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[Short Report]

Unlocking the Yield Barrier in Rice through a Nitrogen-Led Improvement in the Radiation Conversion Factor

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Failure to meet the increasing demand for food from Asia's rising population will result in misery for hundreds of millions. A 40% increase in rice production by 2020 is required and this must come from increased yield per hectare, because the total area of suitable land will change little (Brown, 1997 ; Greenland, 1997 ; Mann, 1999a). For 30 yr, the maximum yield of inbred cultivars of irrigated rice in the tropics has remained at 10 t ha^{-1}, a value regarded as a yield barrier (Kropff et al., 1994a). On average, intensively cultivated rice crops make 2.2 g above-ground (shoot) dry matter from each MJ of photosynthetically active solar radiation intercepted during vegetative growth, a quantity known as the radiation conversion factor (RCF) or radiation use efficiency. The RCF is a primary determinant of yield and 2.2 g MJ^{-1} is consistent with a yield of 10 t ha^{-1} in tropical rice (110-d growth duration) (Kiniry et al., 1989 ; Mitchell et al., 1998) and suggestive of an absolute thermodynamic limit. However, the RCF of wheat, another C3 cereal, is approximately 25% higher than that of rice ; maize, with C4 photosynthesis, is around 50% higher (Kiniry et al., 1989 ; Mitchell et al., 1998), therefore improvements in RCF and yield in rice may be possible. The essential relationship between large leaf area, erect leaves and storage of the large amounts of nitrogen associated with high grain yield has only recently been recognized (Sinclair and Sheehy, 1999), as has the importance of maintaining a minimum (Greenwood et al., 1990) concentration of nitrogen (critical N) for maximal metabolic activity (Horie et al., 1997, Sheehy et al., 1998) and hence maximal use of photosynthetically active radiation (PAR). It is important to test the hypothesis that crops containing at least critical N could increase the RCF and break the yield barrier. However, the critical N for the growth of rice has not been determined with precision. As we wished to achieve an RCF comparable to that of wheat, the parameters derived by Justes et al., (1997) were used to calculate critical N concentrations for rice (Table 1).

At IRRI, Philippines, in the dry seasons of 1997 and 1998, crops of the elite indica-type rice cultivar IR72 and current lines of a new plant type (Peng et al., 1994) were transplanted and irrigated until maturity in the standard way. That the rice crop contains critical N cannot yet be ensured with precision ; not least because potential yield (Yoshida, 1981) is unknown. Thus, to ensure an abundant nitrogen supply, allowing for 50% fertilizer recovery (Cassman et al., 1993), fertilizer was applied at transplanting and then weekly throughout the crop growth period, providing a total amount much larger than current commercial practice (Table 1). To ensure expression of maximum potential yields, N applications were increased further in 1998. At intervals, sample quadrats of shoots were harvested, dried and weighed. Just before each harvest, the fraction of PAR transmitted by the crop was recorded and together with records of incident PAR from the IRRI weather station the amount of intercepted PAR was calculated. The RCF was computed from the slope of a linear regression of shoot dry matter on accumulated intercepted PAR (Kiniry et al., 1989 ; Mitchell et al., 1998). At the final harvest, all spikelets were counted and classified as filled or unfilled, and shoots and grain were dried and weighed.

Both IR72 and the new plant type (NPT) broke the yield barrier with yields of 11.6 t ha^{-1} (Table 1) in 1997, a year without tropical storms and consequent lodging. In 1998, IR72 again yielded 11.6 t ha^{-1} in plots with strings across to prevent lodging, but 10.1 t ha^{-1} in lodged plots. Whilst not lodging, NPT suffered substantial damage (>30% tillers) from the striped stem borer (*Chilo suppressalis* (Walker)) during grain filling, average yield being 10.0 t ha^{-1}. The maximum yield for NPT was estimated as 12.0 t ha^{-1} from the weight of the upper quartile of harvested plots. In 1998, the critical N in both cultivars was exceeded throughout the growing season. However, in 1997, the N concentration in IR72 at panicle initiation was 64% of the critical N and that at five days after flowering was 97% of the critical N. In the NPT,

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Table 1. Yield and its components for rice crops grown at the International Rice Research Institute in the dry seasons of 1997 and 1998.

