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Analysis of yield-attributing traits for high-yielding wheat lines in southwestern Japan

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ABSTRACT

Development of wheat cultivars that achieve high yields despite the short growing season is essential for increasing wheat production in southwestern Japan. The objectives of this study were to assess the genetic progress in grain yield and to clarify yield-attributing traits of high-yielding wheat lines in southwestern Japan. We conducted field experiments for two growing seasons (2012–2013 and 2013–2014) using three commercial wheat cultivars (Shiroganekomugi, Chikugoizumi, and Iwainodaichi) and four high-yielding wheat lines including Hakei W1380 developed in southwestern Japan. In an ancillary field experiment, we compared a commercial cultivar, Shiroganekomugi, and a high-yielding line, Hakei W1380, in the 2014–2015 season. Across the two seasons, grain yield of high-yielding lines was generally higher than commercial cultivars. Hakei W1380 achieved the highest grain yield across the two seasons, and successfully produced more than 900 g m⁻² in the 2013–2014 season. Correlation analysis showed that recent yield progress of wheat lines in southwestern Japan was derived from enhanced biomass production and grain number m⁻². Larger numbers of grains m⁻² in high-yielding lines than in commercial cultivars were associated with higher crop growth rate at the pre-anthesis stage, and therefore higher spike dry weight m⁻² at anthesis. Genotypic differences in crop growth rate from jointing to anthesis resulted mainly from differences in leaf area index. These results indicate that further improvements in grain yield in southwestern Japan could be achieved by increasing the amount of radiation intercepted at the pre-anthesis stage and grain number m⁻².

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Introduction

The self-sufficiency rate of wheat (*Triticum aestivum* L.) in Japan amounted to only 12% in 2013 (MAFF, 2015). As recent breeding programs have shifted emphasis from yield to quality, wheat productivity remained stagnant in Japan: grain yield increased from 2.3 t ha⁻¹ in 1961–1965 to 3.6 t ha⁻¹ in 2008–2012 (FAOSTAT, 2015). Similarly, grain yield increased from 1.9 t ha⁻¹ in 1961–1965 to 3.3 t ha⁻¹ in 2008–2012 in Kyushu, Japan (MAFF, 2015). Kyushu, in the southwestern part of the country, is the second largest wheat-producing area and contributes to 14% of the total wheat production (in 2014; MAFF, 2015) in Japan. In this area, wheat is usually grown in lowland rice–wheat double-cropping systems. After sowing from mid-November to early December, wheat growth slows considerably for 2–3 months during the winter. However, crops must be harvested before the transplanting of rice seedlings and the start of rainy season (early June). Because of the unique characteristics of climate and cropping systems in southwestern Japan, growth duration of wheat is short,

and late-maturing cultivars with high yield potential cannot be grown. Therefore, to increase wheat production in southwestern Japan, it is essential to develop high-yielding cultivars despite the short growing season.

In many regions of the world, wheat productivity has dramatically increased because of the introduction of the semi-dwarf allele and the increase in nitrogen fertilizer, beginning with the Green Revolution (Fischer & Edmeades, 2010). For example, grain yield increased from 4.0 t ha⁻¹ in 1961–1965 to 7.7 t ha⁻¹ in 2008–2012 in the UK, and from 3.1 t ha⁻¹ in 1961–1965 to 8.0 t ha⁻¹ in 2008–2012 in New Zealand (FAOSTAT, 2015). Even in Japan, grain yield increased from 2.0 t ha⁻¹ in 1961–1965 to 4.0 t ha⁻¹ in 2008–2012 in the largest wheat-producing area, Hokkaido (northern Japan; MAFF, 2015). Physio-morphological changes associated with yield progress have been studied intensively using sets of historic cultivars. Most of the studies showed that yield progress depended on harvest index (HI: biomass partitioning to reproductive organs) without major changes in aboveground biomass (Acreche et al., 2008; Austin et al., 1989, 1980; Brancourt-Hulmel et al.,

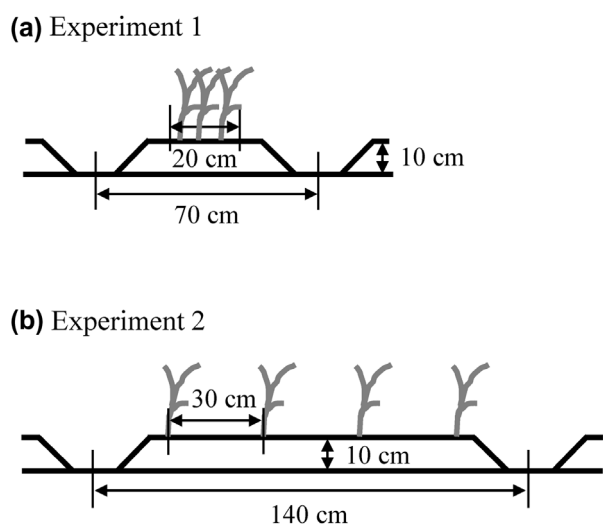


Figure 1. Diagrams of planting systems in (a) Experiment 1 and (b) Experiment 2.

