng *et al.*, 2004; Evans & De Datta, 1979; Islam & Morison, 1992; Dobermann *et al.*, 2000).

Yang *et al.* (2001) observed that a decrease in gibberellin and an increase in abscisic acid enhanced the remobilization of pre-stored carbon to the grains and accelerated grain filling rate. Regulation of grain filling patterns and grain filling percentage by cytokinins in rice grains and roots was reported (Yang *et al.*, 2000).

Studies have been made on the contribution of grain filling duration to grain filling or grain weight in cereal crops such as sorghum, barley, wheat, and rice. Seed-fill duration is regulated by leaf's ability to supply assimilate to the developing seed and by the ability of the seed to use this assimilate for continued growth (Egli, 2004). Cha *et al.* (1997) proposed that at least five genes were involved in the effective grain filling period. Gelang *et al.* (2000) studied the adverse effect of ozone on wheat grain yield and mentioned that flag leaf senescence accelerated by ozone shortened grain filling duration, which consequently caused yield reduction, but not grain filling rate. In spring wheat and sorghum, grain filling duration was not necessarily associated with grain yield (Talbert *et al.*, 2001; Muchow, 1990). However, Egli (2004) proposed that lengthening the seed filling period should be the most promising avenue to higher yield in a given seed fill rate.

Contribution of grain filling duration and rate to grain yield was compared in several crops. Jongkaewwattana & Geng (2001) suggested rate and duration of grain filling in rice affect final grain traits such as weight and density. Negative correlation was found between grain filling duration and grain filling rate in rice and grain weight was determined mainly by the latter (Jones *et al.*, 1979; Cho *et al.*, 1987), while no significant correlation was found between them in tropical maize (Josue & Brewbaker, 2005). Cho *et al.* (1988) further mentioned that rice grains in the bottom part of a panicle had shorter period and slower rate of grain filling than those in the top and middle part of the panicle. But in most cases, including the studies by Cho *et al.* (1987 & 1988) and Jones *et al.* (1979), rate and duration of grain filling were examined on a panicle basis, which did not account for grain filling on unit area basis although the information was useful on a single panicle basis.

This study was designed with aims to (1) seek variations in grain filling duration and rate on area basis, (2) compare the contribution of grain filling duration and rate to grain yield, and (3) examine the influence of temperature and solar radiation for effective grain filling on grain yield in relation to grain filling duration and rate.

MATERIALS AND METHODS

Experiments were conducted at the research farm of National Institute of Crop Science, Rural Development Administration, Suwon, Republic of Korea (37°16' N, 126°59' E, 31 m elevation), a temperate plain area, in 2006. The soil was a Fluvaquentic Endoaquetps with pH 5.1, 18.2 g organic C kg^{-1}, and 7.7 cmol kg^{-1} cation exchange capacity to 30 cm depth (National Institute of Agricultural Science and Technology, 2001).

Sixteen rice genotypes, which cover a wide range of temperate japonica germplasms, were used in this study. Pregerminated seeds were sown on seedling trays to raise uniform seedlings. Thirty-day old seedlings, grown in trays on a seedbed, were manually transplanted on 26 May at a hill spacing of 0.3×0.14 m with three seedlings per hill. Ninety kg N ha^{-1} was split-applied: 50% at basal, 20% at tillering initiation, and 30% at panicle initiation. Forty-five kg P ha^{-1} was applied as a basal fertilizer immediately before puddling the fields. Fifty-seven kg K ha^{-1} was split-applied: 70% at basal and 30% at panicle initiation. Fertilizer application methods conformed to the recommendation by Rural Development Administration.

Plots were laid out in a randomized complete block configuration with four replications. Crop management, including water and weed management, followed the standard cultural practices. Pests were intensively controlled to avoid biomass and yield loss. The experimental fields were flooded and 5～10 cm water depth was maintained until 9～10 days before final harvest, except for one week when they were drained during maximum tillering stage to minimize unproductive tiller development and enhance soil aeration for root growth.

