Contribution of Biomass Partitioning and Translocation to Grain Yield under Sub-Optimum Growing Conditions in Irrigated Rice

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Abstract: The International Rice Research Institute (IRRI) has developed a new plant type (NPT) and F1 hybrids to further increase rice yield potential. In this study we compared yield and yield-related traits among four genotypic groups: indica inbreds, F1 hybrids, NPT and NPT×indica lines; and determined the contribution of biomass partitioning and translocation to grain yield under sub-optimum growing conditions. Field experiments were conducted in 1998 wet season (WS) and 1999 dry seasons (DS) in the Philippines. Forty-seven genotypes in the WS and 46 genotypes in the DS were studied. Growth analyses were done at flowering and physiological maturity and yield, and yield components were measured at physiological maturity. Among the genotypic groups, average grain yield of the F1 hybrids was the highest and that of the NPT lines was the lowest. Grain yield was highly associated with harvest index (HI) with an $r^2$ of 0.73-0.84 in both seasons. The relationship between grain yield and biomass production was relatively weak. A negative relationship was observed between $T_r$, the amount of biomass accumulated before flowering and translocated to the grains during grain filling and $W_r$, the biomass accumulation from flowering to physiological maturity. The NPT lines had the highest average $W_r$ but had the lowest $T_r$ among the genotypic groups, which was opposite of that of the F1 hybrids. Compared to $W_r$, $T_r$ was more closely related to HI and grain yield. Results suggest that under sub-optimum growing conditions such as low total solar radiation increasing $T_r$ and HI is vital for achieving high actual grain yield in irrigated rice.

Key words: Biomass production, Grain yield, Harvest index, Rice, Translocation.

Yield potential of irrigated rice in the tropics has not increased remarkably since the release of IR8 in 1966 (Akita, 1994) and efforts to further improve yield potential still continue. Scientists at the International Rice Research Institute (IRRI) initiated two new approaches to increase yield potential: (1) the development of a new plant type (NPT) using tropical japonica germplasm, and (2) development of indica/indica F1 hybrid rice for the tropical environments. The NPT lines with large panicles, few tillers and dark green leaves have been evaluated in replicated yield trials since 1994 (Peng et al., 2000). The grain yield of NPT lines, however, was disappointing because of their low biomass production and poor grain filling (Peng et al., 2000). The introduction of traits from indica cultivars into NPT lines was initiated in 1996 to broaden the genetic background of the NPT germplasm and to refine the original ideotype design (Peng and Khush, 1996). Some advanced lines from NPT×indica crosses have been selected for replicated observation trials since 1999. The NPT×indica lines have more tillers, smaller panicles, higher grain filling percentage, and greater biomass production than NPT lines (Peng et al., 2000). Some F1 hybrid rice developed by IRRI have shown a yield advantage of about 15% compared with the best inbred cultivars when grown in farmers' fields. These hybrids had a yield potential increase by about 9% under the favorable tropical conditions for rice production (Peng et al., 2000). Recently, these hybrid rice lines were commercialized in India, Vietnam, and the Philippines (Virmani, 1996).

Studies of historical cultivars often show that genetic improvement in yield potential resulted from increases in harvest index (HI) (Lawes, 1977; Austin et al., 1980; Riggs et al., 1981), which is associated with ideotype characters, e.g. short stature in wheat and the uniculm habit in maize and sunflower (Sedgley, 1991). Comparisons between semi-dwarf and traditional rice cultivars attribute improvement in yield potential to the increase in HI rather than to biomass production (Takeda et al., 1983; Evans et al., 1984). When comparisons were made among the improved semi-dwarf cultivars under favorable growing conditions, however, high yield was achieved by increasing biomass production (jiang et al., 1988; Akita, 1989; Amano et al., 1993). In recent years, modern cereal breeding programs presented evidence of the possibility of boosting grain yield by selecting genotypes with higher biomass production (Hughes et
al., 1987; Damisch and Wiberg, 1991; Boukerrou and Rasmussen, 1990). In maize hybrids, for instance, where HI has largely remained constant, increased grain yield was a result of increased biomass production (Tollenaar and Daynard, 1982; Tollenaar, 1989; Tollenaar and Aguilera, 1991). In rice, the increased yield of F₁ hybrids was associated with increased biomass production under favorable growing conditions (Song et al., 1990; Yamauchi, 1994). Under favorable growing conditions such as intensive irrigated rice systems in the DS of the tropics where total solar radiation is high, HI of modern rice cultivars is high (45-55%) and their grain yield approaches the yield potential of 10 t ha⁻¹ (Peng et al., 2000). Further improvement in HI is difficult to achieve. Peng et al. (1999) suggested that further improvement in rice yield potential might come from increased biomass production rather than increased HI. However, we hypothesize that HI is more important in determining grain yield than biomass production under sub-optimum and unfavorable growing conditions even when comparison is made among the modern rice cultivars.

