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Changes in the panicle-related traits of different rice varieties under high temperature condition

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Abstract

The size and structure of panicles are important factors which contribute to both yield and quality of rice. Changes in the panicle-related traits by elevated temperature were studied using 40 rice varieties including 27 *japonica* and 13 Tongil-types (derived from *indica-japonica* crosses). Tongil-type rices showed larger sink size than *japonica* either in ambient and high temperature conditions, mainly due to the higher number of secondary rachis-branches (SRBs) and spikelets on SRBs per panicle, which showed highly positive correlations (>0.95) with the numbers of spikelets and rachis-branches per panicle. On the other hand, percentages of ripened grains and head rice (%) were significantly higher in *japonica* than in Tongil-type under both conditions. Under high temperature, Tongil-type showed significant increase in the numbers of spikelets, rachis-branches, SRBs and spikelets on SRBs per panicle, while *japonica* did not show any significant change in sink size. However, the percentages of ripened grains and head rice were significantly reduced by high temperature in both ecotypes. While the decrease in ripened grains percentage was higher in Tongil-type, head rice percentage reduced more in *japonica* than in Tongil-type. For both ecotypes of rice, the percentage of ripened grains was higher in primary rachis-branches (PRBs) than in SRBs in ambient and high temperature conditions. Moreover, the decrease in the ripened grains percentage by temperature rise was higher in SRBs than PRBs. Therefore, it would be desirable to breed varieties with increased number of PRBs rather than SRBs to minimize the negative impact of warmer climate on the ripening of rice grains.

Keywords: rice, high temperature, panicle, primary rachis-branch, secondary rachis-branch.

Abbreviations:	
PRB	Primary rachis-branch
SRB	Secondary rachis-branch
NS	Number of spikelets per panicle
NR	Number of rachis-branches per panicle
NPr	Number of PRBs per panicle
NSP	Number of spikelets on PRBs per panicle
NSPr	Number of spikelets on a PRB
NSr	Number of SRBs per panicle
NSS	Number of spikelets on SRBs per panicle
NSSr	Number of spikelets on a SRB
S/P	Ratio of SRBs to PRBs
RPP	Ripened grains percentage of PRBs (%)
RPS	Ripened grains percentage of SRBs (%)
RP	Ripened grains percentage per panicle (%)
HP	Head rice percentage (%)
PCA	Principal component analysis
LSD	Least significant difference
SSRG	Starch synthesis-related gene

Introduction

Yield and grain quality of rice, the most important staple crop for a half of the world population, are being deteriorated due to the temperature rise by global warming. According to the Intergovernmental Panel on Climate Change, global average surface temperature was increased by 0.74°C during the last century and is expected to rise by 1.1~6.4°C by 2100 (IPCC, 2007). Elevated temperature influences rice yield and quality mainly during the reproductive and ripening stages, respectively. During flowering, a temperature higher than 33.7°C for an hour induces spikelet sterility and yield decline in rice (Jagadish et al., 2007, 2008). Although there are few heat-tolerant genotypes such as N22, showing more than 60% fertility at temperatures above 36°C, many sensitive varieties exhibit significant sterility under high temperatures mainly due to the hindrance of anther dehiscence and pollen germination (Jagadish et al., 2008, 2009). The high temperatures cause yield loss in rice by increasing respiration and energy consumption while decreasing seed assimilation, grain weight, and harvest index (Prasad et al., 2006; She et al., 2010; Zakaria et al., 2002; Zhu et al., 2005). Furthermore, warmer weather during ripening reduces head rice percentage by enhancing the formation of chalkiness, opaque area in rice grains, which not only deteriorates grain appearance but also worsens palatability (Chun et al., 2009; Kobayashi et al., 2007; Tabata et al., 2007). Therefore, development of adaptable cultivars to increased temperature is one of the most important goals in rice breeding aimed to cope with climate change. Panicle traits such as rachis-branching system and the number of spikelets on primary and secondary rachis-branches have been important for rice breeders because they are crucial determinants of grain yield and quality (Kim et al., 2003a; Matsue et al., 1994, 1995; Yamagishi, 2003). Primary rachis-branches (PRBs) are the branches connected to the central rachis of a panicle, while secondary rachis-branches (SRBs) refer to the branches connected to primary branches (Park et al., 2010). Previous studies on the variations in panicle size and structure since 1950s have been reviewed by Taguchi-Shiobara et al. (2011). Yamagishi et al. (2003) conducted a principal component analysis (PCA) for the panicle traits of 65 *japonica* varieties and distinguished that genotypes with large panicle size have relatively higher number of spikelets on SRBs rather than PRBs. Park et al. (2010) studied the diversity of panicle traits in 178 Korean rice varieties and reported that Tongil-type cultivars (derived from *indica*-*japonica* cross) have larger panicle size than *japonica* cultivars mainly due to the higher numbers of SRBs and spikelets on SRBs. Taguchi-Shiobara et al. (2011) conducted PCA of panicle traits using 136 *indica* and 156 *japonica* varieties and found that *indica* types have fewer PRBs and conversely more SRBs and spikelets compared to *japonica* rices. Although increasing panicle size and weight has been a strategy to boost rice yield, it is important to consider the rachis-branching pattern as well, because increased sink size usually accompanies reduction in ripening percentage (Kim et al., 2003b, c; Yamagishi et al., 2003). Moreover, translocation efficiency differs with the spikelet position and rachis-branching architecture of a panicle (Nagata et al., 2002; Terao et al., 2010). It is reported that ripening percentage was higher in the spikelets on PRBs than those on SRBs, and grain weight was heavier in the spikelets on upper rachis-branches than those on lower rachis-branches (Matsue et al., 1994; Park et al., 2010). Kim et al. (2003c) suggested that the ratio of SRBs to PRBs should be 2.0-2.5 to improve both sink size and ripening. Recently, a fine-mapped QTL called *PBN6* was shown to increase the number of PRBs without changing the number of spikelets per panicle and ripening percentage (Ando et al., 2008). Also, a gene called *APO1* was identified in the *PBN6* region, which enhances translocation efficiency and improves ripening (Terao et al., 2010). In addition to yield and grain filling, rachis-branching system also affects eating and cooking characteristics of rice. According to Matsue et al. (1994, 1995), amylose and protein content, amylographic characteristics, and even palatability showed significant difference depending on the position of spikelets in a panicle. In spite of the significant influences on yield and grain quality, few studies have been conducted on the changes in panicle traits of different rice varieties under higher temperatures. In this study, we investigated the variations in rachis-branching pattern and the percentages of ripened grains and head rice in different rice varieties under ambient and high temperature conditions by conducting clustering analysis and principal component analysis. Relationships among the panicle-related traits under both conditions were analyzed as well. In addition, changes in the panicle traits, ripened grains percentage and head rice percentage by elevated temperature were discussed in terms of different ecotypes and their rachis-branching system.