Five hills from each plot were sampled eight times every week from flowering (FL) to 49 days after FL (DAF) when final sampling for each genotype was made. Plants were separated into leaves, culm+sheath, and panicles after counting panicle number. Panicles were manually threshed into rachis and spikelets. Filled spikelets were separated from unfilled spikelets by submerging them in tap water. Each plant organ was oven-dried at 75℃ to constant weight to determine dry weight. Filled and unfilled spikelets were counted to determine spikelet number and grain filling percentage. Aboveground biomass, sum of dry weight for each organ, and harvest index, partitioning of biomass to rice grain, were calculated from these samples.

Grain filling process was fitted by Richards (1959) growth equation as described by Yang *et al.* (2001) to calculate grain filling duration and rate as a function of time after FL, using SPSS statistical software:

$$W=\frac{A}{(1+Be^{-kt})^{1/N}} \tag{1}$$

where W is the grain weight (g m^{-2}), A the final grain weight, t DAF, and B, k, and N are coefficients determined by regression. Grain filling duration was defined as that when W was from 5% (t_1) to 95% (t_2) of A. The average grain filling rate during this period was calculated from t_1 to t_2. Similarly, grain filling process was again fitted by substituting cumulative air temperature (T) and cumulative solar radiation (R) from FL for t in above equation to calculate cumulative temperature and cumulative solar radiation from 5% (T_1 and R_1) to 95% (T_2 and R_2) of A. The average daily mean temperature and daily solar radiation were calculated by dividing cumulative temperature and cumulative solar radiation for effective grain filling, respectively, by grain filling duration to estimate the grain filling process as the function of temperature and solar radiation for effective grain filling.

Climatic data were collected from Suwon Meteorological Bureau, located about 500 m apart from the experimental fields. Data were analyzed following analysis of variance (SAS, 1982) and means of genotypes were compared based on the Least Significance Difference (LSD) Test at the 0.05 probability level.

RESULTS

Daily mean air temperature increased linearly from transplanting to 80 days after transplanting (DAT) and decreased thereafter (Fig. 1A). Abrupt decreases in daily mean temperature and solar radiation from 50 to 70 DAT were the result of rainy season in summer. Daily solar radiation

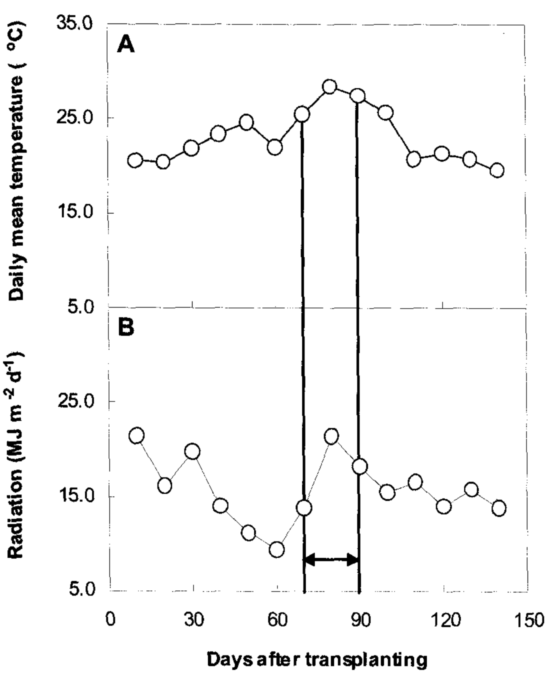

Fig. 1. Daily mean temperature (A) and solar radiation (B) during the growth period of rice plants. The sixteen rice genotypes in this study flowered during the period indicated by an arrow with two heads.

showed a peak at 80 DAT and slowly declined thereafter (Fig. 1B). The sixteen rice genotypes flowered during 70~90 DAT when mean temperature and solar radiation reached a peak throughout the cropping season.

