

CHAPTER 20

PROSPECTS FOR GENETIC IMPROVEMENT TO INCREASE LOWLAND RICE YIELDS WITH LESS WATER AND NITROGEN

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Abstract. Increasing yield potential of lowland rice remains to be the top priority in rice genetic-improvement programmes, because rice farmers' primary concern is still grain yield and world rice production has to increase by 1% annually in the next 20 years to meet the demand of the growing population. Improvements in yield potential of irrigated lowland rice were achieved under ample supply of water and nutrients. Water use efficiency (WUE) and nitrogen use efficiency (NUE) were seldom included in the breeding objectives for irrigated lowland rice. Scarcity of freshwater resources has threatened the production of the flood-irrigated rice crop, and excessive use of N fertilizer is causing environmental concerns. We have to increase lowland rice yield with less water and N. Newly developed crop management strategies have proven to be effective in increasing WUE and NUE. Several water-saving technologies such as alternate wetting and drying (AWD) and aerobic rice system have been developed to increase the water productivity of rice. However, yield penalty occurred when these water-saving technologies were practised with current varieties. New varieties have to be developed to reduce the yield loss under AWD and aerobic rice system in order to increase WUE further. Direct selection for WUE under flood-irrigated lowland conditions may have a negative impact on grain yield under water-saving strategies. Optimizing the timing and rate of N application to synchronize supply and demand of N by the crop has resulted in a great reduction in fertilizer-N input without yield loss and greater NUE. Genetic improvement of NUE has not been achieved in rice. Genotypic variation in NUE has been reported in many studies. Plant traits that are associated with high grain yield and high NUE should be identified so that breeders are able to use these traits easily as selection criteria in the breeding programme to develop N-efficient varieties without sacrificing rice yield potential. New breeding techniques such as development of F₁ hybrids, marker-aided selection, transformation and genetic engineering should be combined effectively with the empirical breeding method in order to increase rice grain yield with less water and N.

INTRODUCTION

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World rice production has to increase by 1% annually to meet the demand of the growing population (Rosegrant et al. 1995). Most of this increase must come from higher yields on existing cropland to avoid environmental degradation, destruction of natural ecosystems, and loss of biodiversity (Cassman 1999). Irrigated lowland contributes more than 75% of total rice production, although it accounts for about 55% of total rice area. In the past, improvement in the yield potential of irrigated lowland rice varieties has contributed greatly to the steady growth of world rice production. Most progress in the improvement of yield potential of irrigated lowland rice varieties was achieved when water and nutrients were amply supplied. Because of water scarcity and environmental pollution caused by over-application of fertilizers, the challenge is to increase rice yield of irrigated lowland with less water and less fertilizer, especially N fertilizer.

Irrigated lowland rice receives 24–30% of global developed freshwater resources (Bouman et al. in press), while in Asia it receives more than 45% of total freshwater used (Tuong and Bouman 2003). However, scarcity of freshwater resources now threatens the production of the flood-irrigated lowland rice crop (Tuong and Bouman 2003), mainly caused by the increasing competition for freshwater resources from urban and industrial sectors. By 2025, 15 out of 75 million ha of Asia's flood-irrigated lowland rice crop are predicted to experience water shortage. At the field level, flood-irrigated rice requires two to three times more water than other cereal crops such as wheat and maize. In the past, crop, land and water management practices were the main considerations to increase rice's water productivity (defined here as the amount of grains produced per unit water supplied by irrigation and rainfall). Several water-saving technologies have been developed that aim to reduce non-beneficial water flows from rice fields during crop growth, namely seepage, percolation and evaporation (Bouman and Tuong 2001): saturated soil culture (Borrell et al. 1997), alternate wetting and drying (Tabbal et al. 2002), groundcover systems (Liu et al. 2005) and aerobic rice (Bouman et al. 2002). In addition, reducing the duration of land preparation and shallow tillage significantly reduce the total water input for wetland preparation. However, very little effort has been devoted to improve the water productivity of irrigated lowland rice at the plant level by developing varieties with intrinsic higher water use efficiency (transpiration efficiency) or by developing varieties that maintain a high yield potential under non-flooded conditions. There is limited information on morpho-physiological characteristics of varieties that are required for superior performance under water-saving crop management.

