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

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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 x single fully ripened grain mass), source size (total available carbohydrate), and source components, non-structural carbohydrate (pre-reserved) at full heading (NSCm) 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 745 g m⁻² throughout two years and under all N regimes examined. Although Y correlated with both sink and source 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 = Cm NSCm + Cd DMP, where Cm and Cd are coefficients of NSC utilization and of DMP utilization for grain filling. Y correlated with DMP more closely than with NSCm. ∆NSC (NSCm - NSCf), where NSCf is NSC at maturity and "Cm" vaguely correlated with the difference between sink size and DMP, showing that NSC is used to compensate for the shortage of DMP to fill grains. At the same time, there were cultivar differences in NSC, and "Cm". The highest yielding cultivar Taknari always had the greatest DMP, relatively high NSC, and stably high values of "Cn". In conclusion, yield variation among rice cultivars correlated with source size more closely than with sink size, and DMP rather than NSC primarily contributed to Y. While NSC tended to be utilized complementarily to DMP, the contribution of NSCm 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 photosynthetic production 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 longevity of the tissue (Yoshida, 1972; Saitoh et al., 1991; Hasegawa et al., 1994; Horie et al., 1997).

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; NSCf, NSC at full heading stage; NSCm, NSC at maturity; ∆NSC, 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. Saitho 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; Saitho 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 was 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 (Haplaquyet) 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 Takahari 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 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 P₂O₅ was applied as basal, while 14 g m⁻² K₂O 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).

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 23, and planting density was 30 × 15 cm with one plant per hill. Application rates of the fertilizer, N : P₂O₅ : K₂O, 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 P₂O₅ and K₂O 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 number of panicles and G is grain weight. Table 1. Type and origin country of rice cultivars used in years 1995 and 2001.

| Cultivar     | Type          | Country            | 1995 | 2001 |
|--------------|---------------|--------------------|------|------|
| Takahari     | Indica × Japonica | Japan            | Used | Used |
| Nipponbare   | Japonica      | Japan            | Used | Used |
| Kodubitori   | Japonica      | Japan            | Used | Used |
| Takamai      | Japonica      | Japan            | Used | Used |
| Yumehikari   | Japonica      | Japan            | Used | Used |
| Azumato      | Indica        | Australia        | Used | Used |
| Blastobot    | Japonica      | U.S.A.           | Used | Used |
| Ch66         | Indica        | China            | Used | Used |
| IR65564-44-2-2 | Indica x Tropical Japonica | Philippines | Used | Used |
| IR72         | Indica        | Philippines      | Used | Used |
| Ningjing1    | Indica        | China            | Used | Used |
| Shengxiantao | Indica        | China            | Used | Used |
| YAD3049      | Indica        | Australia        | Used | Used |
| WAD455-1-B-P-38-HB | Glutinina x Sativa | Core d’Ivire | Used | Used |
| Banten       | Tropical Japonica | Indonesia       | Used | Used |
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 + NSCₘ, (g m⁻²), where DMP is the dry matter production during grain filling and NSCₘ is the content of NSC in the leaves and stems at heading. NSC utilized during grain filling (ΔNSC) was calculated as (NSCₘ−NSCₙ), where NSCₙ is the NSC content at maturity. Yield was further described as Y = C n NSC + C d DMP, and the coefficient “C n” that presents the coefficient of NSCₙ utilization for grain filling was obtained by dividing ΔNSC by NSCₙ. 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
among cultivars in 2001 due to the high spikelet number, and moderate to high single grain mass and filling percentages.

In Fig. 1, Y was plotted against the sink and source sizes, for each experiment conducted in 1995 and 2001. The sink size in 1995 ranged from 419 g m\(^{-2}\) of Banten under L N regime to 935 g m\(^{-2}\) of Amaroo under the HL N regime, and in 2001 from 405 g m\(^{-2}\) of Banten to 971 g m\(^{-2}\) of Takanari. Source size in 1995 ranged from 330 g m\(^{-2}\) of Banten under the HL N regime to 902 g m\(^{-2}\) of Takanari at HE regime, and in 2001 from 313 g m\(^{-2}\) of Banten to 786 g m\(^{-2}\) of Takanari. In the two years, Takanari had the highest source size. Putting the data on all cultivars under all N regimes together, Y in 1995 was more closely correlated with the source size (r = 0.88\(*\*\*) \) than with the sink size (r = 0.64\(*\*\*)\). The correlation coefficients showed that Y was closely correlated with the source size in the plants under high nitrogen applications, HL and HE N regimes (Fig. 1a). The relationship between Y and source or sink size in year 2001 showed significantly positive correlations. The value of correlation coefficient for source was slightly higher than that for sink size (Fig. 1c and d).