For general information on the varieties used in this study, growth duration and crop growth at physiological maturity were summarized in Table 1. Growth duration of rice genotypes varied in a range of 119 days for Junghwa to 139 days for Samgwang and Chucheong, which imposed different climatic conditions during grain filling period to different rice genotypes. Samgwang and Chucheong produced aboveground biomass at physiological maturity more than the others. In general, genotypes with longer growth duration accumulated more biomass (r^2=0.869**, n=16). Harvest index demonstrated genotypic variation in a range of 0.37~0.52. Grain yield at 49 DAF was positively associated with both aboveground biomass at physiological maturity (r^2=0.662**, n=64) and harvest index (r^2=0.365**, n=64). Spikelet number m^{-2} ranged from 27940 for Taeseong to 42371 for Samgwang and grain filling percentage from

Table 1. Growth duration from transplanting to final harvest (49 days after flowering), aboveground biomass production, harvest index, spikelet number per m^2, and grain filling percentage taken at final harvest in different temperate japonica rice genotypes.

Genotype	Growth duration	Aboveground biomass	Harvest index	Spikelets	Grain filling
	d	g m^{-2}		no m^{-2}	%
Junghwa	119	1359	0.42	33771	85.3
Hwadong	120	1351	0.44	31826	85.6
Munjang	122	1349	0.42	34510	83.2
Ungwang	122	1408	0.49	37986	85.6
Taeseong	122	1326	0.41	27940	87.2
Sangmi	126	1339	0.42	37448	75.5
Sura	132	1664	0.42	36213	89.0
Hwayeong	133	1671	0.48	38818	92.5
Gopum	134	1600	0.41	37286	83.5
Dongjin-1	134	1584	0.43	41431	76.0
Onnuri	134	1519	0.52	38470	88.0
Junam	137	1689	0.49	37906	92.8
Nampyeong	138	1789	0.44	36692	94.3
Ilpum	138	1767	0.47	41496	89.3
Samgwang	139	1885	0.45	42371	93.1
Chucheong	139	1853	0.37	33123	94.9
LSD (0.05)		76	0.02	2307	2.9

Data are means of four replications.

75.5% for Sangmi to 94.9% for Chucheong. Both spikelet number m^{-2} and grain filling percentage contributed to grain yield with r^2 values of 0.544** and 0.347** (n=64), respectively.

When fitted by non-linear Richards equation (1959), Hwayeong, Junam, Ilpum, and Samgwang produced grain yield higher than 800 g m^{-2} while Junghwa and Taeseong produced grain yield relatively lower than the other genotypes (Table 2). Effective grain filling duration exhibited highly significant genotypic variation from 11.2 days for Hwadong to 35.5 days for Hwayeong. Grain filling rate during effective filling period was the highest in Hwadong as 46.3 g m^{-2} d^{-1} and lowest in Sura as 20.7 g m^{-2} d^{-1}. Cumulative mean temperature from the temperature where 5% of final grain weight was attained to the temperature where 95% of final grain weight was accumulated demonstrated highly significant genotypic variation from 296℃ for Hwadong to 761℃ for Hwayeong. Daily mean temperature, calculated by dividing cumulative mean temperature by number of days for effective grain filling, was the highest in Ungwang and the lowest in Ilpum, ranging 20.3～27.2℃. In general, early flowering genotypes such as Junghwa and Hwadong were subjected to higher daily mean temperature for effective grain filling than late flowering genotypes such as Samgwang and Chucheong. Cumulative and daily solar radiation for effective grain filling, which were calculated by the essentially same way for cumulative temperature, exhibited wide genotypic variations in the range of 169～595 MJ m^{-2} and 13.8～18.2 MJ m^{-2} d^{-1}, respectively.

When plotted to determine the contribution of grain filling duration and rate to grain yield, final grain weight was associated positively with grain filling duration (Fig. 2A) but negatively with grain filling rate (Fig. 2B). Coefficient of determination in the relationship between grain weight and grain filling duration was greater than that between grain weight and grain filling rate. Negative correlation was observed between grain filling duration and grain filling rate (Fig. 3).

Grain yield linearly increased with the rise in both cumulative mean temperature (Fig. 4A) and cumulative solar radiation for effective grain filling (Fig. 4B). Cumulative

Table 2. Final grain weight (A), grain filling duration (GFD), grain filling rate (GFR), cumulative mean temperature (CT), daily mean temperature (DT), cumulative solar radiation (CR), and daily solar radiation (DR) for effective grain filling, fitted by non-linear Richards equation, in different temperate japonica rice genotypes.