Crop yields world-wide have continuously increased, partly because of the increase in fertilizer nutrient input, especially N fertilizer (Cassman 1999). To maximize grain yield, farmers often apply more N fertilizer than the minimum required for maximum crop growth (Lemaire and Gastal 1997). Global use of N fertilizer increased over sevenfold from 1960 to 2002 with an average growth rate of 5% per year (FAO 2005). About 60% of global N fertilizer is used for producing the world's three major cereals: rice, wheat and maize (Ladha et al. 2005). Rice production accounts for about 20% of global N consumption. Nitrogen use efficiency is relatively low in irrigated lowland rice because of rapid N losses from ammonia volatilization, denitrification, surface run-off and leaching in the soil–

floodwater system (De Datta and Buresh 1989). These N losses are much greater under excessive N use and cause severe environmental consequences, such as groundwater contamination (caused by nitrate leaching from soil), eutrophication of lakes and rivers (because of surface run-off and seepage of N from rice fields), and acid rain (caused by ammonia volatilization). Denitrification contributes to global warming by emitting greenhouse gases such as nitrous oxide (N₂O).

Further increase in rice production has to be achieved with less N fertilizer by improving N use efficiency (NUE) through better N fertilizer management and new rice varieties. Research on improving NUE of the rice crop has been focused on the development of fertilizer management strategies in the past three decades. Great progress has been achieved to reduce N losses by new application methods and modified N sources. Another important research area is optimizing the timing and rate of N application for better synchronization between the supply and demand of N by the crop (Cassman et al. 1998). Some efforts have been devoted to germplasm improvement in NUE, but the impact has not been as great as for the first two approaches.

GENOTYPIC IMPROVEMENT FOR WATER PRODUCTIVITY

Transpiration efficiency (TE) is defined as the ratio of photosynthesis (A) to transpiration. Whole-plant water use efficiency (WUE) can be expressed as the ratio of total biomass or grain production to the amount of water transpired. A close relationship between TE at the single-leaf level and whole-plant WUE was observed in winter wheat (Heitholt 1989) and grain sorghum (Peng and Krieg 1992). Farquhar et al. (1982) developed a theoretical relationship that demonstrated a negative correlation between ¹³C discrimination (Δ) in C₃ plants and the ratio of A to stomatal conductance (g) through the ratio of intercellular and ambient CO₂ partial pressures (p_i/p_a). A negative relationship between Δ and whole-plant WUE has been reported in many crops, including upland rice (Dingkuhn et al. 1991).

Peng et al. (1998) reported that improved tropical *japonica* rice lines had 25–30% higher TE at the single-leaf level than *indica* varieties when grown under flooded conditions. This was because *indica* varieties had a higher transpiration rate than the tropical *japonica* lines whereas the differences in A between the two types were relatively small and inconsistent across growth stages and years compared with the differences in transpiration rate. A smaller Δ in a tropical *japonica* line than in an *indica* variety suggested that the improved tropical *japonica* rice may have greater whole-plant WUE than the *indica* rice. Yeo et al. (1994) observed large differences among *Oryza* species in TE at the single-leaf level. *Oryza australiensis* had significantly higher TE than *Oryza sativa* at the same photosynthetic rates. The potential for exploiting this trait, however, has not been investigated. Varietal differences in TE at the single-leaf level and whole-plant WUE measured by gravimetric determinations of growth and water loss from individual plants were reported in rice by Flowers et al. (1988). However, the high WUE was associated with the non-dwarfed habit and therefore it may not be useful to incorporate this trait into commercial varieties to increase water productivity. Increase in waxiness of rice

leaves was proposed to reduce non-stomatal transpiration but the impact on WUE has not been demonstrated (Lafitte and Bennett 2002).

