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Contribution of Sink and Source Sizes to Yield Variation among Rice Cultivars

Iskandar Lubis, Tatsuhiko Shiraiwa, Masao Ohnishi*, Takeshi Horie and Naoto Inoue**

(Graduate School of Agriculture, Kyoto University, Kitashirakawa, Sakyo-ku, Kyoto 606-8502, Japan;
**Faculty of Life and Environmental Science, Shimane University, 2059 Kami honjyo-cho, Matsue 690-1102, Japan;*
***Faculty of Agriculture, Shinshu University, 8304 Minami-minowa, Nagano 399-4958, Japan)*

Abstract : In order to identify the key factors that arrest yield improvement in rice, we observed fifteen divergent cultivars in a field at Kyoto, Japan in 1995 and 2001 under various nitrogen (N) regimes. The contribution that sink size (spikelet number × single fully ripened grain mass), source size (total available carbohydrate), and source components, non-structural carbohydrate (pre-reserved) at full heading (NSC_h) and dry matter production during grain filling (DMP) had to the variation in yield among cultivars was examined. The dry weight of rough brown rice (Y) ranged from 310 to 743 g m^{-2} throughout two years and under all N regimes examined. Although Y correlated with both sink and ource sizes, it tended to correlate more closely with source size than with sink size. In many cultivars, source size was smaller than sink size at all conditions examined except for the low nitrogen regime. The contribution of source components to Y was analyzed with the equation : $Y = C_n\ NSC_h + C_d$ DMP, where C_n and C_d are coefficients of NSC utilization and of DMP utilization for grain filling. Y correlated with DMP more closely than with NSC_h. ΔNSC (NSC_h - NSC_m), where NSC_m is NSC at maturity and "C_n" vaguely correlated with the difference between sink size and DMP, showing that NSC is used to ompensate for the shortage of DMP to fill grains. At the same time, there were cultivar differences in NSC_h and "C_n". The highest yielding cultivar Takanari always had the greatest DMP, relatively high NSC_h and stably high values of "C_n". In conclusion, yield variation among rice cultivars correlated with source size more closely than with sink size, and DMP rather than NSC_h primarily contributed to Y. While NSC_h tended to be utilized complementarily to DMP, the contribution of NSC_h seemed to depend on the ability of rice cultivars to utilize NSC.

Key words : Dry matter production, Nitrogen application, Non-structural carbohydrate, Sink, Source and Yield.

The yield of rice is controlled by sink size and/or source size. Sink size, also called yield capacity (Yoshida, 1972) or yield potential (Takami et al., 1990), is determined by spikelet number per unit area and single fully ripened grain mass. The source size for grain filling consists of non-structural carbohydrate stored up to the heading stage and dry matter production during that period (Saitoh et al., 1990; Takami et al., 1990; Yamamoto et al., 1991; Tsukaguchi et al., 1996).

Sink size is determined by crop growth performance before heading (Yoshida, 1981; Fujita and Yoshida, 1984). Spikelet number per unit area is a function of plant nitrogen (N) concentration and aboveground dry weight at panicle formation stage (Hasegawa et al., 1994), and the size of hulls that limits the weight of single fully ripened grain mass is also determined before heading (Horie, 2001). On the other hand, the source size is determined by crop growth before and after heading. Non-structural carbohydrate (NSC) accumulates rapidly during the two weeks before heading, and reaches a maximum around the heading stage (Yoshida, 1981). Dry matter production during grain filling (DMP) is the sum of photosynthate produced during that period, being associated with the amount of solar energy absorbed by the crop, plant N nutrition and longevity of the tissue (Yoshida, 1972; Saitoh et al., 1991; Hasegawa et al., 1994; Horie et al., 1997).

A great deal of work has been done to clarify the superior characteristics of high yielding rice cultivars compared with the common cultivars (Weng et al., 1982; Song et al., 1990a; Yamamoto et al., 1991; Amano et al., 1993; Kusutani et al., 1993; Saitoh et al., 1993; Sumi et al., 1996). Amano et al. (1993) attributed the higher yield of a Chinese hybrid variety, compared with a Japanese cultivar, to higher spikelet number per area associated with greater nitrogen accumulation before heading and especially to the larger amount of dry matter translocated from the vegetative part to the grain. Observing one hundred rice cultivars, Kusutani et al. (1993) also characterized the highest yielding type as having a very large sink size (as expressed by volume), high filling percentage (yield per sink volume) and the

Received 22 February 2002. Accepted 6 December 2002. Corresponding author : Iskandar Lubis (Department of Agronomy, Bogor Agricultural University, Kampus IPB Darmaga, Bogor 16680, Indonesia, iskandarlbs@yahoo.com).