Grain yield is a function of biomass accumulation from flowering to physiological maturity (Wₚ) and the amount of biomass accumulated before flowering and translocated to the grains during grain filling (T). The contribution of T and Wₚ to rice yield has been widely studied (Weng et al., 1982; Song et al., 1990; Saitoh et al., 1991; Akita et al., 1992). Increased panicle weight and grain filling percentage were positively correlated with the contribution of T. Weng et al. (1982), but T was larger in improved varieties and was more effective than Wₚ in increasing panicle weight. Mihal et al. (1996) reported that compared with low-yielding varieties, high-yielding varieties had higher accumulation of assimilates before heading and greater translocation of these materials during grain filling. Yoshida (1981) stated that high T supports sustained grain growth and stabilizes grain yield under unfavorable weather conditions.

The objectives of this study were to (1) compare grain yield of indica inbreds, F₁, hybrids, NPT and NPT×indica lines; (2) determine the contribution of biomass production and HI to grain yield under sub-optimum growing conditions during the wet season when total solar radiation is low; and (3) determine the importance of Wₚ and T in relation to HI and grain yield.

Materials and Methods

Field experiments were conducted in the 1998 wet (July-Nov) and 1999 dry (Jan-May) seasons at the IRRI farm, Los Baños (14° 11’ N, 120° 56’ E, elevation 21 m). Rice genotypes from four different groups, namely- indica inbred, indica/indica F₁, hybrid, NPT, and intermediate type from cross between NPT and indica- were used in the study. The NPT are improved tropical japonica rice with large panicles, few tillers, dark green and erect leaves, and sturdy culms for lodging resistance. NPT×indica lines were developed by introducing traits from indica cultivars to broaden the genetic background of the NPT germplasm (Peng and Khush, 1996).

A total of 47 genotypes in the wet season (WS) and 45 in the dry season (DS) were used. In the 1998 WS, NPT lines were not included due to their susceptibility to pests and diseases. Plots were laid out in a randomized complete block design with four replications. Pregerminated seeds were sown on seedling trays to produce uniform seedlings. Fourteen–day–old seedlings were transplanted on 24 June 1998 at a spacing of 20 × 20 cm with four seedlings per hill. Basal fertilizer applied was 30 kg N ha⁻¹, 15 kg P ha⁻¹, 20 kg K ha⁻¹, and 2 kg Zn ha⁻¹, incorporated 1 d before transplanting. Nitrogen was topdressed at 30 kg ha⁻¹ each at midfillering (MT) and panicle initiation (PI). Midfillering stage is defined as the midpoint between transplanting and PI.

