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

Midori Okami*, Hitoshi Matsunaka*, Masaya Fujita*, Kazuhiro Nakamura* and Zenta Nishio*

*Kyushu Okinawa Agricultural Research Center, National Agriculture and Food Research Organization, Fukuoka, Japan; **Institute of Crop Science, National Agriculture and Food Research Organization, Ibaraki, Japan

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.

© 2016 the author(s). Published by Informa UK Limited, trading as Taylor & Francis Group. This is an Open Access article distributed under the terms of the Creative Commons Attribution License (http://creativecommons.org/licenses/by/4.0/), which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited.

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., 2008;...
PLANT PRODUCTION SCIENCE

361

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.

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

Figure 1. Diagrams of planting systems in (a) Experiment 1 and (b) Experiment 2.
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 (Sláfer et al., 1990) were calculated as follows:

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

(1)

\[
\text{Dry matter partitioning to spike} = \frac{\text{(spike dry weight m}^{-2} \text{ at anthesis)}}{\text{(aboveground dry weight m}^{-2} \text{ at anthesis) - aboveground dry weight m}^{-2} \text{ at jointing stage)}}
\]

(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 (x10⁴ 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) |
|------------------|---------------------|-----------------------------|---------------|-----------------------------|------------------------|---------------------------|------------------|-----------------------------|------------------|---------------|----------------|----------------|
| Shirogane komugi | 603                 | 1,140                       | 0.460         | 17.2                        | 508                    | 35                        | 35.2             | 99.2                        | 72.5             | 125           | 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           |
| Hakel W1380      | 782                 | 1,453                       | 0.471         | 21.4                        | 547                    | 40                        | 36.8             | 99.6                        | 79.0             | 139           | 149           | 188           |
| Hakel W1395      | 760                 | 1,364                       | 0.488         | 21.6                        | 538                    | 41                        | 35.9             | 99.0                        | 78.5             | 136           | 147           | 189           |
| Hakel W1415      | 719                 | 1,339                       | 0.468         | 19.4                        | 526                    | 38                        | 36.9             | 99.8                        | 77.7             | 135           | 145           | 186           |

Season

| Year          | Grain yield (g m⁻²) | Aboveground biomass (g m⁻²) | Harvest index | Number of grains (x10⁴ 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) |
|---------------|---------------------|-----------------------------|---------------|-----------------------------|------------------------|---------------------------|------------------|-----------------------------|------------------|---------------|----------------|----------------|
| 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
LSD(5%) Season 23 39 0.004 0.9 29 2 0.9 0.2 1.6
LSD(5%) 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.
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 significantly correlated with grain yield and aboveground biomass at maturity and grain number per unit area in both seasons (Table 2).

### 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                       | 0.65         | 0.49                   | 0.07         | 0.04                   |
| Grain number per unit area | 0.82*       | 0.24                | 0.49          | 0.65                       | 0.49         | 0.49                   | 0.35         | 0.16                   |
| Spike number         | 0.34        | 0.12                | 0.49          | −0.04                      | −0.66        | −0.45                  | −0.26        | −0.10                  |
| Grain number per spike | 0.58      | 0.61                | −0.04         | −0.38                      | −0.45        | −0.28                  | 0.76*        |                        |
| Grain weight         | −0.12       | −0.07               | −0.27         | −0.66                      | −0.45        | −0.28                  | 0.51         |                        |
| 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.

### 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)  
|                      | 2012–2013 | 2013–2014 |
|----------------------|-----------|-----------|
| 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.
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 2(c)).

**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...
difference was observed only in the number of grains per spike, which was larger in Hakei W1380 than in Shiroganekomugi. 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 Shiroganekomugi, 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 Shiroganekomugi.

During the period from jointing to anthesis, mean LAI was significantly higher in Hakei W1380 than in Shiroganekomugi, 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 Shiroganekomugi (Figure 4). SPAD values of Hakei W1380 tended to be higher than those of Shiroganekomugi for pre-anthesis stages but lower for post-anthesis stages (Figure 5).

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

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).