2003; Siddique et al., 1989; Yanagisawa et al., 2007a; Zheng et al., 2011; Zhou et al., 2007). Only a few studies reported that yield progress was associated with an increase in biomass as well as an increase in HI (Beche et al., 2014; Donmez et al., 2001; Shearman et al., 2005). Among yield components, grain number m^{-2} was the major determinant of grain yield (Abbate et al., 1998; Acreche et al., 2008; Austin et al., 1989; Beche et al., 2014; Donmez et al., 2001; Shearman et al., 2005) with a few exceptions (Aisawi et al., 2015; Zheng et al., 2011). Accordingly, compared to older genotypes, newer genotypes could be generally characterized by better biomass partitioning and larger sink size in response to either higher pre-anthesis growth (Shearman et al., 2005) or post-anthesis growth (Calderini et al., 1997).

Only a few studies have reported the yield-attributing traits in southwestern Japan: grain yield was closely associated with aboveground biomass in previous studies conducted from the 1970s to the 1980s (Fujita & Ujihara, 1993; Taya, 1993). Fujita and Ujihara (1993) indicated the importance of post-anthesis growth with enhanced photosynthetic ability for high yield. However, the high-yielding cultivars used in previous studies (Fujita & Ujihara, 1993; Taya, 1993) are currently grown as commercial cultivars (i.e. check cultivars) or have been replaced by other cultivars. In addition, genetic diversity of commercial cultivars has been limited in southwestern Japan because cultivars from northern Japan and foreign countries have not been used often in breeding programs. These cultivars had undesirable characteristics, including late maturation, weak tolerance to *Fusarium* head blight, and pre-harvest sprouting when they were grown in southwestern Japan. Nevertheless, recent intensive breeding has developed some promising lines that are derived from high-yielding cultivars including cultivars from northern Japan and

foreign countries. Consequently, current yield-attributing traits might be different from those in previous studies (Fujita & Ujihara, 1993; Taya, 1993).

The present study aimed to assess the genetic progress in grain yield and to clarify yield-attributing traits by comparing commercial cultivars and high-yielding lines developed in southwestern Japan. The results can aid in the development of future breeding strategies to improve yield potential of wheat cultivars in southwestern Japan.

1. Materials and methods

1.1. Experiment 1

Field experiments were conducted at Kyushu Okinawa Agricultural Research Center of National Agriculture and Food Research Organization (NARO; 33°12'N, 130°30'E), Chikugo, Fukuoka, Japan in the 2012–2013 and 2013–2014 crop seasons. The soil at the experimental site is Typic Endoaquept. The mean temperatures from November to May were 10.6 °C in 2012–2013 and 11.0 °C in 2013–2014 season.

We grew seven genotypes (three commercial cultivars and four high-yielding lines) in drained lowland fields in both seasons. Shiroganekomugi and Chikugoizumi are spring-type soft wheat cultivars released in 1974 and 1994, respectively. Chikugoizumi is a high-yielding cultivar compared to Shiroganekomugi. Iwainodaichi is a high-yielding winter-type soft wheat cultivar released in 2000. Saikai 190 (Chikugoizumi // Hakei 94-4), Hakei W1380 (Saikai 189 // Kitami 81 / Iwainodaichi), Hakei W1395 (Saikai 188 / Jiang Yang // Saikai 188), and Hakei W1415 (Saikai 189 // Kitami 81 / Iwainodaichi) are high-yielding lines derived from high-yielding cultivars such as Chikugoizumi, Iwainodaichi, Kitahonami (formerly Kitami 81; a high-yielding winter type soft wheat cultivar developed in northern Japan), and Jiang Yang (a soft wheat cultivar with large spikes developed in China). We selected these lines because of their yielding performance based on past data taken at NARO Kyushu Okinawa Agricultural Research Center, Japan, where all the genotypes were developed.

The genotypes were arranged in a randomized complete block design with three replicates. Each plot was a 5.0 m row and a 12.0 m row in 2012–2013 and in 2013–2014, respectively. Row spacing was 0.7 m and seeding rate was 5.0 $g m^{-2}$ in both seasons (Figure 1(a)). The sowing date was November 21 in both seasons. We applied an inorganic fertilizer (N, P_2O_5 , and $K_2O = 60, 51$, and 51 $kg ha^{-1}$, respectively) before sowing, and top-dressed ammonium sulfate (N = 30 $kg ha^{-1}$) on 8 February and 7 March 2013 and 5 February and 7 March 2014 (total N = 120 $kg ha^{-1}$). Weeds were controlled by means of herbicide application.

One 0.5-m row (0.35 m²) was harvested from each plot for all genotypes except Hakei W1395 at anthesis in 2012–2013 and for all genotypes at 110 days after sowing and anthesis in 2013–2014. In the 2013–2014 season, 110 days after sowing corresponded to jointing stage. After counting the number of stems and separating all spikes from the culm, samples were oven-dried at 80 °C for at least 72 h to determine dry weights. After the end of stem elongation, culm length was measured from the ground to the neck of the spike.