Genotype	A	GFD	GFR	CT	DT	CR	DR
	g m^{-2}	d	g m^{-2} d^{-1}	℃	℃	MJ m^{-2}	MJ m^{-2} d^{-1}
Junghwa	540	14.6	35.7	393	26.9	262	18.2
Hwadong	572	11.2	46.3	296	26.5	169	15.1
Munjang	569	15.4	33.7	415	26.9	217	14.0
Ungwang	683	21.9	28.6	596	27.2	320	14.5
Taeseong	538	12.4	39.3	335	27.0	171	13.8
Sangmi	575	15.4	33.9	396	25.8	213	13.9
Sura	710	31.0	20.7	715	23.1	539	17.4
Hwayeong	837	35.5	21.5	761	21.4	595	16.7
Gopum	658	23.7	26.0	501	21.1	398	16.8
Dongjin-1	686	22.9	27.3	473	20.7	383	16.8
Onnuri	770	25.0	28.1	527	21.0	430	17.2
Junam	802	25.2	29.2	514	20.4	359	14.2
Nampyeong	777	31.0	22.6	632	20.4	464	14.9
Ilpum	828	26.6	28.2	539	20.3	384	14.4
Samgwang	857	26.2	29.6	538	20.6	376	14.4
Chucheong	704	25.6	25.0	531	20.7	358	13.9
LSD (0.05)	39	4.9	5.9	114	0.4	88	0.9

Data are means of four replications.

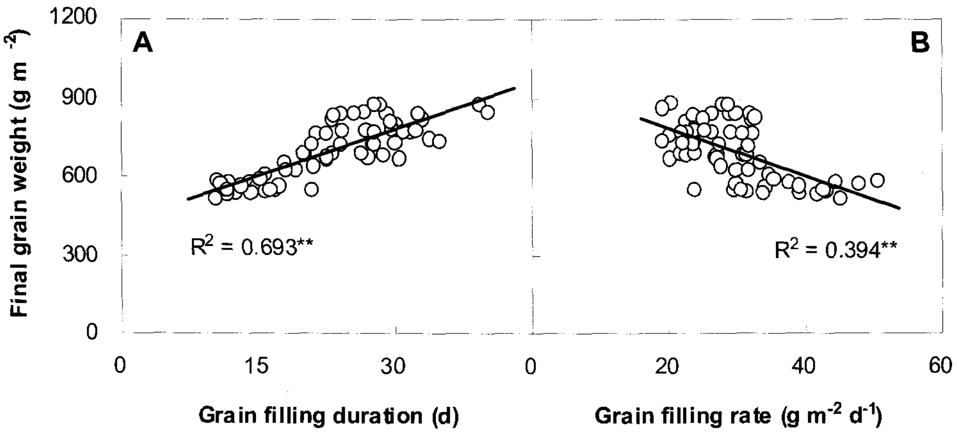

Fig. 2. Relationship of final grain weight with grain filling duration (A) and grain filling rate (B), which were fitted by non-linear Richards equation. Each data point is a replication for sixteen temperate japonica rice genotypes (*n*=64).

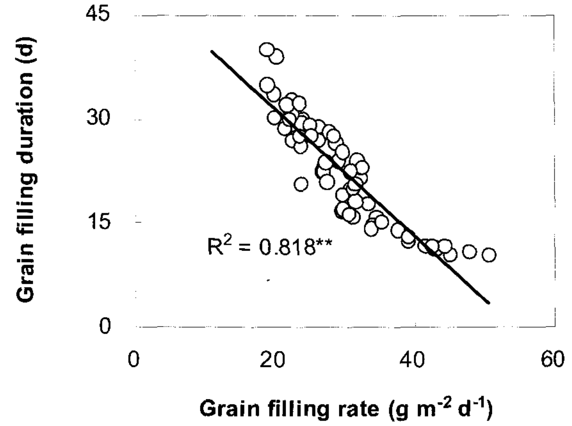

Fig. 3. Relationship between grain filling duration and grain filling rate, both of which fitted by non-linear growth equation. Each data point is a replication for sixteen temperate japonica rice genotypes (*n*=64).