Transforming the C_3 rice plant into a C_4 plant by genetic engineering of photosynthetic enzymes and required anatomic structures was suggested as another approach to improve TE. High-level expression of maize phosphoenolpyruvate carboxylase (PEPC) and pyruvate, orthophosphate dikinase (PPDK) and NADP-malic enzyme (NADP-ME) in transgenic rice plants has been achieved (Agarie et al. 1998). Ku et al. (2000) reported that PEPC and PPDK transgenic rice plants had up to 30 to 35% higher A than untransformed plants. However, this increased A was associated with enhanced stomatal conductance, which reduces the potential for increasing TE by the development of C_4 rice plants. The mechanism underlying the maintenance of higher stomatal conductance by the transgenic plants is unknown.

Development of early maturing and high-yielding varieties of flood-irrigated lowland rice during the Green Revolution in the 1960s and 1970s has increased the average rice yield and reduced crop duration significantly. This has contributed to a three-fold increase in water productivity with respect to total water inputs (Bouman et al. 2006). Hybrid rice varieties have a 9% higher yield potential than inbred varieties with comparable growth duration when grown under flood-irrigated conditions in the tropics (Peng et al. 1999). This yield advantage offers another opportunity to increase the water productivity of flood-irrigated lowland rice (Guerra et al. 1998).

Breeders and crop physiologists in Australia selected specifically for high TE in wheat using carbon isotope discrimination techniques (Richards 2004). Wheat varieties with a 2–23% increase in grain yield over check varieties have been successfully developed for water-limited conditions. Blum (2005) pointed out that high yield under water-limited conditions is generally associated with reduced WUE mainly because of high water use. Plant traits such as small plants (small leaves and reduced tillering) or short growth duration are associated with low yield potential and high WUE because of reduced water use. Therefore, selection for high WUE by using carbon isotope discrimination techniques in a breeding programme will result in smaller or earlier flowering plants that use less water but have low yield potential at the same time (Blum 2005). The challenge is to develop water-efficient genotypes that produce higher yields with limited water supply, and equal or greater yields than current varieties under favourable growth conditions without stress.

Bouman et al. (in press) stated that the possibility of increasing water productivity of irrigated lowland rice is much greater by improving crop, land and water management practices than by developing rice varieties with high TE or whole-plant WUE. Because photosynthesis and transpiration rates are generally proportional, there is only a small difference in TE among rice varieties at the single-leaf level when grown under flooded and aerobic cultivation (Singh and Sasahara 1981). However, developing rice varieties with superior performance under water-saving technologies such as alternate wetting and drying (AWD) and aerobic cultivation could result in a significant improvement in water productivity of irrigated lowland rice.

GENOTYPIC VARIATION IN RESPONSE TO WATER REGIMES

In AWD, irrigation water is applied to achieve intermittent flooded and non-flooded soil conditions. The frequency and duration of non-flooding can be determined by re-irrigating (to achieve flooded conditions) after a fixed number of non-flooded days, when a certain threshold of soil water potential is reached, when the ponded watertable level drops to a certain level below the soil surface, when cracks appear on the soil surface or when plants show visual symptoms of water shortage. AWD is a mature technology that is widely practised in irrigated lowland rice in China (Bouman et al. 2006). A yield increase under AWD is rare. Bouman and Tuong (2001) summarized 31 field experiments on AWD and reported that yield reductions of 0 to 70% were observed in AWD treatments compared with continuously flooded controls in 92% of the experiments. The large variability in the performance of AWD was caused by differences in the irrigation interval, soil properties and hydrological conditions across the experiments. In fact, varieties that were developed for the traditional continuously flooded-irrigated rice system may not be suitable for AWD conditions. In all the experiments, AWD increased water productivity with respect to total water input because the yield reduction was smaller than the amount of water saved.