At physiological maturity, two 0.5-m rows (0.7 m²) of each plot were harvested in both seasons. All spikes were counted and separated from the culm and 60 spikes were randomly selected as a subsample; the others were used as a bulk sample. After threshing and sieving with a 2.0-mm sieve, the number of grains in the subsamples was determined. Grains thicker than 2.0 mm were regarded as plump grains. Both subsamples and bulk samples were oven-dried at 80 °C for at least 72 h to determine dry weights. Grain yield and grain weight were then calculated and expressed at 12.5% moisture content. HI and plump-grain percentage were calculated by dividing grain yield (at 0% moisture content) by aboveground biomass and dividing grain yield (at 0% moisture content) by dry weight of all the grains, respectively.

Fruiting efficiency (Acreche et al., 2008) and dry matter partitioning to spike during pre-anthesis stage (Slafer et al., 1990) were calculated as follows:

$$\text{Fruiting efficiency} = \frac{(\text{number of grains m}^{-2})}{(\text{spike dry weight m}^{-2} \text{ at anthesis})} \quad (1)$$

Dry matter partitioning to spike

$$= \frac{(\text{spike dry weight m}^{-2} \text{ at anthesis})}{(\text{aboveground dry weight m}^{-2} \text{ at anthesis} - \text{aboveground dry weight m}^{-2} \text{ at jointing stage})} \quad (2)$$

1.2. Experiment 2

Field experiments again were conducted at NARO Kyushu Okinawa Agricultural Research Center in the 2014–2015 crop season, as described for Experiment 1. The mean temperature from November to May was 11.3 °C.

We grew two genotypes, a commercial cultivar Shiroganekomugi (a lowest yielding genotype in Experiment 1) and a high-yielding line Hakei W1380 (a highest yielding genotype in Experiment 1), in a drained lowland field. The genotypes were arranged in a randomized complete block design with three replicates. Each plot was 1.4 m wide by 4.5 m long, with one ridge containing four rows (Figure 1(b)). Seeds were drill-sown at 170 seeds m⁻² on 19 November 2014. We applied an inorganic fertilizer (N, P₂O₅, and K₂O = 60, 51, and 51 kg ha⁻¹, respectively) before sowing, and top-dressed ammonium sulfate (N = 30 kg ha⁻¹) on 4 February and 12 March 2015 (total

N = 120 kg ha⁻¹). Weeds were controlled with herbicide application.

After counting the number of stems, we harvested two 0.3–0.5-m rows (0.21–0.35 m²) from each plot at 112 days after sowing, which corresponded to jointing stage, and at anthesis. Fifteen to thirty stems were randomly selected as a subsample; the others were used as a bulk sample. Subsamples were separated into green leaf blades, dead leaf blades, leaf sheaths + culms (if any), and panicles (if any). All spikes of bulk samples were also separated from the culm at anthesis. Green leaf area in the subsamples was determined using a portable area meter (LI-3000A, LI-COR, Lincoln, NE, USA) equipped with a transparent belt conveyer (LI-3050A, LI-COR, Lincoln, NE, USA). Samples were oven-dried at 80 °C for at least 72 h to determine dry weights. Leaf area index (LAI), crop growth rate (CGR), and net assimilation rate (NAR) were then calculated. Leaf weight ratio (LW ratio, g g⁻¹) was calculated by dividing the leaf blade dry matter by aboveground dry matter, and specific leaf area (SLA, cm² g⁻¹) was calculated by dividing leaf blade area by leaf blade dry matter.

At physiological maturity, four 0.5-m rows (0.7 m²) of each plot were harvested. All spikes were counted and separated from the culm. Sixty spikes were randomly selected as a subsample; the others were used as a bulk sample. Grain yield, yield components, fruiting efficiency, and dry matter partitioning to spike were measured as mentioned above.

Non-destructive measurements of tagged area in each plot were also conducted during the growth period. The number of fully expanded leaves was counted periodically.

The duration of spike growth was calculated as the interval from penultimate leaf emergence to anthesis (Fischer, 2011). At anthesis, the length and maximum width of upper three leaf blades on 10 superior tillers were measured with a ruler. Individual leaf area was estimated as length × maximum width × 0.695 (Rodríguez et al., 1998). Leaf N status was monitored by measuring soil plant analysis development (SPAD) values in the uppermost fully expanded leaf on 8–10 superior tillers with a SPAD-502 chlorophyll meter (Konica Minolta Inc., Tokyo, Japan).

1.3. Data analysis

Data from all trials were subjected to analysis of variance (SAS Institute, 2003) using the SAS Add-In for Microsoft Office of AFFRIT, MAFF, Japan. Fisher's least significant difference (LSD) test was used for *post hoc* comparisons of treatment means.

Table 1. Grain yield and agronomic traits of seven genotypes in the 2012–2013 and 2013–2014 growing seasons (Experiment 1).

