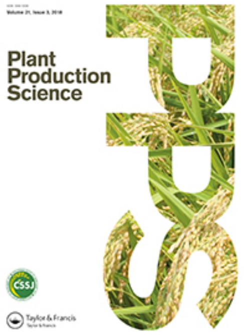

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Characteristics of growth and quality, and factors contributing to high yield in newly developed rice variety 'Akidawara'

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ABSTRACT

The newly developed rice variety 'Akidawara' (AKI) combines the traits of high yield and highly palatability, and its cultivation is expected to spread. We examined characteristics of growth and quality, and factors contributing to high yield in AKI by comparing with 'Nipponbare' (NIP). Grain yield for AKI were 703 g m^{-2} (9% more than NIP) and 781 g m^{-2} (14% more than NIP) under the standard and heavy fertilizer regimes. It was also suggested that increase in the sink capacity was the key contributors to the high yield in AKI resulting from a conspicuous increase in the number of spikelets, which is likely due to introgression of the high-yielding variety allele. Furthermore, AKI achieved the similar degree of sink filling in spite of its larger sink capacity. In this point, panicle dry weight increase during ripening (ΔP) was significantly higher for AKI than for NIP despite the fact that no differences in shoot dry weight increase were observed between varieties. The greater ΔP in AKI might be derived from its larger sink capacity and the difference between varieties involves the translocation of nonstructural carbohydrate. In the grain quality, the reduction in perfect grain ratio was negligible and regarded as a small trade-off for AKI's 14% increase in yield, and grain protein content increased to a lesser degree in AKI at the same yield level. These results suggest that over 700 g m^{-2} high yield can be achieved with relative high grain quality and lower protein content in AKI.

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Introduction

In recent years, high-yielding varieties are increasingly being grown for purposes other than direct human consumption such as rice flour and animal feed (Yoshinaga et al., 2013) in Japan. Although grain yield of most of these varieties has been at the highest level among Japanese varieties but the palatability of boiled rice was out of the target. On the other hand, demand for rice for direct human consumption is also changing, with the share of demand for household consumption as boiled rice declining and the share of demand for consumption at restaurants, and in boxed meals and rice balls from convenience stores increasing. This has fueled demand for so-called 'commercial rice' including for food service industry and home replacement meal, which now accounts for approximately 40% of all rice consumed as boiled rice. With regards to commercial rice varieties, whereas different characteristics maybe emphasized depending on the specific purpose, there is a general expectation that commercial rice should be supplied at lower prices than rice for household consumption. As such, the use of high-yielding varieties and low-cost, high-yielding cultivation methods is favored. These changing consumption patterns have prompted the breeding of high-yielding varieties and increased demand for high-yielding cultivation using these varieties.

One such variety developed by Japan's National Agriculture and Food Research Organization (NARO) and registered in 2011 is 'Akidawara' (AKI). Because AKI combines the traits of high yield and good palatability, its cultivation is expected to spread. Bred by crossing high-yielding and highly palatable varieties, it incorporates the high-yielding 'Akenohoshi' allele (Ando et al., 2011), which increases spikelet number, at the Gn1 QTL (Ashikari et al., 2005), and alleles of 'Koshihikari,' one of Japan's leading varieties in terms of palatability, at palatability QTLs on the third and sixth chromosomes (Takeuchi et al., 2008). Owing to the combination of positive genetic effects, AKI is expected to produce yields that exceed those of reference varieties by over 10% under the same fertilizer regime from 8 to 12 g N m^{-2} (Ando et al., 2011). Although the area planted with AKI is expanding and high yielding of AKI have been demonstrated (Li et al., 2016), the traits related to improved yield have not been clarified. Furthermore,

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the evaluation of the grain quality of AKI at heavy nitrogen application rate is important, since the heavy nitrogen application is necessary to achieve high yield.

Therefore, in this study, we focused on factors contributing to high yield in AKI and the interaction between yield and quality especially at heavy nitrogen application rate and conducted a field experiment in which different fertilizer regimes were executed in each of three years.

