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Evaluation of yield performance in rice near-isogenic lines with increased spikelet number

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ABSTRACT

Rice yield potential is determined by the balance between sink size and source capacity. To clarify the factors that limit yield in *temperate japonica* cultivars, we compared the yield performance of Sasanishiki, a *temperate japonica* cultivar, with those of three near-isogenic lines (NILs) of Sasanishiki with introgression of quantitative trait loci (QTL) derived from a high-yielding *indica* cultivar, Habataki: *qSBN1*, which increases the number of secondary rachis branches; *qPBN6*, which increases the number of primary rachis branches; and a pyramid line that combines these two QTLs. NIL (*SBN1*), NIL (*PBN6*), and NIL (*SBN1* + *PBN6*) produced 28–37%, 9–16%, and 62–65% more spikelets per panicle than Sasanishiki, respectively. However, the NILs with increased spikelet number per panicle did not increase grain yield significantly, because compensation is taken place among different yield components. The pyramid line nevertheless had 4–12% higher yield than Sasanishiki due to greater translocation of carbohydrates from stem to panicle. There was no difference in carbohydrate accumulation before heading or in biomass production among Sasanishiki and the three NILs. The results indicate that increasing sink size does not substantially improve yield in Sasanishiki, which lacks sufficient substrate supply to fully satisfy the increased sink demand that results from the spikelet-number QTLs.

1. Introduction

Rice (*Oryza sativa* L.) is one of the most important crops for world food security. Since the population continues to increase and the cultivated area is reduced by urbanization and other factors, a 40% yield increase will be necessary during the next 40 years to meet global food demand (Murchie et al., 2009). In recent decades, however, improvements in the yield potential of rice have been limited, while consumer demand for high-quality food rice is increasing. Part of the problem is that recently released commercial varieties have narrow genetic backgrounds derived from limited number of popular varieties with stagnant yield potentials in Japan (Nakagahra et al., 1997; Tabuchi et al., 2007; Yamamoto et al., 2010). A similar problem has been reported in China (Peng et al., 2009). The commercial cultivars of *temperate japonica* rice often show low yield and biomass production compared with high-yielding *indica* varieties that have been developed for multiple uses, including both food for humans and livestock forage (Takai et al., 2006; Peng et al., 2009). The introgression of several traits from high-yielding *indica* varieties would therefore provide an opportunity to improve the yield potential of *temperate japonica* cultivars.

A number of efforts have been made to clarify the physiological factors that limit rice yield, with a focus on the relationship between sink size and source capacity: the former is defined as the product of the total spikelet number per unit area and the single-grain weight, whereas the latter combines biomass production with the translocation of accumulated carbohydrates from the stem to the panicles (Takeda et al., 1984; Oka et al., 1987; Kusutani et al., 1999; Song et al., 1990; Ying et al., 1998; Peng et al., 2000). Most studies have reported that grain yields of *temperate japonica* cultivars are primarily limited by their small sink size (Takeda et al., 1984; Oka et al., 1987; Kusutani et al., 1999). On the other hand, recent high-yielding *indica* varieties possess large sink size, high photosynthetic rates, and high translocation of carbohydrates to the rice grains (Takai et al., 2006; Ohsumi et al., 2007; Katsura et al., 2007). It has been proposed that enlarging sink size may enhance the source

Abbreviations: LAI, leaf area index; NIL, near-isogenic line; PRB, primary rachis branches; QTL, quantitative trait locus; SRB, secondary rachis branches.

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Table 1
Panicle architecture and yield components of Sasanishiki, Habataki, and the three QTL-NILs.

Year	Treatment	Variety/line	Spikelet number per panicle (no.)	Ratio of spikelet number on SRB/on PRB	Panicle number (no. m^{-2})	Total spikelet number (no. m^{-2})	Winnowed grain yield (g m^{-2})[#]	Single-grain weight (mg)
2007	N1	Sasanishiki	95.3 (-) a	0.88 (-) a	306(-) a	29157(-) a	525(-)	17.1 (-) a
		NIL(*SBN1*)	122.1 (1.28) b	1.34 (1.52) b	278 (0.91) a	34035 (1.17) ab	557 (1.06)	16.0 (0.93) b
		NIL(*PBN6*)	110.1 (1.16) ab	0.97 (1.10) a	328 (1.07) a	36121 (1.24) ab	538 (1.02)	15.8 (0.93) bc
		NIL(*SBN1* + *PBN6*)	157.7 (1.65) c	1.48 (1.68) b	264 (0.86) a	40858 (1.40) b	589 (1.12)	15.4 (0.90) c
		Habataki	176.8 (1.85) c	1.90 (2.15) c	156 (0.51) b	27473 (0.94) a	456 (0.87) ns	16.8 (0.98) a
	N2	Sasanishiki	91.9 (-) a	0.95 (-) a	355(-) a	33039(-)	572(-)	17.3 (-) a
		NIL(*SBN1*)	118.9 (1.29) b	1.44 (1.51) b	326 (0.92) a	38402 (1.16)	584 (1.02)	16.2 (0.93) b
		NIL(*PBN6*)	100.5 (1.09) ab	0.99 (1.05) a	355 (1.00) a	35800 (1.08)	558 (0.97)	16.3 (0.94) b
		NIL(*SBN1* + *PBN6*)	148.6 (1.62) c	1.47 (1.55) b	312 (0.88) ab	46333 (1.40)	622 (1.09)	15.7 (0.91) c
		Habataki	168.6 (1.84) c	2.08 (2.19) c	207 (0.58) b	34833 (1.05) ns	578 (1.01) ns	17.0 (0.98) a
2008	N2	Sasanishiki	96.1 (-) a	1.08 (-) a	306(-) a	29370(-) a	602(-) a	19.2 (-) a
		NIL(*SBN1*)	131.9 (1.37) c	1.57 (1.46) b	284 (0.93) a	37262 (1.27) b	635 (1.06) ab	17.5 (0.91) b
		NIL(*PBN6*)	110.3 (1.15) b	1.14 (1.06) a	311 (1.02) a	34348 (1.17) ab	576 (0.96) a	17.5 (0.91) b
		NIL(*SBN1* + *PBN6*)	156.2 (1.63) d	1.70 (1.58) b	281 (0.92) a	43836 (1.49) c	627 (1.04) ab	16.8 (0.87) c
		Habataki	214.5 (2.23) e	2.71 (2.52) c	184 (0.60) b	39321 (1.34) bc	683 (1.14) b	16.8 (0.87) c
Analysis of variance								
year			17.0^{++}	38.8^{++}	4.7^{+}	0.2	2.6	123^{++}
variety			80.7^{++}	152.1^{++}	8.4^{++}	4.3^{+}	0.8	46^{++}
year × variety			3.7^{+}	5.7^{++}	0.1	0.4	0.5	12^{++}