Cultivar Year	IR72 1997	IR72 1998 unlodged	IR72 1998 lodged	NPT 1997	NPT 1998 actual	NPT 1998 upper quartile
Yield (t ha^{-1}) at 14% moisture content	11.6 ±0.7	11.6 ±0.3	10.1 ±0.4	11.6 ±0.5	10.0 ±0.3	12.0 ±0.3
Harvest index (%)	55 ±1.0	51 ±0.4	50 ±0.8	40 ±0.1	42 ±0.7	44 ±0.2
Grain filling (%)	77.4 ±1.5	84.0 ±2.3	78.8 ±2.7	63.4 ±1.4	65.9 ±0.9	67.7 ±1.8
Total spikelet number (thousand m^{-2})	56.9 ±2.9	65.1 ±2.1	60.0 ±1.7	79.1 ±4.0	71.1 ±2.6	80.2 ±5.4
Shoot dry matter at harvest (t ha^{-1})	18.7 ±0.8	20.1 ±0.5	18.1 ±0.7	25.8 ±1.2	21.0 ±0.5	24.2 ±0.8
Radiation conversion factor (g MJ^{-1})	2.5	2.5	—	2.7	2.3	2.6
Shoot N content at harvest (kg ha^{-1})	292 ±13	409 ±11	369 ±14	402 ±19	403 ±9	465 ±15
Critical N at harvest (kg ha^{-1})	276	287	271	330	294	319
N applied (kg ha^{-1})	480	820	700	520	1000	1000
Days from transplanting to harvest	102	101	101	116	108	108

In 1997, the breeding line of the new plant type (NPT) was IR65598-112-2 and in 1998 it was IR65564-44-4-1. Values in the table are means and standard errors. There were seven replicates except for the NPT in 1998 where there were 34 replicates and eight in the upper quartile. Harvest index is grain dry matter as a fraction of shoot dry matter. Grain filling is the proportion of spikelets (florets) producing a grain. The radiation conversion factor for the upper quartile of the NPT in 1998 was estimated from the ratio of shoot dry matter (2.3 × upper quartile/actual). Critical N was calculated using the equation $\%N = 5.35\ W^{-0.44}$, where W is shoot dry matter in t ha^{-1}.

the percentage of N concentration to critical N was 82% at panicle initiation and 105% at ten days before flowering. At harvest, the crop nitrogen contents were well above the critical N, and RCF was substantially increased. Thus, we have shown that the yield barrier can be significantly surpassed (16%) and the RCF of rice raised to values comparable with wheat. Ensuring little or no nitrogen constraint enabled these crops to transfer large quantities of nitrogen to the grain whilst sustaining two or three live leaves per tiller through to final harvest, a time when most leaves are usually senescent. Consequently, even at the end of the grain filling period, we calculate (Kropff et al., 1994b) that canopy photosynthesis remained high, approximately 30 g $CH_2O\ m^{-2}\ d^{-1}$.

Nitrogen management is one key to unlock the yield barrier. We can be optimistic that rice cultivars with a yield potential of 12 t ha^{-1} will be bred : for example, the scope for improving the harvest index or the percentage of filled grains of NPT in comparison with that of IR72 (Table 1). Progress will also require improved resistance to lodging and to stem borers. Nitrogen must be managed more effectively to enable new rice cultivars to realize their potential and to raise current farm yields (Cassman et al., 1993) to meet demand. These high experimental rates of application of nitrogen were chosen to achieve critical N and higher yields but are unrealistic for commercial use, not because the cost of fertilizer is an economic limitation (Dawe, 2000) but because environmental considerations are against excessive fertilization. Moreover, meeting the 40% increase in yield is beyond the capacity of rice with its current photosynthetic mechanism. Such a large increase in potential yield will almost certainly require the introduction of low photorespiration or intermediate C3-C4 characteristics from wild rice species (Yeo et al., 1994 ; Tanksley and McCouch, 1997) or introduction of the C4 photosynthetic pathway to rice using biotechnology (Ku et al., 1999 ; Mann, 1999b).

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