Results

Panicle-related traits under ambient condition

Average ambient temperature during the treatment ranged from 21.9 to 24.4^{o}C, depending on the maturity stgae of different varieties (Table 1). Except for the number of PRBs per panicle, there were significant differences in all the investigated traits between *japonica* and Tongil-type under ambient condition (Table 2). Compared with *japonica*, Tongil-type showed higher numbers of spikelets and rachis-branches per panicle, numbers of SRBs and spikelets on SRBs per panicle, number of spikelets on a SRB, and the ratio of SRBs to PRBs. On the contrary, the number of spikelets on PRBs per panicle, number of spikelets on a PRB, ripened grains percentage (of PRBs, SRBs, and total), and head rice percentage were higher in *japonica* than Tongil-type. This was in consistence with the study of Park et al. (2010) and Taguchi-Shiobara et al. (2011), in which Tongil-type and *indica* varieties showed higher sink size-related traits such as the numbers of SRBs and spikelets on SRBs per panicle compared with *japonica* varieties. On variety level, the numbers of spikelets and rachis-branches per panicle were higher in Nampung (216.7, 58.7), Keunseom (205.5, 54.7), and Dasan1 (205.5, 56.0) and low in Daerip1 (102.0, 26.3), Chucheong (112.7, 29.8), and Daeya (112.8, 27.3) (Supplementary data 1). Ripened grains percentage was the highest in Jinbu, Odae1, and Dongan (97.9, 97.1, and 96.8%), and the lowest in Areum, Yongju, and Anda (86.2, 86.9, and 88.5%), respectively. Head rice percentage was the highest in Manchu, Sura, and Hwanam (96.5, 96.0, and 95.3), and the lowest in Dasan1, Dasan, and Jinbu (62.1, 66.4, and 67.3%), respectively. While considering both ripening and head rice, Dongan and Manchu showed the best characteristics with 96.8 and 96.5% ripened grains and 95.2 and 96.5% head rice, respectively. In the clustering analysis using panicle-related traits in ambient condition, 40 rice varieties were clustered into three main groups (Fig. 1A). Group 1 had 12 Tongil-type varieties, Group 2 had 13 *japonica* and one intermediate Tongil-type (Nongan) varieties, and Group 3 had 14 *japonica* varieties. Also, in the studies of Park et al. (2010, 2011), Nongan was clustered into a different group from other Tongil-type varieties in the clustering analyses of panicle traits. Nongan was derived from *japonica*-Tongil cross and has *japonica*-like panicle characteristics, such as relatively low SRBs to PRBs ratio. In the principal component analysis (PCA) with the 13 panicle-related traits, contributions of the first and second principal components (Prin1 and Prin2) were 55.2 and 19.4%, respectively (Table 3). Major loadings of Prin1 were the number of spikelets per panicle (0.35), the number of rachis-branches per panicle (0.35), the number of SRBs per panicle (0.35), the number of spikelets on SRBs per panicle (0.36), and the ratio of SRBs to PRBs (0.34), while those of Prin2 were the number of PRBs per panicle (0.55) and the number of spikelets on PRBs per panicle (0.58) (Table 3). Results of PCA show that varieties with large sink size such as Nampung, Dasan1, and Keunseom were clustered into Group 1. The varieties having high numbers of PRBs and spikelets on PRBs per panicle, such as Nongan, Manchu, Jangan, and Cheongdam, were clustered into Group 2, and those with small sink size such as Daerip1, Chucheong, Daeya, and Hwaseong were clustered into Group 3 (Fig. 1B). Correlation analysis showed that the number of SRBs and spikelets on SRBs per panicle have highly positive correlations (> 0.95) with the numbers of spikelets and rachis-