Genotype	Grain yield (g m ⁻²)	Aboveground biomass (g m ⁻²)	Harvest index	Number of grains (×10 ³ m ⁻²)	Number of spikes (m ⁻²)	Grains per spike (spike ⁻¹)	Grain weight (mg)	Plump-grain percentage (%)	Culm length (cm)	Heading (DAS)	Anthesis (DAS)	Maturity (DAS)
Shiroganekomugi	603	1,140	0.460	17.2	508	35	35.2	99.2	72.5	135	146	186
Chikugoizumi	689	1,282	0.469	17.1	466	37	40.2	99.6	79.9	133	145	186
Iwainodaichi	733	1,377	0.465	18.4	593	32	40.0	99.9	79.4	133	146	186
Saikai 190	736	1,333	0.481	20.5	610	35	36.1	99.3	76.6	132	145	186
Hakei W1380	782	1,453	0.471	21.4	547	40	36.8	99.6	79.0	139	149	188
Hakei W1395	760	1,364	0.488	21.6	538	41	35.9	99.0	78.5	136	147	189
Hakei W1415	719	1,339	0.468	19.4	526	38	36.9	99.8	77.7	135	145	186
Season												
2012–2013	596	1,108	0.469	17.1	429	40	35.5	99.2	73.1	134	145	185
2013–2014	839	1,546	0.475	21.7	654	33	39.1	99.7	82.2	135	147	188
LSD(5%)												
Genotype	83	134	0.010	1.9	46	2	0.9	0.6	2.1			
Season	23	39	0.004	0.9	29	2	0.9	0.2	1.6			
Genotype × Season	NS	189	0.014	NS	NS	NS	1.3	NS	3.0			

Notes: Grain yield and grain weight were expressed at 12.5% moisture content. DAS, days after sowing; NS, not significant; and NA, not available.

Table 2. Phenotypic correlations among yield traits of seven genotypes in the 2012–2013 season ($n = 7$, above the diagonal) and the 2013–2014 season ($n = 7$, below the diagonal) (Experiment 1).

	Grain yield	Aboveground biomass	Harvest index	Grain number per unit area	Spike number	Grain number per spike	Grain weight	Plump–grain percentage
Grain yield		0.98***	0.65	0.90**	0.73	0.29	0.50	0.40
Aboveground biomass	0.98***		0.49	0.81*	0.79*	0.12	0.61	0.51
Harvest index	0.28	0.07		0.83*	0.19	0.80*	−0.08	−0.15
Grain number per unit area	0.82*	0.77*	0.38		0.65	0.49	0.07	0.04
Spike number	0.34	0.24	0.52	0.49		−0.35	0.35	0.16
Grain number per spike	0.58	0.61	−0.04	0.62	−0.38		−0.26	−0.10
Grain weight	−0.12	−0.07	−0.27	−0.66	−0.45	−0.28		0.76*
Plump–grain percentage	−0.20	−0.12	−0.42	−0.50	0.05	−0.58	0.51	

Significant correlations are denoted by * $p < .05$, ** $p < .01$, and *** $p < .001$.

2. Results

2.1. Experiment 1

Grain yield was significantly higher in 2013–2014 than in 2012–2013 (Table 1). However, genotypic difference in grain yield was consistent in both seasons: grain yields of advanced lines were generally higher than those of commercial cultivars. Average grain yield in two seasons was lowest in the commercial cultivar Shiroganekomugi followed by Chikugoizumi. Grain yield of Hakei W1380 was the highest among seven genotypes and significantly higher than that of commercial cultivars Shiroganekomugi and Chikugoizumi by 30 and 14%, respectively. Grain yields of other lines (i.e. Saikai 190, Hakei W1395, and Hakei W1415) were significantly higher than that of Shiroganekomugi by 19–26%. High-yielding lines generally exhibited higher biomass production, higher HI, and larger number of grains m^{-2} compared with commercial cultivars. Highest HI, largest number of grains m^{-2} , and largest number of grains $spike^{-1}$ were achieved in Hakei W1395. However, genotypic differences in HI were relatively small; coefficient of variation, cv was 2.3% in HI

while it was 10.6% in grain yield. Consequently, grain yield was significantly correlated with aboveground biomass at maturity and grain number per unit area in both seasons (Table 2).

Culm length was significantly longer in the 2013–2014 season than in the 2012–2013 season (Table 1). Among seven genotypes, Shiroganekomugi had the shortest culm length in both seasons. On the other hand, Iwainodaichi and Chikugoizumi had longer one. All genotypes had similar growth periods; growth duration from sowing to maturity among genotypes was 186–189. Durations from heading to anthesis and from anthesis to maturity were 10–13 and 40–42, respectively.

Compared to commercial cultivars, high-yielding lines tended to have higher CGRs throughout the growth period, although genotypic differences were not significant in the 2013–2014 season (Table 3). Correlation analysis indicated that genotypic differences in CGR at pre-anthesis stage (especially the period from jointing to anthesis) were closely associated with grain yield and aboveground biomass at maturity (Table 3). Although not significant in the 2013–2014 season, CGR at post-anthesis stage was also

Table 3. Crop growth rate (CGR; $g m^{-2} d^{-1}$) at each phenological stage and its phenotypic correlations with grain yield and aboveground biomass at maturity for 6–7 genotypes in the 2012–2013 and 2013–2014 growing seasons (Experiment 1).