Source and sink sizes in each N regime were compared in Fig. 2. Under the L N regime in 1995, most cultivars had source sizes equal to or higher than respective sink sizes. By contrast, source sizes under the HE and HL N regimes were lower than sink sizes in many cultivars. This trend was further distinctive in 2001. Thus the source and sink sizes were well balanced only under the L N regime in 1995, but not necessarily balanced under the other N regimes, when the productivity was higher than under the L N regime in 1995.

2. Relative contribution of source components to the yield

The source size and its components in each cultivar are shown in Table 3, averaging values across the three N regimes and three replications for 1995 and 2001, respectively. Variability among cultivars and its association with Y was examined for each component calculating their coefficient of variation (C.V.) and coefficient of correlation with Y. NSC\(_{h}\) ranged from 176 g m\(^{-2}\) in Banten to 316 g m\(^{-2}\) in Yumehikari in 1995 and from 62 g m\(^{-2}\) in Koshihikari to 159 g m\(^{-2}\) in NPT in 2001. DMP ranged from 212 g m\(^{-2}\) of Banten to 975 g m\(^{-2}\) of Takanari in 1995, and from 243 g m\(^{-2}\) of Banten to 669 g m\(^{-2}\) of Takanari in 2001. Thus, the highest size of source in Takanari (Table 2) was attributed mainly to high DMP both in 1995 and 2001. DMP had a closer correlation with Y (r = 0.92\(*\*\*) in both years) than NSC\(_{h}\) (r = 0.37\(\cdot\)4 in 1995 and r = 0.38\(\cdot\)3 in 2001), indicating that variation in the yield among rice cultivars depended more on DMP than on NSC\(_{h}\).

Table 3. Relative contribution and utilization efficiency of the source components, mean values of three N regimes in 1995 and of three replications in 2001.

| Cultivar   | NSC\(_{h}\) | DMP | C\(_{n}\) | \(C_{n}\) |
|------------|------------|-----|---------|---------|
| 1995       | g m\(^{-2}\) | g m\(^{-2}\) |         |         |
| Takanari   | 254 ± 62   | 575 ± 56 | 0.55 ± 0.04 | 0.82 ± 0.04 |
| Nipponbare | 215 ± 24   | 435 ± 13 | 0.47 ± 0.14 | 0.84 ± 0.01 |
| Koshihikari | 190 ± 22  | 480 ± 37 | 0.52 ± 0.04 | 0.82 ± 0.17 |
| Yumehikari | 316 ± 39   | 395 ± 93 | 0.45 ± 0.07 | 0.80 ± 0.04 |
| Amaroo     | 191 ± 28   | 557 ± 29 | 0.46 ± 0.02 | 0.77 ± 0.01 |
| Bluebonet  | 194 ± 26   | 352 ± 125 | 0.46 ± 0.11 | 0.86 ± 0.19 |
| Ningning11 | 189 ± 5    | 471 ± 86 | 0.60 ± 0.03 | 0.94 ± 0.10 |
| 2001       | g m\(^{-2}\) | g m\(^{-2}\) |         |         |
| Takanari   | 118        | 669     | 0.91     | 0.95    |
| Nipponbare | 84         | 554     | 0.09     | 0.99    |
| Koshihikari | 62        | 518     | 0.66     | 0.95    |
| Takanari   | 94         | 423     | 0.62     | 1.05    |
| IR72       | 82         | 575     | 0.45     | 1.01    |
| Shungsihako | 135       | 693     | 0.39     | 0.93    |
| NPT        | 159        | 449     | 0.49     | 0.95    |
| WAB        | 64         | 317     | 0.83     | 1.18    |
| Ch86       | (88)       | (202)   | (0.35)   | (1.09)  |
| Banten     | (71)       | (243)   | (0.55)   | (1.21)  |
| LSD        | 33         | 188     | 0.98     | 0.43    |
| P (cultivar) | 0.0001**  | 0.01**  | 0.03*    | 0.79ns  |
| C.V.       | 0.35       | 0.23    | 0.94     | 0.08    |
| Correlation with Y | 0.36**        | 0.43**  | 0.14ns   | 0.52ns  |
3. Relationship between sink size and NSC utilization