Bouman and Tuong (2001) re-analysed the yields of a variety evaluation under AWD conditions by De Datta et al. (1973a; 1973b), who grew 30 different cultivars with irrigation applied when soil water tension in the root zone reached 500 mbar in either the vegetative or reproductive stage. There were six cultivars that had higher yields with AWD in the vegetative stage than in the continuously flooded control. More recently, Virk et al. (2003) evaluated seven hybrids and 37 inbred varieties under AWD and continuously flooded control during the 2003 dry season at IRRI. For the entire growing season, there were six non-flooded soil periods with the first one initiated 21 days after transplanting. With irrigation, 5-cm ponded water depth was imposed, and the field was re-irrigated after the ponded water level had receded to 25 cm below the soil surface. Overall, AWD saved 17% of the water used in the continuously flooded control. Yield losses under AWD ranged from 3 to 23% for hybrids and from -6 to 26% for inbreds. Three out of seven hybrids and 18 out of 37 inbreds did not show any significant yield decline because of AWD. Three hybrids and six inbred varieties that were adapted to AWD conditions were identified. These varieties demonstrated higher water productivity under AWD than under continuously flooded conditions. Both studies, De Datta et al. (1973a; 1973b) and Virk et al. (2003), suggest that genetic variability in tolerance for relatively mild water stress during the vegetative phase exists in both hybrids and inbreds. This trait can be used for the development of new varieties that are more suitable for AWD conditions.

Aerobic rice is high-yielding rice grown under non-flooded conditions in non-puddled and unsaturated (aerobic) soil. It is responsive to high inputs, can be rainfed or irrigated, and tolerates occasional flooding (Bouman and Tuong 2001). In this chapter, aerobic rice refers to rice crops grown in non-flooded and non-puddled lowland soil with supplemental irrigation. Aerobic rice promises substantial water savings by minimizing seepage and percolation and greatly reducing evaporation

(Bouman et al. 2002). Experimentally growing the high-yielding lowland rice varieties under aerobic conditions has shown great potential to save water, but with severe yield penalty. In the early 1970s, De Datta et al. (1973a; 1973b) tested the lowland variety IR20 in aerobic soil under furrow irrigation at IRRI. Water saving was 55% compared with flooded conditions, but the yield fell from about 8 t ha⁻¹ under flooded conditions to 3.4 t ha⁻¹ under aerobic conditions. However, large varietal differences in grain yield exist under aerobic conditions. George et al. (2002) reported that a lowland hybrid variety (Magat) yielded 7.8 t ha⁻¹ compared to 2.1 t ha⁻¹ for a traditional upland rice variety (Lubang Red) when grown under aerobic conditions in the first season with supplemental irrigation. Magat's high yield was because of a harvest index (HI) of 0.43 in contrast to 0.31 of an improved upland rice variety (Apo) and 0.17 of Lubang Red. George et al. (2002) concluded that rice can be highly productive in aerobic soils if crop management is optimized for varieties with high HI and adapted to aerobic conditions. Aerobic rice is grown commercially in highly acidic soil of Brazil, producing about 5 t ha⁻¹ with adequate supply of fertilizers and irrigation in rotational systems (George et al. 2002). In China, aerobic rice yield potential approaches 7 t ha⁻¹ in farmers' fields in the Huang-Huai-Hai Rice Plains (Wang et al. 2002). Yields up to 8.7 t ha⁻¹ were reported for aerobic rice in Jiangsu province, which was only 11% less than the yield under continuously flooded conditions with the same variety (Chu et al. 2004). However, in field experiments around Beijing, maximum aerobic rice yields were only 5.7 t ha⁻¹ (Yang et al. 2005). Still, there is a yield penalty for current varieties when grown under aerobic soil conditions.