	2012–2013		2013–2014	
	Sowing – Anthesis	Anthesis – Maturity	Sowing – Anthesis	Anthesis – Maturity
Shiroganekomugi	3.3	10.6	5.5 (16.6)	13.8
Chikugoizumi	3.8	11.7	5.9 (18.7)	16.7
Iwainodaichi	4.5	16.6	5.2 (16.7)	16.5
Saikai 190	4.1	12.3	5.9 (19.1)	16.9
Hakei W1380	4.3	14.5	6.9 (21.1)	16.8
Hakei W1395	NA	NA	5.4 (17.2)	17.2
Hakei W1415	3.7	12.8	5.7 (17.6)	19.4
Mean	3.9	13.1	5.8 (18.1)	16.8
LSD(5%)	0.5	3.7	NS (NS)	NS
Phenotypic correlation ($n=6-7$)				
Grain yield	0.98***	0.95**	0.68NS (0.78*)	0.73NS
Aboveground biomass	0.96**	0.98***	0.76* (0.82*)	0.71NS

Notes. Values shown in parenthesis are CGRs from 110 days after sowing to anthesis stage in 2013–2014 season. Significant correlations are denoted by * $p < .05$, ** $p < .01$, and *** $p < .001$. NS, not significant; NA, not available.

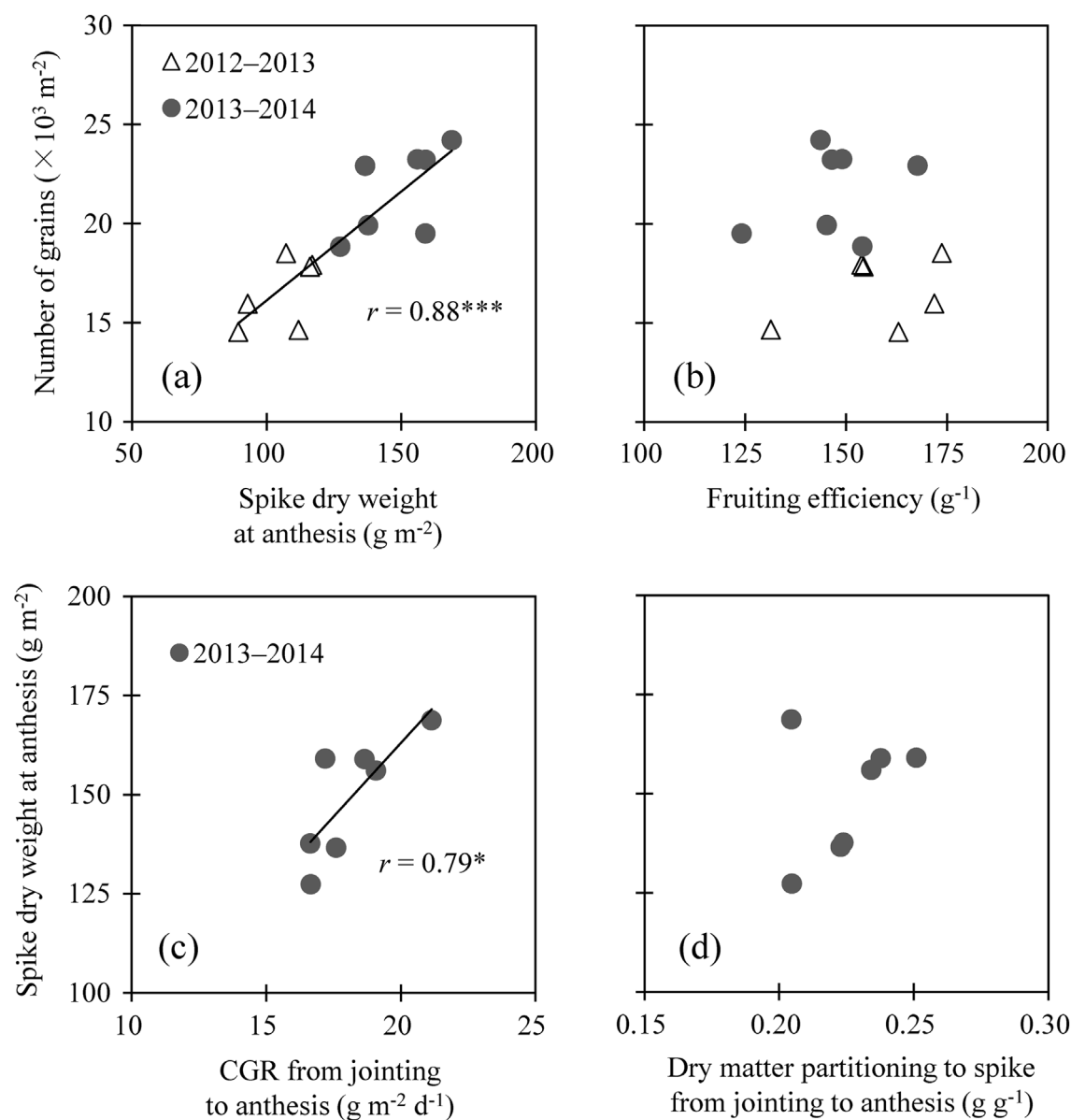


Figure 2. Relationships between (a) spike dry weight at anthesis and grain number, (b) fruiting efficiency and grain number, (c) CGR from jointing to anthesis and spike dry weight at anthesis, and (d) dry matter partitioning to spike from jointing to anthesis and spike dry weight at anthesis (Experiment 1). Fruiting efficiency was calculated by dividing the number of grains m^{-2} by spike dry weight m^{-2} at anthesis. Significant regression is denoted by $*p < .05$ and $***p < .001$ ($n = 13$ in Figure 2(a and b) and $n = 7$ in Figure 2(c and d)).

positively correlated with grain yield and aboveground biomass at maturity.