Materials and methods

Field experimental details

Field experiments were conducted in the experimental field of the Central Region Agricultural Research Center, located in Joetsu, Niigata, Japan (37°07′N, 138 °16′E) from 2013 to 2015. Two Japanese rice (*Oryza sativa* L.) genotypes 'Nipponbare' (NIP) and AKI were grown under irrigated conditions. NIP is a conventional *japonica* high-yielding variety that was released in 1963 and its cultivated area had been largest in 1970s (Nitta, 2010; Yokoo et al., 2005). It is popular for the consumption eaten as boiled rice and a standard variety that shows similar growth duration to that of AKI and enough lodging resistance for heavy nitrogen application. It was utilized for the first rice genome sequence analysis (International Rice Genome Sequencing Project, 2005) and have been frequently used for the evaluation of the characteristics of high-yielding varieties (Ando et al., 2011; Kusutani et al., 1999; Nagata et al., 2016; Oka et al., 1987; Takeda et al., 1984; Tsukaguchi et al., 1996; Yoshinaga et al., 2013).

Seeds were sown in a seedling nursery box, and 25- to 28-day-old seedlings were transplanted, with three seedlings per hill, on 21 May 2013, 19 May 2014 and 2015. The planting density was 22.2 hills m^{-2}, with 30-cm row spacing and 15-cm intra-row spacing, with nil (0N plots), standard (8N plots; total 8 g N m^{-2}), and high nitrogen (16N plots; total 16 g N m^{-2}) application levels (Table 1). In 8N and 16N plots, the basal application contained 4 g N m^{-2}. In 8N, one 4 g N m^{-2} top-dressing was applied at 20 days before heading. In 16N plots, three times 4 g N m^{-2} top-dressing were applied at 30 days after transplanting, and 20 and 10 days before heading. Nitrogen fertilizers were supplied with ammonium sulfate. Phosphorus and potassium (6 g P_2O_5 m^{-2} and 6 g K_2O m^{-2} as fused fertilizer) were applied to all plots before puddling. Weeds, insects, and diseases were controlled using standard herbicides and pesticides as required to avoid yield loss. The experimental plots were arranged in a split-plot design (main and sub plots were nitrogen application and variety, respectively) with three replicates except for 0N application plots with two replications. The size of each plot was 15 m^2.

Table 1. Nitrogen application in each treatment.

Treatments	Basal dressing (g N m^{-2})	Top dressing (g N m^{-2})			Total
		30DAT	20DBH	10DBH	
0N	0	0	0	0	0
8N	4	0	4	0	8
16N	4	4	4	4	16

Notes: DAT: days after transplanting, DBH: days before heading.

Measurement of dry matter production and nitrogen uptake

Plants were sampled at the full-heading stage and the maturity. The full-heading date was defined as the date when about 80% of panicles in a canopy had emerged. Ten hills were sampled at full-heading and matured stage from each plot. Among them, two representative hills with average number of panicles, were selected and separated into four parts: leaf blades, leaf sheaths and culms, panicles, and dead parts. The weights of each part and of the entire shoots were measured after drying for 72 h at 80 °C.

Dried sample of the plant powdered with a sample mill for measuring of nitrogen. The nitrogen content was measured by the combustion method (JM3000CN; J Science Labo, Kyoto, Japan).

Yield, yield components and grain quality

At maturity, plants from 48 hills (2.16 m^2) of each plot were harvested for the determination of yield and yield components. After counting panicle number, panicles were threshed and hulled rice were weighed. Then, grains were screened by a 1.8 mm grain sorter and weighed. Thousand grains weight was calculated with screened hulled grain. The hulled rough grain yield, screened grain yield, and 1000-grain weights were adjusted to 15% moisture content.

Approximately 50 g of subsample was selected from unhulled grain, using Sample Divider (Fujikinzoku, Tokyo, Japan). The number of spikelets per unit area was calculated as the number of spikelets of the subsample divided by the subsample weight and multiplied by the weight of the total amount of unhulled grain per unit area. The number of spikelets per panicle was calculated as the number of spikelets per area divided by the number of panicles per area. Sink capacity was defined as hulled and screened single grain weight multiplied by the number of spikelets per area. Sink filling rate was calculated on the hulled grain yield divided by sink capacity.