[#] At 14% moisture content. PRB, primary rachis branches; SRB, secondary rachisbranches. The values within parentheses indicate the proportion of the value for Sasanishiki. Values in a column followed by different letters differ significantly ($p < 0.05$, Duncan's multiple-range test). ns, no significant difference among cultivars and The N1 treatment was excluded from the ANOVA because it used a different N application. $^{+}$,$^{++}$ indicate F values that are significant at $p < 0.05$ and $p < 0.01$, respectively.

capacity, since sink demand regulates source capacity in several crops (Reynolds et al., 2005; McCormick et al., 2006). However, the relative importance of sink size and source capacity for improved yield of rice has not been clearly determined in previous varietal comparisons because the diversity of the genetic backgrounds of the examined varieties made it difficult to accurately distinguish the effects of sink size and source capacity.

Advances in genomics have revealed a number of genes and quantitative trait loci (QTLs) for traits related to sink size in rice. These include QTLs for spikelet number per panicle (Ashikari et al., 2005; Huang et al., 2009; Wang et al., 2009; Terao et al., 2010), single-grain weight (Wan et al., 2006; Fan et al., 2006; Song et al., 2007; Shomura et al., 2008), and tiller number (Li et al., 2003; Jin et al., 2008; Liu et al., 2009; Fujita et al., 2010). Although the genes and QTLs that have been identified could explain the phenotypic differences in each trait, few studies have demonstrated their contributions to grain yield in rice.

For example, the high-yielding *indica* variety, Habataki, has more spikelets per panicle than the *temperate japonica* cultivar, Sasanishiki, which has an average yield. This has been attributed to the presence of two major QTLs (Nagata et al., 2002; Ando et al., 2008): one (*qSBN1*), on chromosome 1, increases the number of secondary rachis branches (SRB), and the other (*qPBN6*), on chromosome 6, increases the number of primary rachis branches (PRB). Ando et al. (2008) developed three near-isogenic lines (NILs) containing these QTLs from Habataki in the Sasanishiki genetic background: NIL (*SBN1*), NIL (*PBN6*), and the pyramid line NIL (*SBN1* + *PBN6*). They demonstrated that each QTL increased spikelet number per panicle in Sasanishiki, and that the pyramid line produced more spikelets than either single-QTL NIL or the wild-type. However, it is not yet clear whether the increase in spikelet number per panicle contributes to a yield increase in the NILs. Evaluating the yield performance of these NILs would improve our understanding of the relative importance of sink size, source capacity, and their interaction in determining yield.

The objective of the present study was to evaluate the contributions of the Habataki QTLs to increasing the yield of Sasanishiki under field conditions. We investigated the yield and yield components, including spikelet number per panicle, panicle number, and single-grain weight, as well as characteristics of the source capacity, such as photosynthetic rates and developmental changes in the stem carbohydrate content. On the basis of the results, we discuss the effect of increased spikelet number on rice yield in relation to the sink–source balance.

2. Materials and methods

2.1. Plant materials

Field experiments were conducted in a paddy field of the National Institute of Crop Science, Tsukuba, Japan (36°0′N, 140°1′E) for two years to evaluate yield and yield-related traits for three NILs, NIL (*SBN1*), NIL (*PBN6*), and NIL (*SBN1* + *PBN6*), in comparison with their parents, Sasanishiki and Habataki (Ando et al., 2008). NIL (*SBN1*) and NIL (PBN6) contain 3.35-Mb and 390-kb segments, respectively, of chromosomal regions derived from Habataki. The rice seeds were sown in seed beds on 1 May and 28 April and were transplanted on 24 and 22 May in 2007 and 2008, respectively, at a rate of one plant per hill, with a total of three replicates. Plant spacing was 15 cm between plants by 30 cm between rows. Plot size was larger than 3.4 m^2 with five-plant rows in 2007 and than 6.1 m^2 with eight-plant rows in 2008. Plants were grown under continuous irrigation with two levels of N fertilization, designated N1 only in 2007 and N2 in both years. The total amounts of N fertilizer were 5 g m^{-2} for the N1 treatment plots in 2007, using coated urea (a