In the 1999 DS, genotypes from all four groups were transplanted on 22 January. Basal nutrient supply was

| Genotype        | Growth duration (d) | Grain yield (g/ dm²) | Total biomass at PM (g/m²) | Harvest index (%) |
|-----------------|---------------------|----------------------|---------------------------|------------------|
| IR77            | 111                 | 448                  | 1291                      | 36.4             |
| IR46            | 120                 | 462                  | 1309                      | 35.3             |
| IR66            | 117                 | 459                  | 1123                      | 40.8             |
| IR776           | 117                 | 446                  | 1263                      | 33.3             |
| IR98            | 98                  | 423                  | 1037                      | 40.8             |
| IR70            | 114                 | 419                  | 1207                      | 34.7             |
| PSRR254         | 114                 | 416                  | 1287                      | 32.4             |
| PSRR218         | 116                 | 413                  | 1314                      | 31.4             |
| PSRR230         | 117                 | 413                  | 1269                      | 32.4             |
| PSRR252         | 114                 | 410                  | 1253                      | 36.6             |
| IR50            | 104                 | 409                  | 1018                      | 40.3             |
| IR74            | 124                 | 406                  | 1241                      | 32.6             |
| IR54            | 120                 | 399                  | 1213                      | 32.8             |
| PSRR84          | 104                 | 398                  | 984                       | 40.4             |
| IR26            | 114                 | 397                  | 1082                      | 36.5             |
| IR22            | 120                 | 389                  | 1214                      | 32.1             |
| IR8             | 120                 | 378                  | 1220                      | 50.7             |
| IR64            | 104                 | 375                  | 1097                      | 36.8             |
| IR44            | 121                 | 352                  | 1159                      | 35.0             |
| IR20            | 104                 | 351                  | 1071                      | 36.5             |
| IR26            | 111                 | 329                  | 1161                      | 28.4             |
| PSRR4          | 121                 | 324                  | 1224                      | 26.2             |
| IR8             | 138                 | 322                  | 1182                      | 38.2             |
| IR38            | 135                 | 303                  | 1254                      | 22.4             |
| IR40            | 120                 | 291                  | 1213                      | 24.1             |
| IR8             | 117                 | 290                  | 1211                      | 24.1             |
| IR34            | 124                 | 239                  | 1396                      | 17.1             |
| IR62            | 114                 | 238                  | 995                       | 24.0             |
| Mean            | 114                 | 376                  | 1204                      | 31.0             |
| IR420           | 104                 | 546                  | 1248                      | 41.4             |
| IR5902H         | 111                 | 519                  | 1298                      | 36.8             |
| IR71621H        | 111                 | 455                  | 1289                      | 38.4             |
| IR7232K         | 106                 | 455                  | 1190                      | 38.4             |
| IR7386H         | 104                 | 445                  | 1152                      | 38.4             |
| IR7386I         | 104                 | 417                  | 1089                      | 38.3             |
| IR7462I         | 111                 | 405                  | 1194                      | 36.4             |
| IR7462H         | 111                 | 394                  | 1277                      | 32.1             |
| IR7109H         | 114                 | 386                  | 1185                      | 32.3             |
| IR6283H         | 114                 | 349                  | 1220                      | 28.0             |
| Mean            | 114                 | 441                  | 1213                      | 36.3             |
| NPT×indica      | 117                 | 473                  | 1199                      | 39.3             |
| IR7677-161-2-3  | 117                 | 445                  | 1231                      | 36.4             |
| IR7669-191-3-2  | 117                 | 431                  | 1230                      | 34.9             |
| IR7215-133-1    | 120                 | 407                  | 1194                      | 31.2             |
| IR7215-116-6    | 120                 | 384                  | 1294                      | 29.6             |
| IR7216-186-5    | 120                 | 377                  | 1280                      | 29.2             |
| IR7499-307-3-2  | 117                 | 361                  | 1203                      | 30.0             |
| IR7677-179-2-4  | 120                 | 356                  | 1233                      | 30.0             |
| IR7699-136-1-4  | 111                 | 333                  | 1231                      | 27.1             |
| Mean            | 114                 | 396                  | 1245                      | 31.8             |
| Average SE      | 26                  | 41                   | 15                        |                  |

IRRI farm, 1998 wet season.
Table 2. Growth duration, grain yield (oven-dry weight), total biomass at physiological maturity (PM), and harvest index of rice genotypes from different groups.