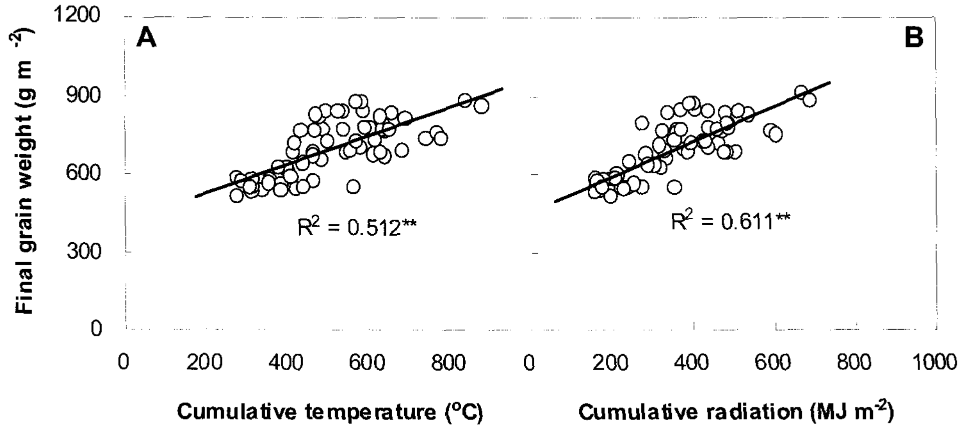

Fig. 4. Relationship of final grain weight with cumulative air temperature (A) and cumulative solar radiation (B) for effective grain filling, fitted by non-linear growth equation. Each data point is a replication for sixteen temperate japonica rice genotypes (*n*=64).

mean temperature for effective grain filling was highly significantly associated with grain filling duration (Fig. 5A). But close association was not found between cumulative mean temperature and daily mean temperature for effective grain filling (Fig. 5B). Greater cumulative solar radiation for effective grain filling was a function of longer grain filling duration (Fig. 6A). Contribution of daily solar radiation to cumulative solar radiation for effective grain filling was not obvious (Fig. 6B).

When plotted to examine the contribution of daily mean temperature and solar radiation for effective grain filling, they were not closely associated with grain filling rate (Fig. 7). Grain filling rate slightly shifted to higher values as daily mean temperature rose from 20℃ to 27℃ but it widely varied at the temperature range of 26~27℃ and 20~22℃ (Fig. 7A).

DISCUSSION

Association of grain filling duration and rate with grain yield shows different patterns depending on crop species. Contribution of grain filling duration and rate to grain yield in rice was previously reported in the comparison of genotypes on a panicle basis (Jones *et al.*, 1979; Cho *et*

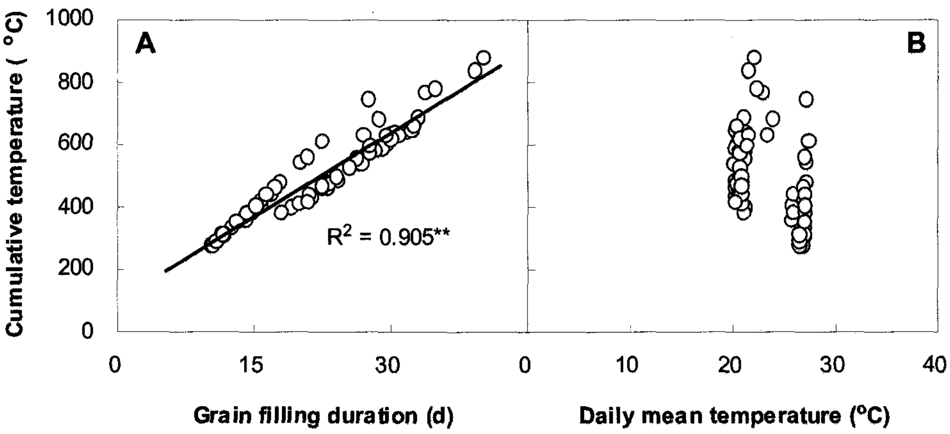

Fig. 5. Relationship of cumulative air temperature for effective grain filling with grain filling duration (A) and daily mean temperature for effective grain filling (B), fitted by non-linear Richards equation. Each data point is a replication for sixteen temperate japonica rice genotypes (*n*=64).