Table 1. Accumulated and average temperatures in the field and greenhouse conditions during high temperature treatment.

Group*	Variety**	Accumulated temperature during the treatment^z (°C) (average temperature)		
		Field (a)	Greenhouse (b)	b - a^y
Ⅰ	GO3, JB, MC, OD1, TS	1216.4 (24.4)	1275.8 (25.5)	59.4 (1.1)
Ⅱ	AR, DS, HS, MP, NA, SR, TB, YJ, YM	1546.3 (23.1)	1634.4 (24.4)	88.1 (1.3)
Ⅲ	AD, CD, DP, DR1, DS1, GB, GO1, HA, HJ, HY, KS, NP	1671.3 (22.6)	1773.9 (24.0)	102.6 (1.4)
Ⅳ	CC, DA, DJ, DJ1, DY, HAR, HG, HM, HN, HP, JG, JS, NC, ON	1775.8 (21.9)	1893.7 (23.4)	117.9 (1.5)

*Varieties were divided into four groups according to their maturity. The number of days for high temperature treatment was 49, 66, 73, and 80 for group Ⅰ, Ⅱ, Ⅲ, and Ⅳ, respectively. ** Full names of the cultivars are listed in Supplementary data 1. ^{z} Accumulated temperature is the sum of daily mean temperatures during high temperature treatment. ^{y} b-a indicates the temperature difference between the field and greenhouse conditions.

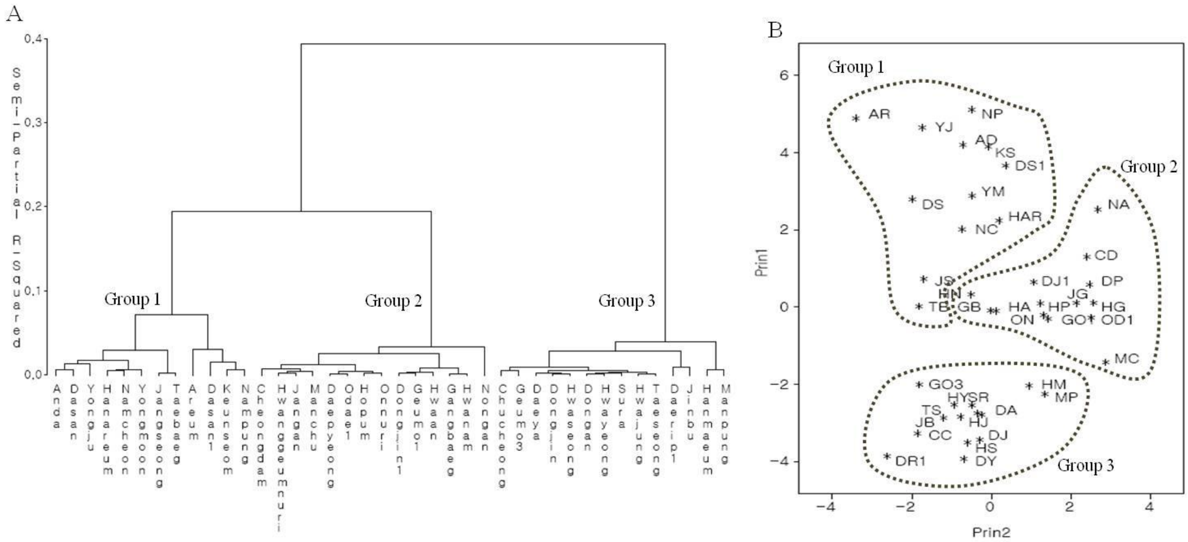

Fig 1. Clustering analysis (A) and principal component analysis (B) of 40 rice varieties based on the 13 panicle-related traits under ambient condition. Prin1 and Prin2 indicate the first and second principal components, respectively, as shown in Table 3. See Supplementary Data 1 for the abbreviations of variety names.

branches per panicle (Table 4). However, the numbers of PRBs and spikelets on PRBs per panicle showed much lower correlations (< 0.62) with the numbers of spikelets and rachis-branches per panicle. Ripened grains percentage was negatively correlated with SRB-related traits; however, PRB-related traits had no significant correlation or weak positive correlation with ripened grains percentage. The SRB-related traits had weak negative correlations with head rice percentage, while PRB-related traits had very weak positive or no significant correlation.