Perfect grain ratio which is an index of grain quality, was measured using Rice Quality Analyzer (RGQ10B, Satake Co. Ltd., Japan). Protein content of brown rice was calculated from nitrogen content multiplied by protein coefficient 5.95, and adjusted to 15% moisture content.

Statistical analysis

Analysis of variance (ANOVA) was performed using 'JMP 12.2.0' (SAS Institute Inc., NC, U.S.A.), to assess varietal differences and the effects of nitrogen application. Then, all the percentage data were analyzed after arcsine transformation.

Results

Heading and climate conditions

Table 2 shows mean temperatures and solar radiation during the growth period, including heading and ripening stages for NIP and AKI, for each of the years of the experiment. The heading stages of NIP and AKI differed by less than two days in all three years, and the climate was roughly the same for the respective growth stages of each variety. Mean temperatures and solar radiation from transplanting to the heading stage were higher than climatic normals in all three years. However, solar radiation during ripening was lower than climatic normals in 2014 and particularly so in 2015. No typhoons or other notable weather events occurred in any of the years of the experiment.

Dry matter production-related traits

Both shoot dry weight and nitrogen uptake increased with increasing fertilizer at full-heading (80% panicle emergence) and maturity. However, no significant difference was observed between the two varieties for either trait, and no interaction between fertilizer regime and variety was evident (Table 3). Both shoot and panicle dry

Table 2. Growth stage and the climate condition in experiment years.

		Growth stage		Mean temperature (°C)				Solar radiation (MJ m^{-2} d^{-1})			
Year	Variety	Heading	Maturity	T-H		H-M		T-H		H-M	
2013	Nipponbare	8.12	9.28	23.7	(+1.3)	23.8	(+.2)	18.6	(+1.9)	15.9	(+2.1)
	Akidawara	8.13	9.30	23.7	(+1.3)	23.6	(+.3)	18.7	(+2.0)	15.8	(+2.2)
2014	Nipponbare	8.12	9.30	22.7	(+0.9)	22.8	(−0.7)	18.9	(+2.2)	15.1	(+1.2)
	Akidawara	8.10	9.29	22.7	(+1.0)	22.9	(−0.7)	19.2	(+2.5)	15.3	(+1.6)
2015	Nipponbare	8.13	9.30	23.3	(+1.0)	22.1	(−1.2)	20.2	(+3.3)	12.8	(−0.8)
	Akidawara	8.11	9.30	23.2	(+1.1)	22.3	(−1.3)	20.0	(+3.5)	12.8	(−1.0)

Notes: T: transplanting time, *H*: heading stage, M: maturity. Values in the parenthesis are the difference from the average of 1981–2010.

Table 3. Characteristics of dry matter production and grain quality of two rice varieties in different nitrogen treatments.

				Shoot dry wt. (g m^{-2})				Increase of dry wt. (g m^{-2})				Nitrogen uptake (g m^{-2})				Grain quality			
Variety	Nitrogen	Harvest Index		FH		M		ΔW		ΔP		FH		M		Perfect grain (%)		Protein content (%)	
Nipponbare	0N	0.37	c	876	c	1327	c	451	b	487	d	7.3	c	9.4	c	87.3	a	5.8	c
	8N	0.39	bc	1060	ab	1645	b	585	a	641	c	11.0	b	12.5	b	77.0	bc	6.2	b
	16N	0.39	bc	1122	a	1771	a	649	a	711	b	15.6	a	17.7	a	69.4	d	7.4	a
Akidawara	0N	0.41	b	884	c	1283	c	399	b	520	d	7.2	c	9.2	c	79.2	b	5.6	c
	8N	0.44	a	1021	b	1616	b	588	a	705	b	10.2	b	12.6	b	75.1	c	6.1	b
	16N	0.44	a	1135	a	1782	a	646	a	800	a	15.2	a	17.0	a	66.6	d	7.2	a
Average	Nitrogen																		
	0N	0.39	b	880	c	1305	c	425	c	503	c	7.2	c	9.3	c	83.2	a	5.7	c
	8N	0.41	a	1040	b	1631	b	586	b	673	b	10.6	b	12.5	b	76.1	b	6.1	b
	16N	0.41	a	1129	a	1776	a	647	a	756	a	15.4	a	17.3	a	68.0	c	7.3	a
	Variety																		
	Nipponbare	0.38	b	1019	a	1581	a	562	a	613	b	11.3	a	13.2	a	77.9	a	6.5	a
	Akidawara	0.43	a	1014	a	1560	a	544	a	675	a	10.9	a	12.9	a	73.6	b	6.3	b
ANOVA																			
Year (A)		**		**		**		**		**		**		ns		**		**	
Nitrogen (B)		**		**		**		**		**		**		**		**		**	
Variety (C)		**		ns		ns		ns		**		ns		ns		**		**	
A X B		ns		ns		*		ns		ns		ns		ns		**		ns	
B X C		ns		ns		ns		ns		ns		ns		ns		**		ns	
C X A		ns		ns		*		ns		ns		**		ns		**		ns	
A X B X C		ns		ns		ns		ns		ns		ns		ns		**		ns	