Abbreviations : DMP, dry matter production during grain filling; G, single fully ripened grain mass; N, nitrogen; n, spikelet number; NPT, IR65564-44-2-2; NSC, non-structural carbohydrate; NSC_h, NSC at full heading stage; NSC_m, NSC at maturity; ΔNSC, NSC utilized during grain filling; WAB, WAB 450-1-B-P-38-HB; Y, dry weight of rough brown rice.

great contribution of pre-heading reserves to yield. They considered that high yield is not necessarily correlated with a large DMP. Saitoh et al. (1993) showed that Milyang 23, the highest yielding cultivar among 14 entries, had a largest sink size and highest carbohydrate concentration in the stem at heading. Including these studies, many authors agreed that the high yielding ability in rice is supported by a large sink size (Yoshida, 1972; Song et al., 1990a; Saitoh et al., 1991; Shi et al., 1996), and is associated with efficient utilization of carbohydrate pre-reserved at heading (Weng et al., 1982; Song et al., 1990b; Sumi et al., 1996).

In a theoretical work, Takami et al. (1990) introduced a hypothesis on rice yield that grain yield equals the sink size when source size equals or is greater than the sink size and they assumed that the plant loses pre-reserved dry matter to fill a deficit of the DMP for the sink demand. Dingkuhn and Le Gal (1996) observed the dry matter change during grain filling under varied water regimes, and supported this model to some extent, although they also suggested that reserves are not necessarily fully mobilized whenever there is a shortage of DMP to fill sink demand. The compensatory utilization of pre-reserved matter proposed above implies that NSC can contribute to the yield when there is a great demand for assimilates by the large sink.

On the other hand, using 12 cultivars bred at IRRI since 1966, Peng et al. (2000) observed that an increase in yield of cultivars released before 1980 was mainly due to the improvement of harvest index (HI), while that of cultivars released after 1980 were associated with an increase in total biomass. The higher yield potential of indica/indica hybrids compared with indica inbred cultivars was also attributed to greater biomass production rather than harvest index (Peng et al., 1999).

These findings indicate that the key factors that arrest yield improvement in rice has not been fully identified, especially in terms of the relative contribution of sink size and source size to yield. A comprehensive analysis of sink and source relationship and the contribution of their components to the yield may be helpful in generalizing the factors necessary to achieve a higher yield and breeding strategy to reach the highest possible yields. This study aims to clarify the cultivar difference in the yield in relation to source size and sink size, and to examine the contribution of source components to the yield.

Materials and Methods

Experimental results obtained in two years were analyzed using a total of 15 rice cultivars with a wide range of genetic differences from a local cultivar of tropical japonica to the new plant type bred at IRRI.

1. Experiment in 1995

Nine rice cultivars (Table 1) were grown in 1995 in a paddy field at Kyoto University, latitude 35.0° N, longitude 135° E with an elevation of 20 m from the sea level. The soil type was classified as alluvial sandy loam and grey lowland soil (Haplaquept) containing 3.1 and 0.22% of total carbon and nitrogen (N), respectively (unpublished data). The planting date was May 23, and planting density was 30×15 cm with 2 plants per hill (except for the Takanari under HL N regime (see below) where the density was only 1 plant per hill). N was applied at three different rates, namely Low (L), High-early (HE) and High-late (HL) to each cultivar without replication. N was applied at the rates of 4, 0, 1, 1 and 1 g m^{-2} (L), 4, 0, 4, 4 and 2 g m^{-2} (HL) and 4, 4, 2, 2 and 2 g m^{-2} (HE) at pre-transplanting, tillering and 26, 16 and 0 days before heading, respectively. Under every N regime, 10 g m^{-2} P_2O_5 was applied as basal, while 14 g m^{-2} K_2O was applied together with N. The aboveground plant material was harvested at full heading, 15 days after full heading and maturity, and dry weight was determined separately for the leaf blade, leaf sheath + culm and panicle after oven drying at 80°C for 48 hours. Contents of N and non-structural carbohydrate (NSC) were determined for the sampled materials with a near infrared reflectance analyzer (Bran+Luebbe InfraAlyzer 500), and for calibration, N content was measured by the Kjeldahl method, and NSC content by the α amylase method (Abe, et al., 1984).