Although not significant in each season ($r = 0.58$, $p = 0.228$, $n = 6$ in 2012–2013 season and $r = 0.61$, $p = 0.150$, $n = 7$ in 2013–2014 season), the number of grains m^{-2} was positively and significantly correlated with spike dry weight at anthesis for the combined data of two seasons (Figure 2(a)). On the other hand, the number of grains m^{-2} was not correlated with fruiting efficiency (Figure 2(b)). Spike dry weight at anthesis was positively and significantly correlated with CGR from jointing to anthesis in the 2013–2014 season (Figure 2(c)). Genotypes with higher partitioning

of dry matter to spike tended to achieve higher spike dry weight at anthesis, except Hakei W1380 in the 2013–2014 season (Figure 2(d)).

The number of grains m^{-2} was positively and significantly correlated with CGR from anthesis to maturity for the combined data of two seasons (Figure 3).

2.2. Experiment 2

Anthesis date of Hakei W1380 was 3 days later than that of Shiroganekomugi (Table 4). Hakei W1380 exhibited significantly higher grain yield (by 24%) than Shiroganekomugi

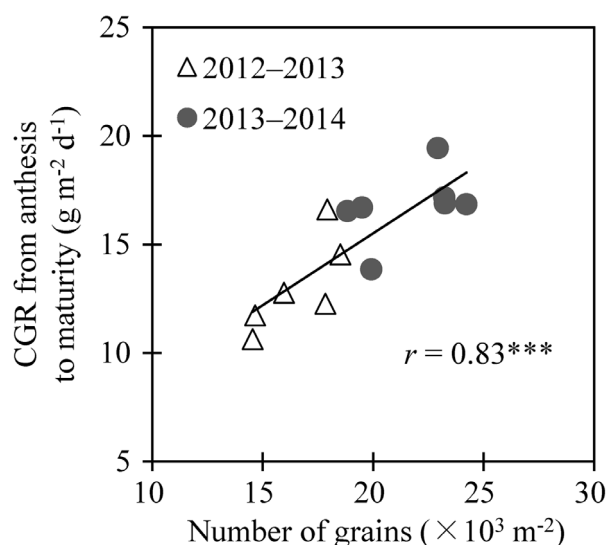


Figure 3. Relationship between the number of grains m^{-2} and CGR from anthesis to maturity (Experiment 1). Significant regression is denoted by *** $p < .001$ ($n = 13$).

because of higher aboveground biomass with similar HI. Among yield components, a significant genotypic

difference was observed only in the number of grains per spike, which was larger in Hakei W1380 than in Shiroganeekomugi. However, Hakei W1380 tended to produce larger numbers of grains m^{-2} and larger numbers of spikes m^{-2} .

Spike dry weight at anthesis was higher in Hakei W1380 than in Shiroganeekomugi, whereas fruiting efficiency did not significantly differ between genotypes (Table 5). Among the traits related to spike dry weight at anthesis, only CGR from jointing to anthesis was significantly higher in Hakei W1380 than in Shiroganeekomugi.

During the period from jointing to anthesis, mean LAI was significantly higher in Hakei W1380 than in Shiroganeekomugi, although NAR did not differ between genotypes (Table 6). Neither mean SLA nor mean LW ratio differed significantly between genotypes from jointing to anthesis. Both flag leaf and second leaf of Hakei W1380 were significantly larger than those of Shiroganeekomugi (Figure 4). SPAD values of Hakei W1380 tended to be higher than those of Shiroganeekomugi for pre-anthesis stages but lower for post-anthesis stages (Figure 5).

Table 4. Grain yield and yield components of Shiroganeekomugi and Hakei W1380 in the 2014–2015 season (Experiment 2).

	Anthesis date (DAS)	Grain yield (g m^{-2})	Aboveground biomass (g m^{-2})	Harvest index	Number of grains ($\times 10^3 \text{ m}^{-2}$)	Number of spikes (m^{-2})	Grains per spike (spike^{-1})	Grain weight (mg)	Plump–grain percentage
Shiroganeekomugi	144	568	1,135	0.44	17.1	521	33	35.2	97.9
Hakei W1380	147	703	1,404	0.44	20.6	561	37	35.4	98.7
Significance		*	NS	NS	NS	NS	*	NS	NS

Notes. Grain yield and grain weight were expressed at 12.5% moisture content. * indicates significant difference between Shiroganeekomugi and Hakei W1380 at $p < .05$. NS, not significant; DAS, days after sowing.

Table 5. Fruiting efficiency, spike dry weight at anthesis, duration of spike growth, CGR, and dry matter partitioning to spike of Shiroganeekomugi and Hakei W1380 in the 2014–2015 season (Experiment 2).

	Fruiting efficiency ^a (g^{-1})	Spike dry weight at anthesis (g m^{-2})	Duration of spike growth ^b	CGR ^c ($\text{g m}^{-2} \text{ d}^{-1}$)	Dry matter partitioning to spike ^e (g g^{-1})
Shiroganeekomugi	151	113	37	14.5	0.24
Hakei W1380	142	146	32	19.7	0.21
Significance	NS	**	NS	*	*

* and ** indicate significant difference between Shiroganeekomugi and Hakei W1380 at $p < .05$ and $p < .01$, respectively. NS, not significant.