Table 4. Grain yield and yield components of Shiroganekomugi 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 (×10³ m⁻²) | Number of spikes (m⁻²) | Grains per spike (spike⁻¹) | Grain weight (mg) | Plump-grain percentage |
|---------------------|---------------------|-----------------------------|---------------|-----------------------------|------------------------|---------------------------|------------------|------------------------|
| Shiroganekomugi     | 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 Shiroganekomugi 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 Shiroganekomugi and Hakei W1380 in the 2014–2015 season (Experiment 2).

| Fruiting efficiency (g⁻¹) | Spike dry weight at anthesis (g m⁻²) | Duration of spike growth (d) | CGR (g m⁻² d⁻¹) | Dry matter partitioning to spike (mg) |
|---------------------------|-------------------------------------|-------------------------------|-----------------|--------------------------------------|
| Shiroganekomugi           | 151                                 | 113                           | 37              | 14.5                                 | 0.24                   |
| Hakei W1380               | 142                                 | 146                           | 32              | 19.7                                 | 0.21                   |
| Significance              | NS                                  | NS                            | NS              | *                                    |                        |

* and ** indicate significant difference between Shiroganekomugi 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 Shiroganekomugi and Hakei W1380 from jointing to anthesis in the 2014–2015 season (Experiment 2).

| NAR (g m⁻² d⁻¹) | Mean LAI (m² m⁻²) | Mean SLA (cm² g⁻¹) | Mean LW ratio (g g⁻¹) |
|-----------------|-------------------|-------------------|----------------------|
| Shiroganekomugi | 4.3               | 3.41              | 266                  | 0.32                  |
| Hakei W1380     | 4.8               | 4.17              | 262                  | 0.33                  |
| Significance    | NS                | *                 | NS                   | NS                    |

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

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
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.

Acknowledgments

We thank the staff of NARO Kyushu Okinawa Agricultural Research Center for their technical assistance. We also thank Dr. A. Oyanagi (NARO Kyushu Okinawa Agricultural Research Center) and Dr. Y. Kato (International Rice Research Institute) for providing valuable comments on an early version of our manuscript.

Disclosure statement

No potential conflict of interest was reported by the authors.

References

Abbate, P. E., Andrade, F. H., Lázaro, L., Bariffi, J. H., Barardocc, H. G., Inza, V. H., & Marturano, F. (1998). Grain yield increase in recent Argentine wheat cultivars. *Crop Science, 38,* 1203–1209.

Acreche, M. M., Briceño-Félix, G., Sánchez, J. A. M., & Slafer, G. A. (2008). Physiological bases of genetic gains in Mediterranean bread wheat yield in Spain. *European Journal of Agronomy, 28,* 162–170.

Acreche, M. M., & Slafer, G. A. (2009). Grain weight, radiation interception and use efficiency as affected by sink-strength in Mediterranean wheats released from 1940 to 2005. *Field Crops Research, 110,* 98–105.

Aisawi, K. A. B., Reynolds, M. P., Singh, R. P., & Foulkes, M. J. (2015). The physiological basis of the genetic progress in yield potential of CIMMYT spring wheat cultivars from 1966 to 2009. *Crop Science, 55,* 1749–1764.

Austin, R. B., Bingham, J., Blackwell, R. D., Evans, L. T., Ford, M. A., Morgan, C. L., & Taylor, M. (1980). Genetic improvements in winter wheat yields since 1900 and associated physiological changes. *The Journal of Agricultural Science, 94,* 675–689.

Austin, R. B., Ford, M. A., & Morgan, C. L. (1989). Genetic improvement in the yield of winter wheat: a further evaluation. *The Journal of Agricultural Science, 112,* 295–301.

Beche, E., Benin, G., da Silva, C. L., Munaro, L. B., & Marchese, J. A. (2014). Genetic gain in yield and changes associated with physiological traits in Brazilian wheat during the 20th century. *European Journal of Agronomy, 61,* 49–59.

Brancourt-Hulmel, M., Doussinault, G., Lecomte, C., Bérard, P., Le Buanc, B., & Trottet, M. (2003). Genetic improvement of agronomic traits of winter wheat cultivars released in France from 1946 to 1992. *Crop Science, 43,* 37–45.

Calderini, D. F., Drecrer, M. F., & Slafer, G. A. (1997). Consequences of breeding on biomass, radiation interception and radiation-use efficiency in wheat. *Field Crops Research, 52,* 271–281.
Shearman, V. J., Sylvester-Bradley, R., Scott, R. K., & Foulkes, M. J. (2005). Physiological processes associated with wheat yield progress in the UK. *Crop Science, 45*, 175–185.

Siddique, K. H. M., Belford, R. K., Perry, M. W., & Tennant, D. (1989). Growth, development and light interception of old and modern wheat cultivars in a Mediterranean-type environment. *Australian Journal of Agricultural Research, 40*, 473–487.