Panicle-related traits under high temperature condition

A greenhouse experiment was set up for the high temperature treatment eight weeks after transplanting. Compared with the ambient condition, accumulated and average temperatures in the greenhouse during the treatment were 59.4-117.9°C and 1.1-1.5°C higher, respectively (Table 1). Except for the number of spikelets on PRBs per panicle, there were significant differences in all the traits between *japonica* and Tongil-type under high temperature (Table 2). Similar to the ambient, Tongil-type showed higher numbers of spikelets and rachis-branches per panicle and SRB-related traits. Although there was no significant difference between *japonica* and Tongil-type in the number of PRBs per panicle under ambient condition, it was significantly higher in Tongil-type under high temperature condition. The number of spikelets on a PRB, ripened grains percentage (of PRBs, SRBs, and total), and head rice percentage were significantly higher in *japonica* than in Tongil-type, which were similar with the results from ambient condition (Table 2). Under high temperature, the numbers of spikelets and rachis-branches, SRBs and spikelets on SRBs per panicle were higher in Dasan1 (257.5, 67.3, 55.0, 195.7), Yongmun (246.7, 60.2, 48.5, 181.7), and Nampung (241.5, 62.3, 51.2, 182.0) and low in Daeya (111.0, 27.0, 17.2, 51.8), Chucheong (112.3, 29.2, 20.7, 62.2), and Daerip1 (114.0, 29.5, 19.8, 56.8) (Supplementary data 2). Ripened grains percentage was maximum in Jinbu, Odae1, and Manchu (98.6, 97.6, and 96.6%) and the lowest in Jangseong, Dasan, and Anda (72.5, 72.7, and 73.7%), respectively. Head rice percentage was the highest in Dongjin, Yongju, and Dongan (87.1, 86.4, and 86.0%) and the lowest in Areum, Taebaeg, and Taeseong (50.2, 61.8, and 62.2%), respectively. As in ambient condition, Manchu also showed high percentages of ripened grains (96.6%) and head rice (85.3%) under high temperature. However, ripened grains percentage of Dongan was decreased to 90.6% under high temperature although its head rice

Table 2. Average and range of the panicle-related traits of 40 rice varieties in ambient and high temperature conditions.

Ecotype (n^*)	NS**	NR	NPr	NSP	NSPr	NSr	NSS	NSSr	S/P	RPP	RPS	RP	HP
Field													
japonica	145.4a^z	37.8a	11.3a	65.0a	5.8a	26.6a	80.4a	3.0a	2.3a	96.5a	94.0a	95.1a	90.5a
(27)	(102-183)	(26-50)	(9-14)	(53-77)	(5.5-6.0)	(17-36)	(49-111)	(2.7-3.3)	(1.6-3.0)	(93.8-98.8)	(87.9-97.4)	(90.6-97.9)	(67.3-96.5)
Tongil	188.8b	48.4b	11.5a	62.1b	5.4b	36.9b	126.7b	3.4b	3.2b	91.7b	90.6b	90.9b	77.9b
(13)	(149-217)	(36-59)	(10-15)	(49-78)	(4.7-5.9)	(25-48)	(87-158)	(3.0-3.8)	(2.3-4.2)	(86.4-96.1)	(84.6-96.1)	(86.2-95.9)	(62.1-90.9)
Total	159.5	41.3	11.3	64.1	5.7	29.9	95.5	3.2	2.6	95.0	92.9	93.8	86.4
(40)	(102-217)	(26-59)	(9-15)	(49-78)	(4.7-6.0)	(17-48)	(49-158)	(2.7-3.8)	(1.6-4.2)	(86.4-98.8)	(84.6-97.4)	(86.2-97.9)	(62.1-96.5)
Greenhouse													
japonica	151.3a	39.4a	11.3a	65.5a	5.8a	28.1a	85.8a	3.0a	2.5a	94.7a	90.6a	92.4a	76.8a
(27)	(111-222)	(27-57)	(9-14)	(50-83)	(5.5-6.1)	(17-44)	(52-146)	(2.7-3.3)	(1.8-3.4)	(88.4-98.3)	(82.8-99.0)	(85.8-98.6)	(62.2-87.1)
Tongil	207.4b	52.6b	11.9b	65.4a	5.5b	40.7b	142.0b	3.5b	3.5b	85.2b	80.0b	81.6b	71.9b
(13)	(154-258)	(37-67)	(10-16)	(46-88)	(4.5-6.1)	(27-55)	(92-196)	(3.0-3.7)	(2.2-4.6)	(71.4-93.5)	(69.7-90.9)	(72.5-91.9)	(50.2-86.4)
Total	169.5	43.7	11.5	65.5	5.7	32.2	104.1	3.2	2.8	91.6	87.2	88.9	75.2
(40)	(111-258)	(27-67)	(9-16)	(46-88)	(4.5-6.1)	(17-55)	(52-196)	(2.7-3.7)	(1.8-4.6)	(71.4-98.3)	(69.7-99.0)	(72.5-98.6)	(50.2-87.1)