Notes: Data indicate the mean of three years with three replications. Δ*W*: Increase of shoot dry wt. at ripening period. Δ*P*: Increase of panicle dry wt. at ripening period. FH is full-heading and M is maturity. * and **, significant at the 0.05 and the 0.01 level; ns, not significant by ANOVA. Values within a column followed by the same letter are not significantly different at the 0.05 probability level by Tukey's test or *t*-test.

Table 4. Yield and yield components of two rice varieties in different nitrogen treatments.

		Grain yield															
Variety	Nitrogen	Hulled (g m^{-2})		Screened (g m^{-2})		Pan-icles (m^{-2})		No. of spikelet /panicle		No. of spikelet (x10^3 m^{-2})		1000 grain wt. (g)		Sink capacity (g m^{-2})		Sink filling (%)	
Nipponbare	0N	507	d	496	d	345	cd	69	d	23.4	e	23.3	a	544	d	93.1	a
	8N	668	c	643	c	412	ab	81	c	33.2	c	22.5	b	747	c	89.5	bc
	16N	719	b	683	b	443	a	84	c	37.1	b	22.5	b	831	b	86.4	c
Akidawara	0N	545	d	525	d	265	e	101	b	26.8	d	21.5	bc	576	d	94.6	a
	8N	732	b	703	b	333	d	111	a	36.8	b	21.4	c	791	bc	92.5	ab
	16N	829	a	781	a	393	bc	110	a	43.0	a	21.8	bc	936	a	88.7	bc
Average	Nitrogen																
	0N	526	c	511	c	305	c	85	b	25.1	c	22.4	a	560	c	93.9	a
	8N	700	b	673	b	372	b	96	a	35.0	b	22.0	b	769	b	91.0	b
	16N	774	a	732	a	418	a	97	a	40.1	a	22.2	ab	884	a	87.6	c
	Variety																
	Nipponbare	631	b	607	b	400	a	78	b	31.2	b	22.8	a	707	b	89.7	b
	Akidawara	702	a	670	a	330	b	107	a	35.6	a	21.6	b	768	a	92.0	a
ANOVA																	
Year (A)		**		**		**		**		**		**		**		**	
Nitrogen (B)		**		**		**		**		**		*		**		**	
Variety (C)		**		**		**		**		**		**		**		**	
A X B		ns		ns		ns		ns		ns		**		ns		*	
B X C		**		**		ns		ns		ns		*		*		ns	
C X A		**		**		ns		ns		ns		ns		ns		**	
A X B X C		ns		ns		ns		*		ns		ns		ns		ns	

Notes: Data indicate the means of three years with three replications. 1.8 mm sorter is used for the screened grain yield. * and **, significant at the 0.05 and the 0.01 level; ns, not significant by ANOVA. Values within a column followed by the same letter are not significantly different at the 0.05 probability level by Tukey's test or *t*-test.

weight increase from full-heading to maturity (ΔW and ΔP) increased with elevated fertilizer, with ΔP exceeding ΔW in both varieties for all fertilizer regimes. Whereas ΔW did not differ between varieties, mean ΔP was approximately 10% higher for AKI (675 g m^{-2}) than for NIP (613 g m^{-2}) (Table 3).