| Genotype (F) | Growth duration (d) | Grain yield (g m⁻²) | Total biomass at PM (g m⁻²) | Harvest index (%) |
|-------------|---------------------|---------------------|-----------------------------|------------------|
| IR72158-114-1 | 117 | 644 | 1605 | 41.3 |
| IR72158-114-2 | 122 | 638 | 1593 | 41.3 |
| IR72158-114-3 | 117 | 574 | 1543 | 37.0 |
| IR72158-114-4 | 117 | 563 | 1439 | 29.2 |
| IR66499-161-2-3-3-2 | 122 | 356 | 1411 | 38.0 |
| IR72964 | 124 | 321 | 1665 | 21.1 |
| IR64 | 111 | 477 | 1347 | 35.4 |
| IR12 | 117 | 467 | 1437 | 33.4 |
| IR68 | 122 | 465 | 1599 | 29.6 |
| IR66158-172-2-3-3 | 111 | 413 | 1291 | 32.1 |
| IR36 | 109 | 408 | 1149 | 35.4 |
| Mean | | 599 | 1449 | 39.8 |

Harvest index (HI) was calculated based on the following equations:

1. \[ W_T = \frac{W_G}{W_F} \times 100 \]

2. \[ H_I = \frac{100 \times W_T}{W_F} \]

Fig. 1. Relationship between grain yield (oven-dry weight) and harvest index of rice cultivars and lines grown in the 1998 wet season (RWS) and 1999 dry season (RDS).

Each data point is a mean of four replications in each season.

70°C to constant weight for determining grain (oven-dried rough rice) yield. Grain filling percentage (100 × filled spikelet number / total spikelet number) and HI were calculated.

The contribution of biomass accumulation before flowering to grain yield was estimated by the difference between grain dry weight at physiological maturity and biomass accumulation from flowering to physiological maturity. This calculation was based on the assumption that biomass accumulation after flowering was allocated entirely to the grains. Biomass accumulation from flowering to physiological maturity (\( W_T \)) and biomass that was accumulated before flowering and translocated to the grains during grain filling (\( T \)) were calculated based on the following equations:

\[ W_T = \text{Biomass at physiological maturity} \]

\[ T = \text{Grain yield} - W_T \]

\[ \text{Data were analyzed and genotypic means were compared based on the average standard error (SE) across genotypes, i.e. two means whose different falls below the SE are not statistically different.} \]

Results

Growth duration of tested genotypes ranged from 98 to 138 d in 1998 WS and from 109 to 131 d in 1999 DS (Tables 1 and 2). Significant differences in grain yield, total biomass, and HI were observed among genotypes. The highest yield of 546 g m⁻² was produced by IR73409H in 1998 WS and IR71622H recorded the highest yield of 546 g m⁻² in 1999 DS. In 1998 WS, average grain yield of F₁ hybrids was higher than that of indica inbred cultivars and NPT x indica lines although...
observed in 1998 WS and associated with HI in both seasons with an 0.84 (Fig. 1). The relationship between grain yield and lowest among the four genotypic groups due to their Regression analysis indicated that grain yield was highly was attributed to high HI and not to biomass produc­ tion. The average grain yield of NPT lines was the poor HI. Average biomass at physiological maturity was relatively weak in indica inbred cultivars and NPT X indica lines. In there was no significant difference among the three groups in the average biomass at physiological maturity. Therefore, the average HI was greater in F1 hybrids than in indica inbred cultivars and NPT X indica lines. In 1999 DS, average grain yield of F1 hybrids was also the highest among the four genotypic groups if IR64615H was not considered. The high grain yield of F1 hybrids was attributed to high HI and not to biomass production. The average grain yield of F1 hybrids was the lowest among the four genotypic groups due to their poor HI. Average biomass at physiological maturity was not significantly different across genotype groups. Regression analysis indicated that grain yield was highly associated with HI in both seasons with an r² of 0.73–0.84 (Fig. 1). The relationship between grain yield and biomass at physiological maturity was relatively weak in 1999 DS (r²=0.38), whereas no relationship between grain yield and biomass at physiological maturity was observed in 1998 WS (r²=0.00).