[*] The numbers of varieties belonging to each ecotype are shown in parentheses. [**] See the Abbreviations. [z] Values with a different letter are significantly different at $P < 0.05$.

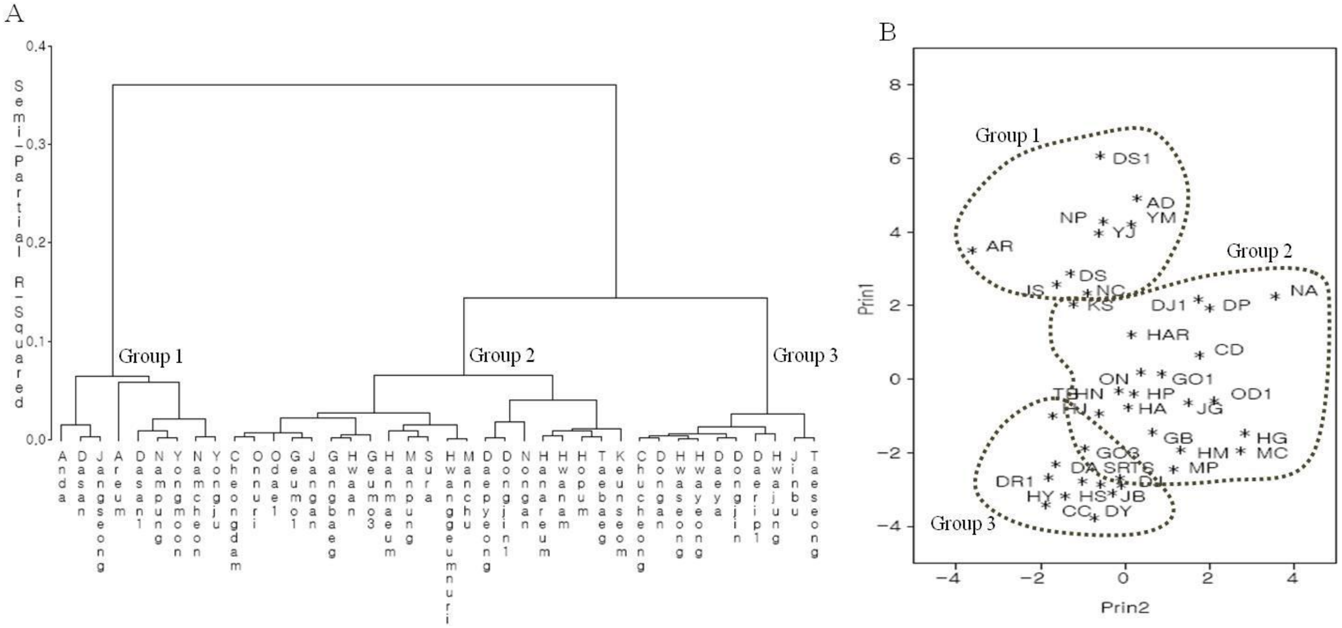

Fig 2. Clustering analysis (A) and principal component analysis (B) of 40 rice varieties based on the 13 panicle-related traits under high temperature condition. Prin1 and Prin2 indicate the first and second principal components, respectively, as shown in Table 3. See Supplementary Data 1 for the abbreviations of variety names.