^aGrain number per gram of spike at anthesis.

^bDays from penultimate leaf emergence to anthesis.

^cValues from 112 days after sowing to anthesis.

Table 6. NAR, mean LAI, mean SLA, and mean leaf weight ratio (LW ratio) of Shiroganeekomugi and Hakei W1380 from jointing to anthesis in the 2014–2015 season (Experiment 2).

	NAR ($\text{g m}^{-2} \text{ d}^{-1}$)	Mean LAI ($\text{m}^2 \text{ m}^{-2}$)	Mean SLA ($\text{cm}^2 \text{ g}^{-1}$)	Mean LW ratio (g g^{-1})
Shiroganeekomugi	4.3	3.41	266	0.32
Hakei W1380	4.8	4.17	262	0.33
Significance	NS	*	NS	NS

* indicates significant difference between Shiroganeekomugi and Hakei W1380 at $p < .05$. NS, not significant.

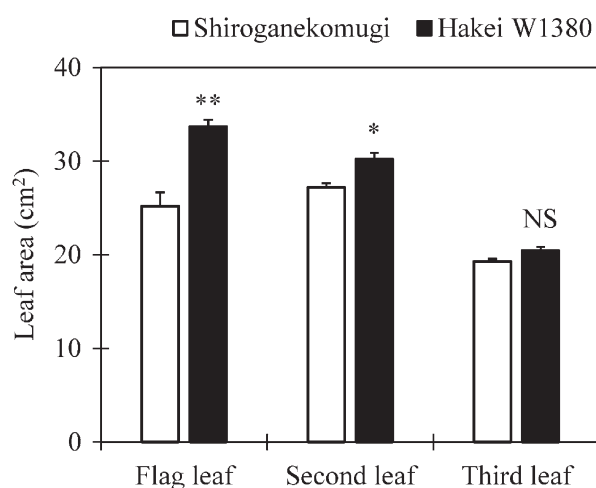


Figure 4. Individual leaf area of Shiroganekomugi and Hakei W1380 in the 2014–2015 season (Experiment 2). Values are means + S.E. ($n = 3$). * and ** indicate significant difference between Shiroganekomugi and Hakei W1380 at $p < .05$ and $p < .01$, respectively. NS, not significant.

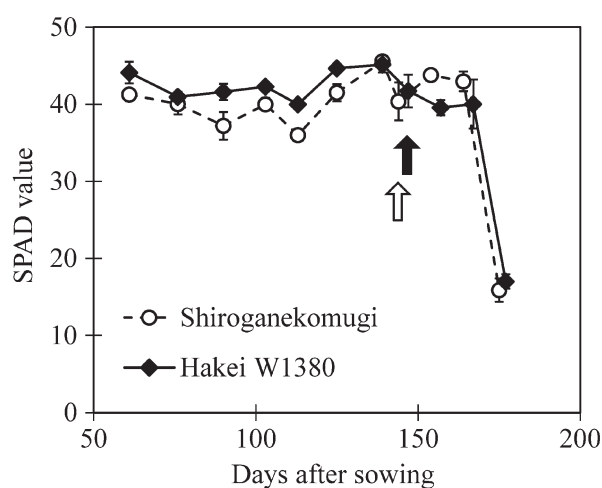


Figure 5. Seasonal change in SPAD value for Shiroganekomugi and Hakei W1380 in the 2014–2015 season (Experiment 2). Values are means \pm S.E. ($n = 3$). White and black arrows indicate anthesis dates of Shiroganekomugi and Hakei W1380, respectively.

3. Discussion

The present study revealed that recent genetic progress in grain yield was associated with biomass production rather than HI in southwestern Japan (Table 2), and this trend has been observed at least since 1970s (Fujita & Ujihara, 1993; Taya, 1993). The HI of 0.44–0.50 achieved in this study (Tables 1 and 4) was comparable or even higher than that of modern cultivars in previous studies (Acreche et al., 2008; Beche et al., 2014; Brancourt-Hulmel et al., 2003; Donmez et al., 2001; Shearman et al., 2005; Siddique et al., 1989; Zheng et al., 2011; Zhou et al., 2007). Despite a theoretical upper limit (0.62; Austin et al., 1980), it appears

difficult to achieve HI of values higher than 0.50 (Fischer & Edmeades, 2010). Hence, future genetic gains in grain yield would depend on increasing biomass production while maintaining HI in southwestern Japan as well as other countries (Austin et al., 1980).

Among yield components, grain yield was strongly associated with grain number m^{-2} (Table 2), as reported in previous studies (Abbate et al., 1998; Acreche et al., 2008; Beche et al., 2014; Donmez et al., 2001; Shearman et al., 2005). An increase in grain number m^{-2} could be accompanied by a decrease in grain weight due to a lack of enough assimilates available to fill grains (Kato & Osawa, 2013; Kato & Yamagishi, 2011). However, significant relationships were not detected between grain number m^{-2} and grain weight in the present study (Table 2). These results were in agreement with previous reports that grain yield was mostly sink-limited during grain filling in optimal conditions (Serrago et al., 2013; Slafer & Savin, 1994). Therefore, increasing sink size could be essential for producing high yield in southwestern Japan.