Yield and yield components

Both hulled grain and screened grain yield increased with increasing fertilizer (Table 4). The magnitude of grain yield increase was significantly larger for AKI than for NIP. Screened grain yield for AKI was 703 g m^{-2} (9% more than NIP) and 781 g m^{-2} (14% more than NIP) under the 8N and 16N fertilizer regimes, respectively, (Table 4). The number of panicles, spikelets per panicle, total number of spikelets and sink capacity all increased with increasing fertilizer and the means differed significantly between varieties. Although AKI produced significantly fewer panicles than NIP, because the mean of the number of spikelets per panicle was markedly higher for AKI, the means of total number of spikelets and sink capacity were significantly higher for AKI than for NIP. Sink filling rate decreased with increasing fertilizer and the means differed significantly between varieties. In spite of the large sink capacity in AKI, sink filling rate was significantly larger than that in NIP. The interactions between nitrogen application and variety for the yield and sink capacity were indicated, due to the larger yield increase by heavy nitrogen application (16N) in AKI than in NIP.

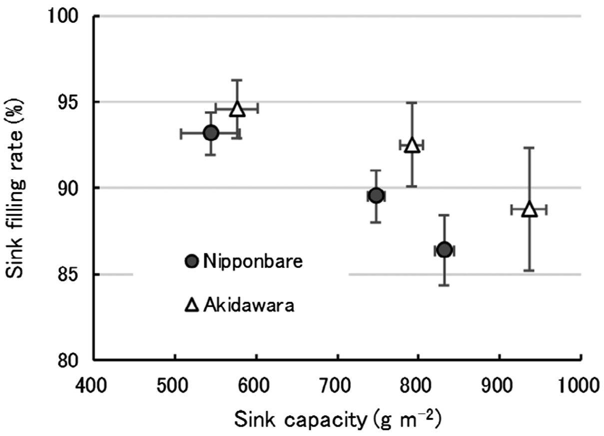

Figure 1. Relationship between sink capacity and sink filling rate of two rice varieties in different nitrogen treatments.
Notes: Sink capacity (g m^{-2}) = No. of spikelets (m^{-2}) × 1000 grain wt.(g)/1000. Sink filling rate (%) = 100 × Grain yield (g m^{-2})/Sink capacity (g m^{-2}). Data are the means of three years' experiments. Error bars indicate SE from three years (n = 3).

Figure 1 shows the relationship between sink capacity and sink filling rate. Although sink filling rate for both NIP and AKI declined with increasing sink capacity (which increased with increasing fertilizer), sink filling rate with respect to sink capacity was higher for AKI than for NIP. Both sink and grain production efficiency per unit of

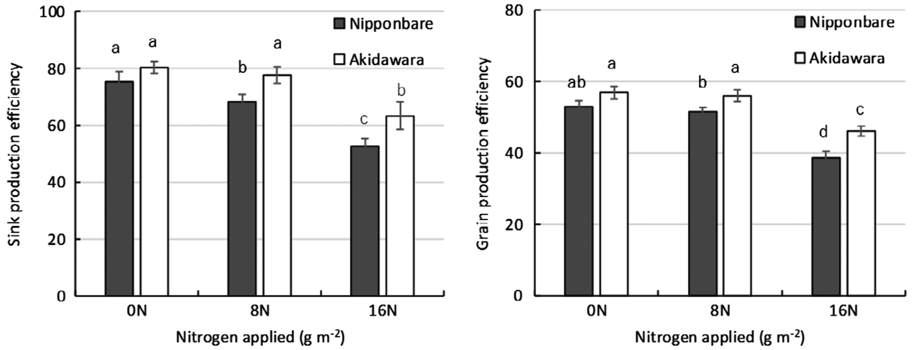

Figure 2. Sink and grain production efficiency per absorbed nitrogen of two rice varieties in different nitrogen treatment.

Notes: Sink production efficiency = Sink capacity (g m^{-2})/Nitrogen absorbed (g m^{-2}) at full-heading. Grain production efficiency = Grain yield (g m^{-2})/Nitrogen absorbed (g m^{-2}) at maturity. Data are the means of three years' experiments. Error bars indicate SE from three years (*n* = 3). Same letters are not significantly different at the 0.05 probability level by Tukey's test.

absorbed nitrogen decreased with increasing fertilizer in both varieties (Figure 2). However, both of the traits in 8N and 16N were significantly higher for AKI than for NIP, and the magnitude of difference between varieties increased with increasing fertilizer (Figure 2).