Table 1. Type and origin country of rice cultivars used in years 1995 and 2001.

Cultivar	Type	Country Origin	1995	2001
Takanari	Indica x Japonica	Japan	Used	Used
Nipponbare	Japonica	Japan	Used	Used
Koshihikari	Japonica	Japan	Used	Used
Takenari	Japonica	Japan	-	Used
Yumehikari	Japonica	Japan	Used	-
Amaroo	Indica	Australia	Used	-
Bluebonet	Japonica	U. S. A.	Used	-
Ch86	Indica	China	-	Used
IR65564-44-2-2	Indica x Tropical Japonica	Philippines	-	Used
IR72	Indica	Philippines	-	Used
Nanjing11	Indica	China	Used	-
Shanguichao	Indica	China	-	Used
YA83049	Indica	Australia	Used	-
WAB450-1-B-P-38-HB	*Glaberrima* x *Sativa*	Cote d'Ivoire	-	Used
Banten	Tropical Japonica	Indonesia	Used	Used

2. Experiment in 2001

Ten rice cultivars (Table 1) were grown on the same paddy field as in 1995 using a randomized block design with three replications. The planting date was May 25, and planting density was 30×15 cm with one plant per hill. Application rates of the fertilizer, N : P_2O_5 : K_2O, was 5 : 12 : 12 g m^{-2} for Cultivar Banten and Ch86, and 12 : 12 : 12 g m^{-2} for the other cultivars. Nitrogen was applied as top dressing in five divided doses, and P_2O_5 and K_2O as basal. The aboveground crop dry weight was measured at full heading, 15 days after full heading and maturity. Nitrogen and NSC contents were determined as in the experiment in 1995.

3. Data analysis

Sink size was calculated as n G (g m^{-2}), where n is the

Table 2. Yield and yield components of rice cultivars grown under three N fertilization regimes in 1995 and under the same N fertilization regime with three replications in 2001.

Cultivar and Treatment	Rough brown rice	Number of spikelet	Single grain mass	Filling percentage	Growth duration	Cultivar and Treatment	Rough brown rice	Number of spikelet	Single grain mass	Filling percentage	Growth duration
	g m^{-2}	1000 m^{-2}	mg	%	d		g m^{-2}	1000 m^{-2}	mg	%	d
1995, L						1995, HE					
Takanari	569	38.0	18.2	82.3	128	Takanari	670	43.3	18.8	82.1	128
Nipponbare	434	29.5	19.6	75.0	123	Nipponbare	491	35.7	19.1	72.0	123
Koshihikari	428	27.0	19.8	80.1	113	Koshihikari	497	31.2	19.7	81.0	113
Yumehikari	417	30.2	17.3	79.9	135	Yumehikari	456	32.1	17.3	82.2	135
Amaroo	462	34.8	18.9	70.3	131	Amaroo	531	45.2	18.9	62.3	131
Bluebonet	343	27.0	18.0	70.5	135	Bluebonet	385	38.7	18.8	53.0	135
Nanjing11	514	30.9	20.1	82.6	114	Nanjing11	593	39.0	20.7	73.7	114
YA83049	414	35.8	18.6	61.9	116	YA83049	376	38.2	18.3	53.7	116
Banten	316	22.2	18.8	75.4	135	Banten	320	27.3	18.5	63.5	135
Mean	433	32.1	18.9	71.3	124	Mean	471	40.3	19.2	60.7	124
1995, HL						2001					
Takanari	606	48.3	18.5	68.0	128	Takanari	743	50.2	19.3	76.7	131
Nipponbare	487	34.2	19.4	73.4	123	Nipponbare	553	33.0	20.0	83.7	119
Koshihikari	513	32.0	20.5	78.1	113	Koshihikari	494	35.6	18.6	74.7	105
Yumehikari	510	38.3	17.1	77.8	135	Takenari	503	37.1	17.8	76.4	132
Amaroo	489	48.6	19.2	52.3	131	IR72	649	51.1	18.8	67.7	124
Bluebonet	414	37.4	18.2	60.6	135	Shanguichao	668	59.5	14.2	79.3	113
Nanjing11	544	36.4	20.6	72.6	114	NPT	502	34.5	20.0	72.9	129
YA83049	359	38.4	19.2	48.7	116	WAB	426	32.0	20.8	63.8	111
Banten	310	32.4	18.9	50.8	135	Ch86	(349)	(25.4)	(18.8)	(73.3)	(119)
Mean	423	38.6	19.2	57.0	126	Banten	(339)	(20.2)	(20.0)	(83.7)	(126)
						Mean	567	41.6	18.7	74.4	121
						LSD	75	3.4	0.5	10.1	0