The number of grains m^{-2} is determined by a combination of spike dry weight at anthesis and fruiting efficiency when it is assumed that the number of grains m^{-2} is limited by assimilate supply (Fischer, 1984). In addition, spike dry weight at anthesis is determined by a combination of duration of spike growth, CGR during spike growth period, and dry matter partitioning to spike during the spike growth period (Fischer, 1984). Accordingly, genotypes with large numbers of grains m^{-2} may have (i) a long duration of spike growth, (ii) high CGR during spike growth period, (iii) large partitioning of dry matter to spike, and/or (iv) many grains per gram of spike (Fischer, 1984). Although previous studies reported that newer genotypes have improved ability to produce grains per unit biomass (i.e. fruiting efficiency) in Argentina (Abbate et al., 1998) and Spain (Acreche et al., 2008), fruiting efficiency was poorly related to grain number m^{-2} in the present study (Figure 2(b)). On the other hand, close relationships between grain number m^{-2} and spike dry weight m^{-2} at anthesis and between spike dry weight m^{-2} at anthesis and CGR from jointing to anthesis were observed (Figure 2(a and c)). These results indicated that larger numbers of grains m^{-2} in high-yielding lines than in commercial cultivars resulted from higher CGR at the pre-anthesis stage and higher spike dry weight at anthesis (Figure 2, Table 5). Therefore, achievement of high grain number m^{-2} through high biomass production at the pre-anthesis stage would be prerequisite for high yield in southwestern Japan. In Experiment 1, grain number m^{-2} was significantly associated with CGR at the post-anthesis stage (Figure 3), suggesting that achievement of high grain number m^{-2} would contribute to high carbohydrate assimilation at post-anthesis stage. Our results supports the previous claims that the number of grains m^{-2} is the

main driver for post-anthesis growth through its effects on sink strength and photosynthetic ability at the post-anthesis stage (Acreche & Slafer, 2009; Calderini et al., 1997).

The CGR at the pre-anthesis stage increases with increase in maximum LAI up to around LAI = 6 in wheat (Fischer, 1984; Taya, 1993); at lower LAI values, the plants cannot fully cover the ground and intercept all available radiation. In Experiment 1, LAI among genotypes at anthesis was 4.06–5.73 m² m⁻² and mean LAI was positively related to CGR from jointing to anthesis in the 2013–2014 season ($r = 0.68$, $p = 0.09$, $n = 7$). In addition, the higher CGR of Hakei W1380 compared with Shiroganekomugi was derived from the larger LAI (Table 6) accompanied by larger upper leaves (Figure 4). These results suggest that leaf area growth and the amount of radiation intercepted are still the primary constraints for biomass production in southwestern Japan. In this region, most farmers grow wheat in raised-bed planting systems in order to avoid injury from waterlogging stress after heavy rain. In such a system, genotypes with high LAI would have the advantage in capturing radiation in the gap between beds (Aisawi et al., 2015). Improved photosynthetic ability and radiation use efficiency, which are regarded as important traits in other countries (Fischer et al., 1998; Shearman et al., 2005), might be subsequent breeding targets for wheat in southwestern Japan.

In the present study, we selected Hakei W1380 as a high-yielding genotype. Grain yield of Hakei W1380 was significantly higher than those of commercial cultivars Shiroganekomugi and Chikugoizumi by 30 and 14%, respectively (Table 1). In addition, it tended to be higher than those of other genotypes, although the differences were not significant.

The higher yield of Hakei W1380 compared with other genotypes can be attributed to the following: (1) higher biomass production (Tables 1 and 4), especially at the pre-anthesis stage (Tables 3 and 5); (2) larger leaf area growth at the pre-anthesis stage (Table 6); (3) better leaf nitrogen status (i.e. higher SPAD value) at the pre-anthesis stage (Figure 5); and (4) higher sink size (i.e. grain number m⁻²; Tables 1 and 4). Such characteristics might come from a donor parent, Kitahonami, which is a high-yielding cultivar for northern Japan (Yanagisawa et al., 2007b). Availability of Kitahonami considerably increased potential yield in northern Japan: Kitahonami exhibited higher yields than an older cultivar, Hokushin, by 16–18% because of improved biomass, HI, and grain number m⁻² (Yanagisawa et al., 2007a).

The pedigree of Kitahonami is traced to a winter wheat cultivar, Norman, in the UK (Yanagisawa et al., 2007b). Accordingly, it was possible that yielding ability of Hakei W1380 was originally introduced from Norman because Norman exhibited high yield and large sink size in the UK in

1980s (Austin et al., 1989). The present study suggests that introgression of traits of high yield from cultivars in northern Japan and foreign countries would be effective for the development of high-yielding cultivars using Hakei W1380 as a parent in breeding programs in southwestern Japan.

Future research should also focus on genotypic differences in nitrogen uptake and nitrogen utilization because these characteristics might play an important role in yield formation of wheat in southwestern Japan.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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*In Japanese with English summary.

**In Japanese.