Quality-related traits

The perfect grain ratio of both varieties decreased with increasing sink capacity, which resulted from increasing fertilizer (Figure 3, Table 3). Although the means of perfect grain ratios were significantly lower for AKI, which has a large sink capacity, than for NIP, the magnitudes of these deficits were small: 1.9% and 2.8% for the 8N and 16N fertilizer regimes. Grain protein content increased with increasing fertilizer and was significantly lower for AKI than for NIP (Table 3), even when yield was increased (Figure 4).

Discussion

Factors for high yield

In this study, we compared the growth and yield of AKI, a high-yielding variety with good palatability (Ando et al., 2011), with those of NIP, a standard variety that takes approximately the same number of days to mature. Much research has been conducted on the factors limiting yield in rice, particularly on the relationship between yield and photosynthetic performance or increase in sink capacity. For temperate *japonica* varieties, it has been reported that insufficient sink capacity is the primary factor limiting yield (Kusutani et al., 1999; Oka et al., 1987; Takeda et al., 1984). The results of this study also suggest that increase in the sink capacity was the key contributors to the high yield in AKI by comparing with NIP. The increase of the sink capacity in AKI results from a conspicuous increase in the number of spikelets per panicle, despite the fact that the number of panicles and 1000-grain weight were smaller than those

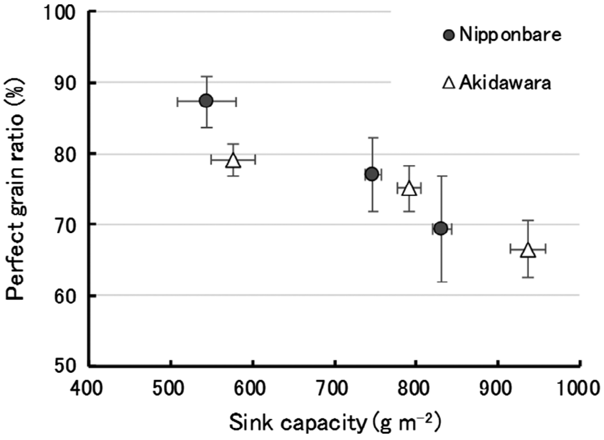

Figure 3. Relationship between sink capacity and perfect grain ratio.

Notes: Sink capacity (g m^{-2}) = No. of spikelets (m^{-2}) × 1000 grain wt.(g)/1000. Data are the means of three years' experiments. Error bars indicate SE from three years (*n* = 3).

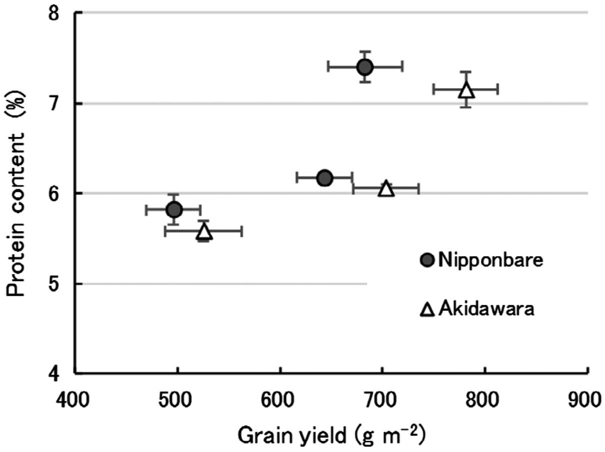

Figure 4. Relationship between grain yield and protein content of brown rice.