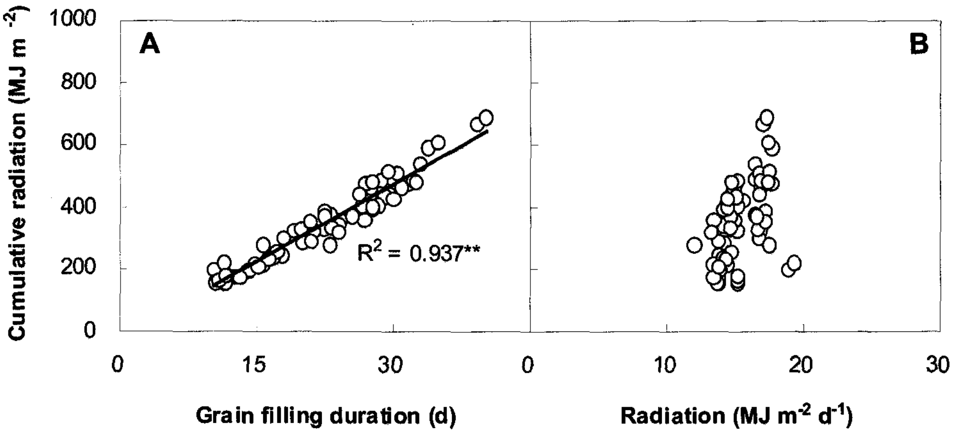

Fig. 6. Relationship of cumulative solar radiation for effective grain filling with grain filling duration (A) and daily solar radiation for effective grain filling (B), fitted by non-linear Richards equation. Each data point is a replication for sixteen temperate japonica rice genotypes (*n*=64).

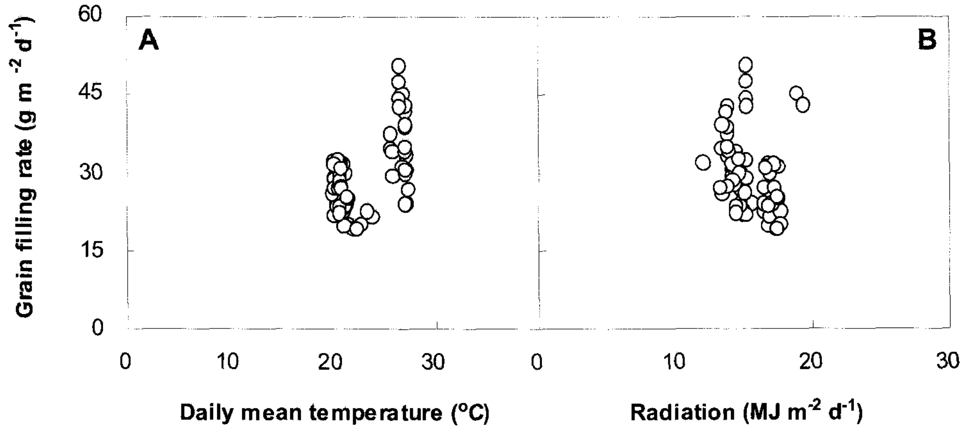

Fig. 7. Effect of daily mean temperature (A) and daily solar radiation (B) for effective grain filling on grain filling rate, fitted by non-linear Richards equation. Each data point is a replication for sixteen temperate japonica rice genotypes (n=64).

al., 1987). In their studies, grain yield was mainly determined by grain filling rate. But grain filling duration obviously influenced grain weight in a positive manner while grain filling rate did in a negative manner when examined on area basis in this study (Fig. 2 & Table 1), unlike previous observations by Jones *et al.* (1979) and Cho *et al.* (1987). Jones *et al.* (1979) further stated that grain filling rate determined grain filling duration. It is logical because rate of grain filling should be determined earlier than duration. In this present study, grain filling duration was associated negatively with grain filling rate (Fig. 3), which was a result similar to the previous report by Cho *et al.* (1987). This negative correlation between the rate and duration of grain filling in rice makes it difficult to improve grain yield by achieving both high grain filling duration and grain filling rate.