The yield of cultivar Takanari was the highest among the cultivars used in this study due to high spikelet number, and moderate to high single grain mass and filling percentage. Figures 1 showed significant positive

0.33 in Banten to 0.60 in Nanjing 1 in 1995, and from zero in Koshihikari to 0.91 in Takanari in 2001. Although the correlation between NSC, and Y were not significant, there was a significant positive correlation between “Cn” and Y in 1995 (r=0.69*). The analysis of variance of rice cultivars used in 2001 showed that there were significant cultivar differences in DMP, NSC, and “Cn”, and the C.V. of “Cn” showed the highest value (0.64, 2001) among the variables presented in Table 3.
correlations between sink size and yield. These observations are in agreement with the suggestion by many authors that larger sink size is required for rice to produce a higher yield (Yoshida, 1972; Song et al., 1990a; Saitoh et al., 1991; Shi et al., 1996). However, the coefficient of correlation of the yield with source size, \( \Delta \text{NSC} + \Delta \text{DMP} \), was higher than that with sink size. Source size was considerably lower than the sink size in many cultivars, particularly in the experiment in 2001. According to mean yields at respective conditions, the yield in 2001 was the highest and under the L N regime in 1995 was the lowest. This suggests that, the source size relative to sink size decreases in all cultivars as the environment becomes more productive, and supports the suggestion by Peng et al. (2000) that further increases in rice yield potential will be achieved by increasing dry matter production.

The relationship between source components and \( Y \) (Table 3) showed that \( Y \) was primarily determined by DMP. Thus, DMP was suggested to be more important factor than NSC, for variation in yield among cultivars. The variation of DMP seems to be associated to some extent with duration of grain filling, which is significantly correlated with DMP (\( r = 0.42^{**}, \) data not shown).

However, NSC also would have a substantial contribution to the cultivar difference in yield. There was a significant positive correlation between the coefficient of utilization of NSC and \( Y \) in 1995 (\( r = 0.69^{*} \)). There were also significant differences among rice cultivars in accumulation and utilization of NSC (\( p = 0.0001^{***} \) and 0.03*) in 2001 (excluding Banten and Ch 86).

Although it was very limited, there were three cultivars whose results could be compared between the experiments in the two years. Cultivar Takanari accumulated a relatively large amount of NSC and utilized it efficiently and stably in both years. On the other hand, cultivar Nipponbare and Koshikihari accumulated a medium to small amount of NSC and utilized it well in 1995, but virtually did not utilize it in 2001 (Table 3). These results suggest that there exists a cultivar difference not only in accumulation of NSC but also in the ability to utilize NSC (pre-reserved) at heading.

Although it was not significant, the difference between sink size and DMP tended to have a positive correlation with \( \Delta \text{NSC} \) (Fig. 4), and with \( "C_o" \) (Fig. 5). These results suggest that the pre-reserved NSC is utilized complementarily with DMP to fulfill the carbohydrate supply to the sink. This feature of NSC utilization has been suggested in recent studies. From observation of 13 rice cultivars, Sumi et al. (1996) suggested that the change in stem dry matter during grain filling varied among rice cultivars as if NSC was utilized to compensate for the shortage of DMP to fill grains. Dingkuhn and Le Gal (1996), using a local rice cultivar I Kong Pao, also observed that reserves (bulk decrease in dry weight of all vegetative organs) buffered the supply deficit that resulted from water shortage during grain filling. Moreover, Nagata et al. (2001), using cultivar Takanari cultivated with various amount of nitrogen and various shading conditions, showed that carbohydrate translocation from vegetative organs to the sink had a significant positive correlation with the shortage of DMP to sink demand. Our results are in agreement with their findings. In this study, however, the correlation of NSC utilization with the difference between sink size and DMP was less distinct than that observed in the above studies. This would be because a wide range of genotypes was used in this study and, as discussed above, there existed a cultivar difference in the ability of NSC utilization. It is suggested that NSC can potentially contribute to high yield but only when the cultivar was endowed with a genetic trait for its efficient utilization.

From the above results and discussion, we conclude that yield variation among rice cultivars is more associated with source size (DMP + NSC) than with sink size (spikelet number × grain mass). The contribution of DMP to the yield was much higher than that of NSC pre-reserved at heading. NSC may be utilized for grain filling to compensate the shortage of DMP. However, the complementarity was not very distinct and the cultivars had different ability to utilize NSC, which was associated with a part of cultivar variation in yield.

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