Notes: Data are the means of three years' experiments. Error bars indicate SE from three years (*n* = 3).

of NIP. The increase in spikelet number per panicle is likely due to introgression of the high-yielding 'Akenohoshi' allele (Ando et al., 2011), which increases spikelet number, at the Gn1 locus on the first chromosome. It is also believed to account for the increase in sink production efficiency in AKI. On the other hand, although sink capacity generally contributes to yield increase, sink capacity increase on its own has been shown to be unable to sufficiently increase yield because it is accompanied by a decline in sink filling (Ohsumi et al., 2011). This study comparing NIP and AKI growth under the same fertilizer regime, however, showed that AKI achieved the similar degree of sink filling to that in NIP, despite the fact that its spikelet number and sink capacity increased (Figure 1, Table 4). And its grain production efficiency and harvest index improved (Figure 2, Table 3). In addition to shoot dry weight increase during ripening (Δ*W*), the translocation of non-structural carbohydrate (NSC) from culm and leaf sheath to panicle has been reported to strongly influence the degree and stability of grain filling in rice (Nagata et al., 2001; Tsukaguchi et al., 1996). In the present study, panicle dry weight increase during ripening (Δ*P*) was significantly higher for AKI than for NIP despite the fact that no differences in Δ*W* were observed between varieties (Table 3). The greater Δ*P* in AKI might be derived from its larger sink capacity and the difference between varieties involves the translocation of NSC. Although we did not investigate NSC dynamics, it is assumed that AKI possesses traits that are favorable for NSC translocation. In an investigation of the relationship between the accumulation and translocation of NSC and sink filling, Morita and Nakano (2011) speculated that NSC accumulation up to heading and NSC translocation during ripening contribute to improved yield and quality by improving sink filling of the new variety 'Nikomaru' with high yield and high palatability. Our results suggest that similar investigation of NSC dynamics is warranted for AKI. Also, given the importance of lodging resistance as a trait for achieving high yields, note that during the three years of this experiment, no conspicuous lodging occurred in AKI despite its cultivation under high fertilizer, high-yielding conditions (maximum yield of 842 g m^{-2}). This result suggests that AKI possesses a certain degree of lodging resistance, which is another characteristic important to high-yielding varieties.

Characteristics of grain quality

The demand for low-priced commercial rice calls for the application of cultivation methods aimed at generating high yields. However, the pursuit of such high-yield methods should be balanced with efforts to simultaneously ensure high quality. As mentioned above, although AKI produces high yields through increased spikelet number, increase in spikelet number is generally accompanied by decline in external appearance (Kobata et al., 2004). In this study, perfect grain ratio decreased with increasing sink capacity (Figure 3) and was lower for AKI, which had higher spikelet numbers, than for NIP. However, in the comparison of perfect grain ratio between 16N in NIP and 8N in AKI, of which yields were around 700 g m^{-2} without significant difference (Table 4), the average perfect grain ratio of 8N in AKI was 75.1% and significantly higher than that of 16N in NIP (Table 3).

A negative correlation exists between grain protein content, a palatability trait, and the stickiness of cooked rice, with increased protein content adversely influencing perceived taste by reducing the stickiness of cooked rice (Song et al., 2012). Thus, analyzing changes in grain protein content is important when attempting to achieve high rice yields by increasing fertilizer application. As shown in Figure 4, the grain protein content of both varieties increased under high-yield conditions, but grain protein content increased to a lesser degree in AKI than in NIP. This is thought to be because, even though the amount of absorbed nitrogen translocated to panicles was higher in AKI (data not shown), the increase in panicle dry weight during ripening (Δ*P*) was rather large, nullifying the increase in protein content. It is notable that AKI exceeded grain yield over 700 g m^{-2} with protein content of 6.1% under standard nitrogen condition (8N) (Tables 3 and 4). In NIP, protein content was 7.4% under high nitrogen condition (16N) although its grain yield was around 700 g m^{-2}, which is equivalent to AKI under standard nitrogen condition (Table 3 and 4). These lines of evidence related to the perfect grain ratio and grain protein content strongly highlight that AKI makes high-yield potential and high grain quality compatible.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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References

Ando, I., Nemoto, H., Kato, H., Ohta, H., Hirabayashi, H., Takeuchi, Y., … Aoki, N. (2011). A new rice cultivar 'Akidawara' with high yield, good grain appearance, and good eating quality. *Breeding Research, 13*, 35–41 (In Japanese).

Ashikari, M., Salalibara, H., Lin, S., Yamamoto, T., Takashi, T., Nishimura, A., … Matsuoka, M. (2005). Cytokinin oxidase refulates rice grain production. *Science, 309*, 741–745.