In the dry season of 2004, we compared the performance of four varieties under continuously flooded and aerobic conditions at the IRRI farm. The field was grown with flooded lowland rice in previous seasons and it was the first season to grow aerobic rice. The four varieties were lowland *indica* inbred (PSBRc80), lowland *indica* hybrid (Magat) and improved upland rice (Apo and UPLRi7). Flooded plots were puddled and kept continuously flooded from transplanting until two weeks before harvest. The aerobic plots were dry-ploughed and harrowed but not puddled during land preparation. One day before transplanting, the aerobic plots were soaked with irrigation water to facilitate transplanting. Afterwards, the aerobic plots were flash irrigated with about 5 cm water when the soil moisture tension at 15 cm depth reached -30 kPa. Around flowering, the threshold for irrigation was reduced to -10 kPa to prevent spikelet sterility. Twenty-days-old seedlings from wet-bed nurseries were transplanted at the rate of three seedlings per hill and at a spacing of 25 × 10 cm for both aerobic and flooded rice plots. Adequate P, K and Zn were applied and incorporated in all plots one day before transplanting. Fertilizer N was applied in three equal splits of 50 kg ha⁻¹, one day before transplanting and at 25 and 45 days after transplanting. Insects, diseases and weeds were adequately controlled to achieve high yields. A maximum of 7.2 t ha⁻¹ was produced by PSBRc80 under aerobic conditions, which was only 8% less than when grown under flooded conditions (Table 1). A large difference in aerobic rice yield existed among the four varieties. The varietal difference in yield was associated with HI, not with biomass production.

Table 1. Comparison of yield parameters among four varieties under continuously flooded and aerobic conditions at the IRRI farm in the dry season of 2004

Variety	Growth duration (d)	Plant height (cm)	Harvest index (g g ⁻¹)	Grain yield (t ha ⁻¹)
<i>Continuously flooded conditions</i>				
PSBRc80	117	97	0.48	7.84
Magat	113	99	0.49	8.12
Apo	117	137	0.47	7.78
UPLRi7	117	121	0.38	6.33
<i>Aerobic conditions</i>				
PSBRc80	124	91	0.47	7.22
Magat	117	85	0.49	6.68
Apo	117	117	0.45	6.32
UPLRi7	124	108	0.42	5.13
LSD (0.05)		5	0.03	0.71

Breeding rice varieties for adaptation to lowland aerobic cultivation is relatively new compared with development of drought-resistant varieties for upland and rainfed lowland environments. Several promising aerobic rice varieties have been developed in China (Wang et al. 2002), but the mechanism of their aerobic adaptation is not clear. Apparently, short plant height associated with high HI should be an important target. However, not all semi-dwarf varieties have high HI and high yield under aerobic condition. For example, short-stature IR72 produced only 4.9 t ha⁻¹ with a HI of 0.28, which was lower than that of the tall upland variety Apo (George et al. 2002). Apparently, IR72 does not have the same aerobic adaptation as PSBRc80 and Magat, although they are all semi-dwarf varieties and produce similar biomass under aerobic conditions. The physiological basis of the yield gap between aerobic and flooded rice has not been studied in detail. Furthermore, it is not clear what physiological traits contribute to aerobic adaptation. One possible candidate is reduced sensitivity of grain filling to mild water stress during the grain development phase. Bouman et al. (2006) suggested that the relatively high yields of aerobic rice cultivars developed in China may be attributed to their capacity to maintain a high HI through high spikelet fertility under aerobic conditions. In IRRI's aerobic rice-breeding programme, crosses are being made between lowland semi-dwarf *indica* and upland tall varieties for achieving aerobic adaptation (Atlin et al. 2006). Identifying the physiological and morphological traits associated with aerobic adaptation is vital to support the selection and breeding of high-yielding aerobic rice varieties. In addition, aerobic rice-breeding nurseries should be managed at optimum level to avoid stresses other than those imposed by aerobic culture so that aerobic yield potential can be fully expressed.

Yield decline under monocropping of aerobic rice has been reported by George et al. (2002) and Peng et al. (2006). The causes of yield decline in the continuous aerobic rice system remain unclear. It could be related to the build-up of nematodes and soil pathogens under aerobic conditions (Ventura et al. 1981), changes in soil

mineral nutrients (Lin et al. 2005) or growth inhibition by toxic substances from root residues (Nishio and Kusano 1975). Crop management strategies to mitigate or prevent the yield decline of continuous aerobic rice can only be developed when the causes of yield decline are clearly identified. New aerobic rice varieties with a minimum yield gap compared with flooded rice, and crop management strategies that can prevent the yield decline of continuous aerobic rice must be developed before the aerobic rice technology can be widely adopted in large areas of the irrigated tropical lowlands.