percentage was still one of the highest (Supplementary data 1 and 2). In the clustering analysis shown in Fig. 2A, three main groups were distinguished under high temperature as well. Although all varieties in Group 1 were Tongil-types as in ambient condition, Hanareum, Taebaeg, and Keunseom (belonged to Group 1 in the ambient) were clustered into Group 2 under high temperature (Fig. 1A and 2A). Compared with other Tongil-type varieties, increases in the numbers of spikelets and rachis-branches per panicle were relatively low (or even decreased) by the elevated temperature in these three varieties (Supplementary data 1 and 2). All 14 varieties belonged to Group 2 in ambient condition were clustered into the same group under high temperature as well. However, Geumo3, Hanmaeum, Manpung, and Sura (clustered into Group 3 in the ambient) were clustered into Group 2 when temperature rose (Fig. 1A and 2A). These four varieties showed relatively high numbers of rachis-branches and PRBs per panicle compared to the varieties remaining in Group 3 under elevated temperature (Supplementary Data 2). In the principal component analysis, factor loadings for Prin1 and Prin2 were very similar to those in ambient condition. For example, the number of spikelets per panicle (0.35), the number of rachis-branches per panicle (0.35), the number of SRBs per panicle (0.35), the number of spikelets on SRBs per panicle (0.36), and the ratio of SRBs to PRBs (0.32) for Prin1, and the number of PRBs per panicle (0.57) and the number of spikelets on PRBs per panicle (0.61) for Prin2 were similar in both conditions, respectively (Fig. 2B, Table 3). Contributions of Prin1 and Prin2 were 55.1 and 17.3%, respectively. Similar to the ambient, the numbers of SRBs and spikelets on SRBs per panicle showed highly positive correlations (> 0.96) with the numbers of spikelets and rachis-branches per panicle and negative correlations with the percentages of ripened grains and head rice (Table 4). However, the numbers of PRBs and spikelets on PRBs per panicle had lower correlations (< 0.58) with the numbers of spikelets and rachis-branches per panicle and no or positive correlations with the percentages of ripened grains and head rice.

Discussion

Except for the number of PRBs per panicle and the number of spikelets on a SRB, all panicle-related traits showed significant increase by temperature elevation (Table 5). On the other hand, the percentages of ripened grains and head rice were significantly reduced when temperature rose. Compared with the grains on PRBs, those on SRBs showed more decrease in ripened grains percentage by high temperature. Kim et al. (2003b) and Oh et al. (2005) suggested that sink capacity should be improved by increasing the numbers of PRBs and spikelets on PRBs per panicle instead of SRBs because the numbers of SRBs and spikelets on SRBs per panicle have highly negative correlations (< -0.8) with the percentage of ripened grains. This matter was also confirmed in this study under both ambient and high temperature conditions (Table 4). Since percentage of ripened grains decreased more in SRBs than PRBs under high temperature (Table 5), it would be desirable to breed varieties with increased number of PRBs and decreased number of SRBs for better ripening under rising temperature caused by global warming. On ecotype level, the numbers of spikelets, rachis-branches, SRBs and spikelets on SRBs per panicle were significantly increased in Tongil-type under high temperature while those in *japonica* did not show any significant change (Table 5). However, the percentages of ripened grains and head rice were significantly decreased under high temperature in both ecotypes. Notably, decrease in ripened grains percentage by elevated temperature was higher in Tongil-type than *japonica*. The sink size of Tongil-type was increased under high temperature more than *japonica* due to the significant increase in the numbers of SRBs and spikelets on SRBs per panicle, which caused more severe reduction in ripened grains percentage. According to Nagata et al. (2002), an *indica* allele (QTL) of a major sink size increased the number of spikelets per panicle mainly by increasing the number of SRBs, which subsequently reduced ripened grains percentage. Further study is needed to investigate if Tongil-type varieties used in this study inherited *indica* alleles associated with increased SRBs and sink size, which possibly cause more severe deterioration in ripening under high temperature condition compared to *japonica*. Unlike percentage of ripened grains, decrease in head rice percentage was higher in *japonica* than in Tongil-type under elevated temperature, which was mainly due to the sharp rise in the occurrence of chalkiness (Table 5, Fig. 3), rather than broken milled rice. In *japonica*, the percentage of chalky grains was markedly increased by 427% under high temperature, whereas increased by only 94% in Tongil-type. When temperature rises during grain filling, activity of starch-synthesizing enzymes slows down and the structure of starch granules becomes loosely-packed, which causes rice grains look milky and opaque (Chun, 2009; Kobayashi et al., 2007; Tabata et al., 2007; Yamakawa et al., 2007). It would be interesting to study if the expression of starch synthesis-related genes (SSRGs) decreases more in *japonica* than in Tongil-type by high temperature, which might cause more reduction in head rice percentage in *japonica*. Zhou et al. (2003) showed that an *indica* allele of Granule-Bound Starch Synthase I gene (*GBSSI*) could reduce the chalkiness level. Thus, identifying useful SSRG alleles in *indica* germplasms and transferring them to *japonica* would be also helpful for developing *japonica* varieties with good grain appearance under high temperature.