The F1 hybrids had a slightly higher biomass at flowering in 1998 WS (r²=0.73), whereas F1 hybrids had a slightly higher biomass at flowering (w, r). Biomass at flowering (w, r), T, and grain filling percentage of rice genotypes from different groups.

Table 4. Biomass at flowering, biomass production after flowering and grain filling percentage of rice genotypes from different groups.

Table 3. Biomass at flowering, biomass production after flowering (Wf), biomass translocated from straw to grain (T), and grain filling percentage of rice genotypes from different groups.

IRRI farm, 1998 wet season.
both seasons (Fig. 2). Grain yield and HI were associated with \( T \) more closely than with \( W_r \) (Fig. 3).

Grain filling percentage was generally low in both seasons with maximum value of 77.8%. Variation in grain filling percentage was greater within genotypic groups than across genotypic groups (Tables 3 and 4). Harvest index was closely related to grain filling percentage in both seasons (Fig. 4). Grain yield was also positively associated with grain filling percentage (\( r^2 = 0.33 \) in 1998 WS and \( r^2 = 0.58 \) in 1999 DS). In 1998 WS, the top-ten yielding genotypes produced 58% higher grain yield than the bottom-ten yielding genotypes (Table 5). This yield difference increased to 96% in 1999 DS. The differences in \( W_r \), \( T \), HI, and grain filling percentage between the top- and bottom-ten yielding genotypes were responsible for yield differences. Between the top- and bottom-ten yielding genotypes, the difference in grain filling percentage ranged from 28 to 39%, that in \( W_r \) from 12 to 17%, and that in HI from 44 to 48%. However, the difference in \( T \) was much greater than in \( W_r \) between the top- and bottom-ten yielding genotypes.

**Discussion**

Maximum grain yield is 6 t ha\(^{-1}\) in the WS and 10 t ha\(^{-1}\) in the DS in tropical irrigated rice systems under normal climatic conditions (Yoshida, 1981). In this study, the highest grain yield expressed at 14% moisture level was 6 t ha\(^{-1}\) in 1998 WS and 8 t ha\(^{-1}\) in 1999 DS. Grain yield was significantly lower in the 1999 DS than in a normal DS. This was because the mean daily total solar radiation during the 1999 DS was only 18.6 MJ m\(^{-2}\), about 10% lower than the 10-year average from 1989 DS to 1998 DS. Likewise, biomass production, HI, and grain filling in the 1999 DS were also significantly lower than those of rice crops grown in normal DS. The highest HI was 42.9% and the highest grain filling was 77.8% in 1999 DS, while HI of 50% and grain filling of 90% were very common in the rice crop that produced 9 to 10 t ha\(^{-1}\) under normal DS conditions (Peng et al., 2000). The highest grain yield of 1998 WS reached the typical maximum grain yield in the WS in tropical irrigated rice systems and 1998 WS is considered as a normal WS. In general, the WS is unfavorable for rice production due to reduced total solar radiation compared with the normal DS. Therefore, both 1998 WS (with mean total solar radiation of 18.2 MJ m\(^{-2}\)) and 1999 DS (with mean daily total solar radiation of 18.6 MJ m\(^{-2}\)) are considered as sub-optimum for rice production.
In this study, grain yield was highly and positively related to HI and the relationship between grain yield and biomass production was relatively weak. The importance of biomass production and HI in determining grain yield has been a controversial issue. The contribution of biomass production and HI to genetic gains in grain yield potential varied with the study. Comparisons between semi-dwarf and traditional rice cultivars attributed improvement in yield potential to the increase in HI rather than to biomass production (Takeda et al., 1983; Evans et al., 1984). When comparisons were made among the improved semi-dwarf cultivars under favorable growing conditions, however, high yield was achieved by increasing biomass production (Jiang et al., 1988; Akita, 1989; Amano et al., 1993). Results from this study suggest that HI is more important than biomass production in determining grain yield under sub-optimum growing conditions. Hybrid rice has about a 15% higher yield than inbred cultivars mainly due to an increase in biomass production rather than in HI (Song et al., 1990; Yamauchi, 1994). However, if F₁ hybrids and inbred cultivars are compared under low total solar radiation, the F₁ hybrids will have less reduction in HI than the inbred cultivars. Under our field experimental conditions, F₁ hybrids had a higher yield than other genotypic groups mainly due to their higher HI. Therefore, further improvement in rice yield potential under favorable growing conditions might come from increased biomass production rather than increased HI. Under sub-optimum growing conditions, however, maintaining a high HI could be more important than increasing biomass production to achieve a high actual grain yield.