Slafer, G. A., & Savin, R. (1994). Source-sink relationships and grain mass at different positions within the spike in wheat. *Field Crops Research, 37*, 39–49.

Donmez, E., Sears, R. G., Shroyer, J. P., & Paulsen, G. M. (2001). Genetic gain in yield attributes of winter wheat in the Great Plains. *Crop Science, 41*, 1412–1419.

FAOSTAT. (2015). *Food and Agriculture Organization of the United Nations*. Retrieved August, 2015, from http://faostat3.fao.org/home/E

Fischer, R. A. (1984). Wheat. In W. H. Smith & S. J. Banta (Eds.), *Potential productivity of field crops under different environments* (pp. 129–154). Los Baños: IRRI.

Fischer, R. A., Rees, D., Sayre, K. D., Lu, Z. M., Condon, A. G., & Saavedra, A. L. (1998). Wheat yield progress associated with higher stomatal conductance and photosynthetic rate, and cooler canopies. *Crop Science, 38*, 1467–1475.

Fischer, R. A., & Edmeades, G. O. (2010). Breeding and cereal yield progress. *Crop Science, 50*, S-85–S-98.

Fischer, R. A. (2011). Wheat physiology: A review of recent developments. *Crop and Pasture Science, 62*, 95–114.

Fujita, M., & Ujihara, K. (1993). Some traits correlated with high yielding ability of wheat in the south-western area of Japan. *Bulletin of the Kyushu National Agricultural Experiment Station, 28*, 29–43.*

Kato, Y., & Yamagishi, J. (2011). Long-term effects of organic manure application on the productivity of winter wheat grown in a crop rotation with maize in Japan. *Field Crops Research, 120*, 387–395.

Kato, Y., & Osawa, M. (2013). Manipulation of the availability of assimilates for kernel growth in wheat in Japan: Effects of crop thinning and planting geometry. *European Journal of Agronomy, 49*, 74–82.

MAFF. (2015). *Ministry of Agriculture, Forestry and Fisheries*. Retrieved August, 2015, from http://www.maff.go.jp/j/zyukyu/fbs/index.html

Rodríguez, D., Keltjens, W. G., & Goudriaan, J. (1998). Plant leaf area expansion and assimilate production in wheat (*Triticum aestivum* L.) growing under low phosphorus conditions. *Plant and Soil, 200*, 227–240.

SAS Institute. (2003). *SAS User’s Guide: Statistics, Version 9.1 ed.*, 2002-2003. Cary, NC.

Serrago, R. A., Alzueta, I., Savin, R., & Slafer, G. A. (2013). Understanding grain yield responses to source-sink ratios during grain filling in wheat and barley under contrasting environments. *Field Crops Research, 150*, 42–51.

Shearman, V. J., Sylvester-Bradley, R., Scott, R. K., & Foulkes, M. J. (2005). Physiological processes associated with wheat yield progress in the UK. *Crop Science, 45*, 175–185.

Siddique, K. H. M., Belford, R. K., Perry, M. W., & Tennant, D. (1989). Growth, development and light interception of old and modern wheat cultivars in a Mediterranean-type environment. *Australian Journal of Agricultural Research, 40*, 473–487.

Slafer, G. A., Andrade, F. H., & Satorre, E. H. (1990). Genetic-improvement effects on pre-anthesis physiological attributes related to wheat grain-yield. *Field Crops Research, 23*, 255–263.

Slafer, G. A., & Savin, R. (1994). Source-sink relationships and grain mass at different positions within the spike in wheat. *Field Crops Research, 37*, 39–49.

Taya, S. (1993). Breeding of early maturing wheat varieties with higher grain yield in southwestern regions of Japan. *Bulletin of the Kyushu National Agricultural Experiment Station, 27*, 333–398*.

Yanagisawa, A., Yoshimura, Y., Amano, Y., Kobayashi, S., Nishimura, T., Nakamichi, K., … Sato, N. (2007b). A new winter wheat variety “Kitahonami”. *Bulletin of the Hokkaido Prefectural Agricultural Experiment Station, 91*, 1–13*.

Yanagisawa, A., Yoshimura, Y., Kobayashi, S., Nishimura, T., Maeno, S., & Watanabe, Y. (2007a). A study on high-yielding winter wheat breeding: A case study on ‘Kitahonami’. *Report of the Hokkaido Branch, the Japanese Society of Breeding and Hokkaido Branch, the Crop Science Society of Japan*, 48, 73–74**.

*In Japanese with English summary.

**In Japanese.