International Rice Genome Sequencing Project. (2005). The map-based sequence of the rice genome. *Nature, 436*, 793–800.

Kobata, T., Uemuki, N., & Kagata, H. (2004). Shortage of assimilate supply to grain increases the proportion of milky white rice kernels under high temperatures. *Japanese Journal of Crop Science, 73*, 315–322. (In Japanese with English summary).

Kusutani, A., Ueda, K., Asanuma, K., & Toyota, M. (1999). Studies on varietal difference in yielding ability in rice –relationship between source-sink ratio and yield. *Japanese Journal of Crop Science, 68*, 24–18. (In Japanese with English summary).

Li, D., Nanseki, T., Matsue, Y., Chomei, Y., & Yokota, S. (2016). Variation and determinants of rice yields among individual paddy fields: Case study of a large-scale farm in the Kanto region of Japan. *Journal of the Faculty of Agriculture, Kyushu University, 61*, 205–214.

Morita, S., & Nakano, H. (2011). Nonstructural carbohydrate content in the stem at full heading contributes to high performance of ripening in heat-tolerant rice cultivar Nikomaru. *Crop Science, 51*, 808–828.

Nagata, K., Ohsumi, A., Yoshinaga, S., & Nakano, H. (2016). Cultivar difference in the yield response to climatic conditions after heading stage in high-yielding rice cultivars. *Japanese Journal of Crop Science, 85*, 367–372. (In Japanese with English summary).

Nagata, K., Yoshinaga, S., Takanashi, J., & Terao, T. (2001). Effects of dry matter production, translocation of nonstructural carbohydrates and nitrogen application on grain filling in rice Cultivar Takanari, a cultivar bearing a large number of spikelets. *Plant Production Science, 4*, 173–183.

Nitta, Y. (2010). Japanese rice producers' shift from high yield to high palatability and quality –characteristics of highly palatable rice–. *Journal of Developments in Sustainable Agriculture, 5*, 96–100.

Ohsumi, A., Takai, T., Ida, M., Yamamoto, T., Arai-Sanoh, Y., Yano, M., … Kondo, M. (2011). Evaluation of yield performance in rice near-isogenic lines with increased spikelet number. *Field Crops Research, 120*, 68–75.

Oka, M., Sumi, A., & Takeda, T. (1987). Relation between sink capacity and sink/source ratio, representing sink capacity per leaf area at heading time, in various types of rice cultivars. *Japanese Journal of Crop Science, 56*, 265–267. (In Japanese with English summary).

Song, Y., Choi, I., Sharma, P. K., & Kang, C. (2012). Effect of different nitrogen doses on the storage proteins and palatability of rice grains of primary and secondary rachis branches. *Plant Production Science, 15*, 253–257.

Takeda, T., Oka, M., & Agata, W. (1984). Characteristics of dry matter and grain production of rice cultivars in Japan II. Comparison of grain production between old and new types of rice cultivars. *Japanese Journal of Crop Science, 53*, 12–21. (In Japanese with English summary).

Takeuchi, Y., Hori, K., Suzuki, K., Nonoue, Y., Takemoto-Kuno, Y., Maeda, H., … Ishii, T. (2008). Major QTLs for eating quality of an elite Japanese rice cultivar, Koshihikari, on the short arm of chromosome 3. *Breeding Science, 58*, 437–445.

Tsukaguchi, T., Horie, T., & Ohnishi, M. (1996). Filling percentage of rice spikelets as affected by availability of non-structural carbohydrates at the initial phase of grain filling. *Japanese Journal of Crop Science, 65*, 445–452. (In Japanese with English summary).

Yokoo, M., Hirano, M., & Imai, T. (2005). Annual change in leading rice varieties between 1956 and 2000 in Japan. *Bulletin NARO Institute of Crop Science, 67*, 19–125. (In Japanese with English summary).

Yoshinaga, S., Takai, T., Arai-Sanoh, Y., Ishimaru, T., & Kondo, M. (2013). Varietal differences in sink production and grain-filling ability in recently developed high-yielding rice (*Oryza sativa* L.) varieties in Japan. *Field Crops Research, 150*, 74–82.