Effective translocation of accumulated biomass before flowering to the grains (i.e. $T$) and high biomass production during ripening (i.e. $W_r$) have been considered in breeding high-yielding rice cultivars (Nishiyama, 1989; Wu and Tsiu, 1989). High $W_r$ and $T$ are both needed for achieving high grain yield. However, our
study indicated a negative relationship between $T$ and $W_r$. This negative relationship indicates a trade-off between $T$ and $W_r$ in terms of yield contribution—i.e., an increase in each component will not necessarily result in increased yield. Furthermore, $T$ was more closely related to grain yield and HI than $W_r$. Increased panicle weight and grain filling percentage were positively correlated with $T$ and $W_r$ (Weng et al., 1982), but $T$ was larger in improved varieties and was more effective than $W_r$ in increasing panicle weight. Miah et al. (1996) reported that the high-yielding indica varieties had higher $T$ than low-yielding japonica varieties. Yoshida (1981) stated that high $T$ supports sustained grain growth and stabilizes grain yield under unfavorable weather conditions. This is because when the current supply of assimilates is limited by cloudy or rainy weather, the accumulated carbohydrates are easily translocated to the grains (Yoshida, 1981). Such a compensatory effect has been reported in instances where the supply of carbohydrate during grain filling is limited (Kobata and Takami, 1983; Sumi et al., 1996), as in cases of unfavorable conditions during grain filling, such as water deficits (Kobata and Takami, 1983), shaded conditions (Nagata et al., 2001), and low total solar radiation in our study. This was why $T$ averaged across cultivars was 51% higher in the WS than in the DS. It is unknown if a negative relationship between $W_r$ and $T$ also exists under favorable growing conditions. If it does, breaking this negative linkage between $W_r$ and $T$ through genetic manipulation and achieving high $W_r$ and $T$ at the same time could be an effective approach to increase rice yield potential under favorable growing conditions. On the other hand, under sub-optimum and unfavorable growing conditions, increasing $T$ seems a practical strategy for achieving high grain yield.

The development of NPT with large panicles, few tillers, and sturdy stems using tropical japonica germplasm aimed at increasing rice yield potential (Peng et al., 1994). However, the average grain yield of NPT lines was the lowest among the genotypic groups due to their low HI. This result is consistent with the report of Lee and Ha (1999) that the NPT line produced the lowest grain yield due to low HI and grain filling. In addition, in our study, the NPT lines had the highest average $W_r$ but had the lowest $T$ among genotypic groups. Ten out of 12 NPT lines had negative values of $T$, suggesting that the biomass produced during the ripening phase did not entirely contribute to grain yield and that some of it remained in the straw in these NPT lines. This speculation is supported by the evidence that new tillers continue to emerge at physiological maturity in the NPT lines, especially when total solar radiation is low. The inability of the sink to fill despite higher available source caused the poor grain filling of the NPT lines. In a temperate environment, the lower translocation of accumulated carbohydrates in the NPT line compared with the Tongil type cultivars was due to its weaker sink strength (Lee and Ha, 1999). The NPT × indica lines had higher $T$ than the NPT lines (suggesting improvement in translocation), but the values are still lower than those of the indica inbred cultivars and F1 hybrids. In order for the NPT × indica lines to fully express their yield potential, translocation of biomass from stem reserves to the grain has to be increased while maintaining high level of current biomass production during the ripening phase.

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