Grain filling duration accounts for number of days for effective grain filling. Therefore, grain filling duration will be solely useful only when genotypes flower on a same date. However, since the varieties in this study flowered at 70 to 90 DAT, they were subjected to different environment for grain filling, e. g. early flowering genotypes to higher daily mean temperature and late flowering genotypes to lower temperature, as depicted in Fig. 1. Hence, grain filling duration will precisely account for grain yield when it is considered in association with circumstances, to which rice plants are subjected during grain filling. When plotted, final grain weight increased with the rise in cumulative mean temperature and cumulative solar radiation for effective grain filling (Fig. 4), indicating that grain yield was influenced by all of grain filling duration, cumulative temperature, and cumulative solar radiation (Fig. 2A & Fig. 4). Cumulative mean temperature for effective grain filling is the function of grain filling duration and daily mean temperature for effective grain filling. Similarly, grain filling duration and daily solar radiation for effective grain filling are the components of cumulative solar radiation. When dissected in this study, cumulative mean temperature and cumulative solar radiation for effective grain filling were highly positively correlated with grain filling duration (Fig. 5A & 6A), but not apparently with daily-based temperature and radiation for effective grain filling (Fig. 5B & 6B). Therefore, it is suggested that longer grain filling duration imposed both higher cumulative mean temperature and higher cumulative solar radiation to grain filling of rice, which consequently contributed to better grain filling for yield improvement.

Although grain filling rate was correlated with grain weight negatively in this study, it is a component that will contribute to grain yield in a given grain filling duration and grain filling is generally associated with temperature as suggested by Kim (1983) and Lee (1995). When plotted to examine the effect of daily mean temperature and daily solar radiation for effective grain filling, they did not show a certain relationship with grain filling rate (Fig. 7), even though the range of grain filling rate shifted to higher values as daily mean temperature rose from 20℃ to 27℃ (Fig. 7A). Since this comparison was made with rice genotypes that had different grain filling duration, there could be an interference of grain filling duration on the relationship of daily mean temperature and solar radiation for effective grain filling with grain filling rate. Hence, relationship between them was examined in selected rice genotypes with similar grain filling duration. When compared Sura and Nampyeong, both of which had grain filling duration of 31 days, Sura was subjected to higher daily mean temperature and higher daily solar radiation than Nampyeong (Table 2). But Nampyeong demonstrated higher grain filling rate than Sura. When compared Ungwang, Gopum, and Dongjin-1 that had similar grain filling duration of 21.9~23.7 days, Ungwang that had daily mean temperature for effective grain filling higher than the other two genotypes did not show grain filling rate remarkably higher than the others. Moreover, Gopum and Dongjin-1 that were subjected to higher daily solar radiation than Ungwang demonstrated a grain filling rate slightly lower than Ungwang. Similarly, Sangmi that had lower daily mean temperature for effective grain filling and similar grain filling duration, compared to Munjang, exhibited a grain filling rate similar to Munjang. Therefore, both daily mean temperature and daily solar radiation seem to have little effect on grain filling rate even in a given grain filling duration when comparison was made among different genotypes, suggesting that changes in genetic effect for grain filling rate in field-grown rice to varying environments is relatively small, unlike sorghum (Muchow, 1990) and wheat (He & Rajaram, 1993). Effects of daily mean temperature and solar radiation on grain filling rate need to be elaborated further for individual varieties to estimate the effects of environmental components in a given genetic background.

Consequently, higher grain yield on unit area basis was achieved mainly by both higher cumulative mean temperature and cumulative solar radiation for effective grain filling as a result of longer grain filling duration. Apparently, longer grain filling duration provided rice plants with more natural resources for grain filling. Comparison of grain filling duration and rate between on a single panicle basis and on unit area basis awaits further investigation. And maintenance of source activity such as photosynthesis, leaf nitrogen concentration, and leaf mass needs to be further elaborated on area basis in relation to grain filling duration, since they are factors associated with grain filling processes in many crops (Park & Lee, 2003a, 2003b; Ryu & Lee, 1994; Murchie *et al.*, 2002).

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