GENOTYPIC VARIATION IN NITROGEN USE EFFICIENCY

Nitrogen use efficiency can be separated into different component indices (Ladha et al. 2005). All indices that have been used for studying NUE of rice genotypes can be divided into three groups: uptake efficiency, utilization efficiency and NUE-related traits (Table 2). Different NUE indices can be used for different purposes. Apparent uptake efficiency of fertilizer-N (RE_N) is the percentage of fertilizer-N recovered in above-ground plant biomass at the end of the cropping season. Both the N-difference and ^{15}N -dilution method can be used to quantify RE_N but the estimate is typically higher with the difference method than with the ^{15}N -dilution method (Ladha et al. 2005). There are many ways to define N utilization efficiency. The most widely used for comparing different genotypes is the N utilization efficiency for grain production (NUE_g). The quantification of NUE_g does not need a zero-N plot. Agronomic N use efficiency (AE_N) and partial factor productivity of applied N (PPF_N) are mainly used by agronomists to evaluate the NUE of different crop management practices. The determination of AE_N requires a control plot to estimate the grain yield without fertilizer N application. Compensation takes place among different components of NUE because of the interactions among traits related to NUE. Indigenous N supply capacity and N fertilizer input rate have a large influence on NUE. Growing conditions that govern plant growth and crop yield will also affect NUE. There is no common standard system to evaluate NUE of different genotypes, making it very difficult to compare results across studies.

In rice, genotypic variation in NUE has been reported by many researchers. Broadbent et al. (1987) studied NUE_g of 24 genotypes with and without fertilizer-N application. They estimated NUE_g using the ratio of panicle weight to total N uptake (WP/TN) and reported that there were significant differences in WP/TN among the genotypes. WP/TN was well correlated with other NUE-related parameters and provided genotypic rankings that did not differ greatly from multiple-parameter rankings. Tirol-Padre et al. (1996) compared NUE_g of 180 genotypes without fertilizer N application. There were significant differences in NUE_g among the 180 genotypes, ranging from 38 to 82 kg kg⁻¹. They also confirmed the presence of genetic variability within a maturity class for N acquisition. Singh et al. (1998) compared the N responses of 20 genotypes under fertilizer N rates of 0, 50, 100, 150 and 200 kg ha⁻¹. They identified N-efficient genotypes that produced high grain yield at both low and high levels of N application, N-inefficient genotypes that produced low yields at low N levels but responded well to N application, and N-

inferior genotypes that gave low yields at both low and high N levels. Although 75% of the variation in grain yield was explained by total N uptake, genotypic differences in NUE_g were observed. Inthapanya et al. (2000) determined the differences in NUE_g among 16 genotypes grown under rainfed lowland conditions at three locations with and without N application. There was a significant effect of genotype and an insignificant effect of genotype \times location interaction for NUE_g . Mean NUE_g of the 16 genotypes ranged from 55 to 84 kg kg⁻¹. Koutroubas and Ntanos (2003) studied NUE_g of five cultivars with N application under Mediterranean conditions. They reported that *indica* cultivars generally had higher NUE_g than *japonica* cultivars. In a recent study (Samonte et al. 2006), NUE_g of Lemont, Teqing and 13 advance recombinant inbred lines obtained from a Lemont \times Teqing cross was determined under high N application level. There was a significant variation in NUE_g among the 15 genotypes, ranging from 25 to 64 kg kg⁻¹. The large genotypic variation in NUE_g was probably caused by some genotypes with low yield potential. When only high-yielding varieties were compared, the genotypic variation in NUE_g could be much smaller.