Materials and methods

Plant materials

A total of 40 Korean rice varieties including 27 *japonica* and 13 Tongil-types were used in this study (Supplementary data 1). The seeds were sown on April 30th of 2009 at the Rice Experimental Station of the Department of Rice and Winter Cereal Crop, National Institute of Crop Science, Iksan, Korea. On May 29th, the seedlings were transplanted into the field in two separate plots with the planting density of 30 × 15 cm, one plant per hill. For each cultivar, 25 plants were transplanted in a row in both plots. Fertilization of N-P_2O_5-K_2O was 90-45-57 kg ha^{-1} and the split ratio of basal : tillering : panicle initiation was 50 : 20 : 30% for N, 100% basal for P_2O_5, basal : panicle initiation as 70 : 30 for K_2O. Eight weeks after transplanting (July 24th), a greenhouse was set up for high temperature treatment and the plants were grown in the greenhouse until harvest. Overheating was avoided by using side wall windows and ventilating fans with temperature sensor installed in the greenhouse. Average temperature difference between the field and greenhouse was maintained as 1.1-1.5 ºC (Table 1).

Panicle-related traits

Upon maturity, six plants with relatively even growth were selected and harvested for each variety and treatment. Panicles from the longest culms in each harvested plant were sampled to investigate panicle-related traits. The numbers of primary and secondary rachis-branches (PRBs and SRBs) and the numbers

Table 3. Eigenvectors for the principal components from the 13 panicle-related traits of 40 rice varieties in ambient and high temperature conditions.

Trait	Eigenvector					
	Field			Greenhouse		
	Prin1[*]	Prin2	Prin3	Prin1	Prin2	Prin3
NS[**]	**0.35**[z]	0.20	0.06	**0.35**	0.19	0.07
NR	**0.35**	0.20	0.12	**0.35**	0.15	0.17
NPr	0.15	**0.55**	-0.12	0.16	**0.57**	-0.09
NSP	0.03	**0.58**	-0.28	0.08	**0.61**	-0.25
NSPr	-0.27	0.10	-0.34	-0.21	0.16	-0.46
NSr	**0.35**	0.13	0.14	**0.35**	0.07	0.20
NSS	**0.36**	0.07	0.13	**0.36**	0.05	0.14
NSSr	0.24	-0.12	0.05	0.28	-0.04	-0.10
S/P	**0.34**	-0.09	0.19	**0.32**	-0.18	0.27
RPP	-0.26	0.23	0.34	-0.25	0.30	0.42
RPS	-0.24	0.20	0.53	-0.29	0.16	0.43
RP	-0.28	0.25	0.47	-0.29	0.22	0.41
HP	-0.16	0.27	-0.28	-0.10	0.12	-0.14
Eigenvalue	7.18	2.52	1.18	7.17	2.25	1.60
Contributaion (%)	55.2	19.4	9.1	55.1	17.3	12.3
Cumulative contribution (%)	55.2	74.6	84.7	55.1	72.5	84.8

[*] Prin1, Prin2, and Prin3 represent the first, second, and third principal components, respectively.

[**] See the Abbreviations. [z] Eigenvectors with relatively high factor loading (>0.30) are emphasized with bold letters.

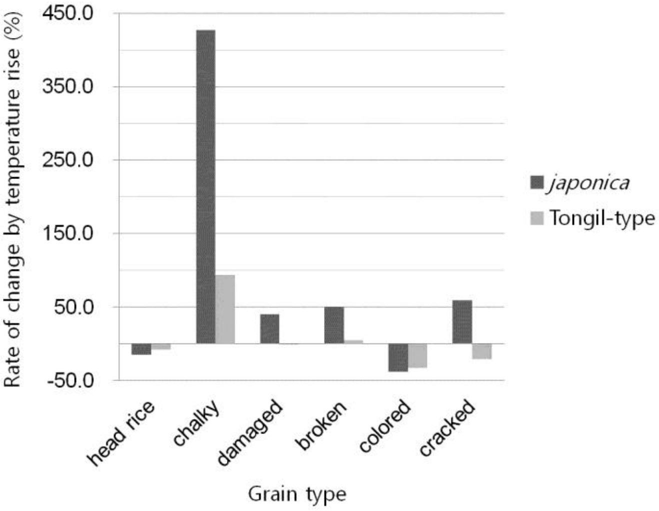

Fig 3. Rate of change in milled rice grain types of *japonica* and Tongil by high temperature.

of spikelets on PRBs and SRBs were counted in all the sampled panicles and averaged to represent a variety in each treatment. Also, the numbers of filled and unfilled/immature spikelets on PRBs and SRBs were counted to measure ripened grains percentages of PRBs and SRBs per panicle. The rest of the panicles from the harvested plants were hand-threshed, dehulled with SY88-TH (Ssangyong Co., Korea), and milled with VP-32T (Yamamoto Co., Japan). Grain appearance of milled rice including the percentages of head, chalky, damaged, broken, colored, and cracked rice was examined with RN-300 (Kett Co., Japan).

Statistical analysis

All statistical analyses were conducted using SAS software version 9.1 (SAS Institute, NC, USA). Differences in the investigated traits according to temperatures, ecotypes, and varieties were calculated by the least significant difference (LSD) test. Clustering analysis was performed with Ward's method after standardizing all data (Ward, 1963). For principal component analysis (PCA), correlation matrix from the 13 panicle-related traits were used to calculate eigenvectors.