spikelet number per unit area (m^{-2}), and G is the single grain mass of fully ripened brown rice (g) (with specific gravity higher than 1.06 for japonica, 1.03 for indica and the mass at 0% moisture). Filling percentage (FP) was calculated as $FP = Y/(n\ Go)\ 100\ (\%)$, where Y = rough brown rice yield (g m^{-2}, 0% moisture), and Y in year 2001 was calculated assuming hull weight to be 17% of grain weight. Source size was calculated as $DMP + NSC_h$ (g m^{-2}), where DMP is the dry matter production during grain filling and NSC_h is the content of NSC in the leaves and stems at heading. NSC utilized during grain filling (ΔNSC) was calculated as (NSC_h-NSC_m), where NSC_m is the NSC content at maturity. Yield was further described as $Y = C_n\ NSC_h + C_d\ DMP$, and the coefficient "$C_n$" that presents the coefficient of NSC_h utilization for grain filling was obtained by dividing ΔNSC by NSC_h. The coefficient "C_d" is then the coefficient of DMP utilization, which was calculated from the equation above.

For cultivar comparison, the analysis of variance with a completely randomized block design was conducted only for the experiment in 2001, in which triplicated data were available. In this analysis, data for cultivars Ch86 and Banten were not included because they received N application different from that in the others. In 1995, due to lack of replications for each N regime, the statistical test for cultivar difference was not conducted. However, the variability of measurement values was presented in Table 3 for each cultivar with a standard deviation among the three N regimes.

Results

1. Cultivar difference in yield in relation to sink and source sizes

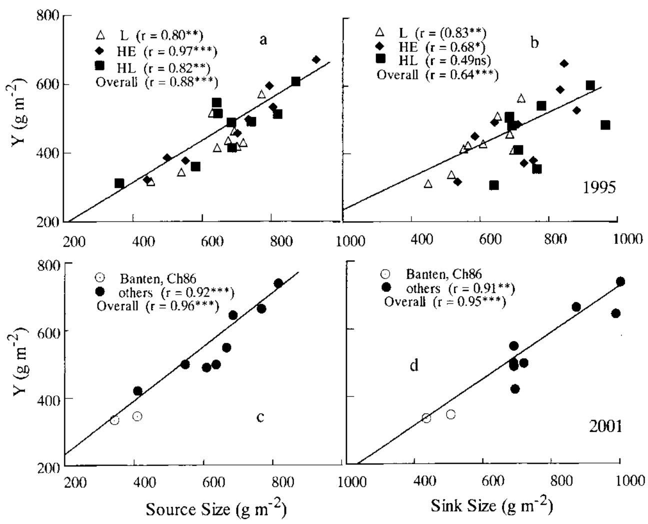

Fig. 1. Correlation of the dry weight of rough brown rice (Y) with source (a, c) and sink (b, d) in the cultivars grown under three N fertilization regimes in 1995, Low (L), High-early (HE) and High-late (HL) application and under N fertilization at 5 g m^{-2} for Banten and Ch86 and 12 g m^{-2} for the others in 2001. ns, *, ** and *** denote not significant and significant at 5%, 1% and 0.1% level, respectively.

Rough brown rice yield at 0% moisture (Y) of rice cultivars planted in 1995 ranged from 310 g m^{-2} of Banten under the HL N regime to 670 g m^{-2} of Takanari under the HE N regime, and from 339 g m^{-2} of Banten to 743 g m^{-2} of Takanari in 2001 (Table 2). Growth duration of cultivars used in the experiments ranged from 105 days of Koshihikari in 2001 to 135 days of Banten, Bluebonet and Yumehikari in 1995. The yield of cultivar Takanari, an indica of intermediate growth duration, was highest under all N regimes in 1995 and