Table 4. Correlation coefficients among the panicle-related traits in ambient and high temperature conditions.

	NR^{z}	NPr	NSP	NSPr	NSr	NSS	NSSr	S/P	RPP	RPS	RP	HP
NS	0.97** (0.97**)^{y}	0.61** (0.57**)	0.42** (0.45**)	-0.36** (-0.28**)	0.96** (0.96**)	0.97** (0.97**)	0.58** (0.69**)	0.80** (0.76**)	-0.30** (-0.29**)	-0.30** (-0.44**)	-0.38** (-0.44**)	-0.21 (-0.14)
NR		0.59** (0.54**)	0.37** (0.37**)	-0.46** (-0.42**)	0.99** (0.99**)	0.95** (0.96**)	0.42** (0.55**)	0.85** (0.82**)	-0.27** (-0.28**)	-0.32** (-0.41**)	-0.38** (-0.42**)	-0.20 (-0.18)
NPr			0.90** (0.93**)	-0.13* (-0.11)	0.47** (0.41**)	0.42** (0.37**)	0.08 (0.14*)	0.09 (-0.03)	-0.03 (0.02)	-0.02 (-0.12)	-0.02 (-0.07)	0.10 (-0.04)
NSP				0.31** (0.27**)	0.25** (0.24**)	0.20** (0.22**)	-0.05 (0.08)	-0.13* (-0.19**)	0.07 (0.07)	0.05 (-0.04)	0.09 (0.01)	0.26* (0.07)
NSPr					-0.48** (-0.43**)	-0.48** (-0.38**)	-0.25** (-0.11)	-0.51** (-0.46**)	0.21** (0.16*)	0.17** (0.18**)	0.26** (0.20**)	0.34** (0.30**)
NSr						0.97** (0.98**)	0.44** (0.57**)	0.91** (0.89**)	-0.29** (-0.30**)	-0.34** (-0.42**)	-0.41** (-0.44**)	-0.23* (-0.19)
NSS							0.64** (0.72**)	0.90** (0.88**)	-0.34** (-0.33**)	-0.34** (-0.46**)	-0.44** (-0.49**)	-0.30** (-0.17)
NSSr								0.46** (0.55**)	-0.33** (-0.35**)	-0.19** (-0.45**)	-0.32** (-0.48**)	-0.36** (-0.10)
S/P									-0.32** (-0.35**)	-0.40** (-0.41**)	-0.48** (-0.46**)	-0.29** (-0.18)
RPP										0.37** (0.72**)	0.74** (0.88**)	0.20 (0.13)
RPS											0.89** (0.96**)	0.15 (0.14)
RP												0.21 (0.16)

* and ** indicate significance at $P < 0.05$ and $P < 0.01$, respectively. ^{z} See the Abbreviations. ^{y} Values in parentheses indicate the correlation coefficients under high temperature, while the other are from the ambient.

Table 5. Relative ratio (%) of the panicle-related traits of 40 rice varieties in high temperature condition to those in ambient condition.

Ecotype (n^{y})	NS^{z}	NR	NPr	NSP	NSPr	NSr	NSS
Japonica (27)	104.0	104.1	100.3	100.7	100.5	105.7	106.7
Tongil (13)	109.9**	108.8*	103.6	105.4	101.5	110.4*	112.1**
Total (40)	106.3**	105.9**	101.4	102.2**	100.8*	107.6**	109**
Ecotype	NSSr	S/P	RPP	RPS	RP	HP	
japonica	100.7	105.9	98.1**	96.4**	97.1**	84.9**	
Tongil	100.8	107.7	92.9**	88.3**	89.8**	92.3*	
Total	100.7	106.6**	96.4**	93.9**	94.8**	87.1**	

* and ** indicate significant difference between the ambient and high temperature conditions at $P < 0.05$ and $P < 0.01$, respectively. ^{z} See the Abbreviations.^{y} The numbers of varieties belonging to each ecotype are shown in parentheses.

Conclusion

Both in ambient and high temperature conditions, ripened grains percentages were higher in spikelets on primary-rachis branches (PRBs) than those on secondary-rachis branches (SRBs). Moreover, spikelets on PRBs maintained better ripening under high temperature compared to those on SRBs. Therefore, decreasing the ratio of SRBs to PRBs would be an effective rice breeding strategy to avert negative impact of global warming on grain filling. Changes in the percentages of ripened grains and head rice under high temperature were different among ecotypes as well. The ripened grains percentage reduced more in Tongil-type whereas head rice percentage decreased more in *japonica* in higher temperatures. It would be desirable to combine beneficial characteristics from each ecotype to improve ripening and grain appearance under increasing temperature by climate change.

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