Table 2. Components of nitrogen use efficiency (NUE) and their related traits

No.	Parameter	Symbol	Calculating equation	Unit
<i>N uptake efficiency</i>				
1 ^a	Apparent uptake efficiency of fertilizer N	RE _N	100 \times N uptake from fertilizer N / Fertilizer N input	%
<i>N utilization efficiency</i>				
2	N utilization efficiency for grain production	NUE_g	Grain yield / Total N uptake	kg kg ⁻¹
3 ^b	Fertilizer N utilization efficiency for grain	FNUE _g	Grain yield increase / N uptake from fertilizer N	kg kg ⁻¹
4	N utilization efficiency for biomass production	NUE_b	Total dry matter / Total N uptake	kg kg ⁻¹
5 ^b	Fertilizer N utilization efficiency for biomass	FNUE _b	Total dry-matter increase / N uptake from fertilizer N	kg kg ⁻¹
6 ^b	Agronomic N use efficiency	AE _N	Grain yield increase / Fertilizer N input	kg kg ⁻¹
7	Partial factor productivity of fertilizer N	PFP _N	Grain yield / Fertilizer N input	kg kg ⁻¹
8	Photosynthetic N use efficiency	PNUE	Photosynthetic rate / Leaf N concentration	$\mu\text{mol g}^{-1} \text{s}^{-1}$
<i>NUE-related traits</i>				
9	N harvest index	NHI	Grain N content / Total N uptake	
10	N translocation ratio	NTR	Grain N content / Plant N content at flowering	
11 ^b	N productivity index	NPI	Grain yield at zero N \times NUE_g	
12	Harvest index	HI	Grain yield / Total dry matter	

^a Requiring zero-N plot to estimate indigenous N supply or ¹⁵N labelling technique to estimate N uptake from fertilizer N.

^b Requiring zero-N plot to estimate indigenous N supply, grain yield and total dry matter without fertilizer N application.

PHYSIOLOGICAL UNDERSTANDING OF NITROGEN USE EFFICIENCY

Several factors can cause the differences in N acquisition among rice genotypes (Ladha et al. 1998). Genotypic differences existed in N uptake from various soil depths (Kundu and Ladha 1995). Rice genotypes differed in their ability to stimulate plant associative N₂ fixation (Ladha et al. 1998). Rice genotypes had different rhizosphere effects on the extent and pattern of soil N mineralization (Kundu and Ladha 1997). These differences could be related to differences in rooting characteristics such as root surface area, root mass, root depth, root number and root length density (Kirk and Bouldin 1991).

On the other hand, many physiological processes affect N utilization efficiency for biomass production (NUE_b) and NUE_g (Ladha et al. 1998). NUE_b is largely affected by critical concentrations (internal N requirement) for expansion and organ formation, N partitioning between leaves and stems, vertical N distribution in a canopy, efficiency of N use in converting CO₂ to carbohydrate through photosynthesis, rubisco activity and leaf senescence. Grain N concentration, sink capacity, unproductive tillers, HI and the ability to remobilize the absorbed N from straw to grain determine N harvest index (NHI) and NUE_g.

Leaf N plays a major role in biomass production through photosynthesis. Leaf N content is closely correlated with single-leaf photosynthetic rate (Peng et al. 1995). Canopy photosynthetic rate is affected by leaf N through leaf area expansion. High plant N content delays leaf senescence and therefore increases photosynthetic duration (Makino et al. 1984). Increasing leaf N content and delaying N efflux from leaf (i.e., delaying leaf senescence), especially the flag leaf, could improve NUE_b if the ratio of photosynthesis to respiration was not decreased. A large proportion of radiation is intercepted by the top layers of the canopy, especially in the rice crop with high leaf area index. Matching vertical N distribution and light distribution in the canopy is another approach to achieving high NUE_b. In the leaf, N is concentrated in the chloroplasts, mainly as the enzyme protein rubisco. Rubisco accounts for more than 50% of total soluble protein and over 25% of total N of leaves (Makino et al. 1984). Therefore, leaf is a major storage organ for N. The major source of N for developing leaves of mature rice plants is the N mobilized from older, senescing leaves. Out of total N translocated from vegetative tissues to the panicle, 64% was from leaf blades, 16% from leaf sheaths and 20% from stems (Mae and Ohira 1981). Therefore, efficiency in N remobilization from old to new leaf and from straw to grain will affect both NUE_b and NUE_g.

Unproductive tillers could reduce NUE_g, especially when mutual shading occurs. Unproductive tillers capture solar radiation and absorb soil N during early stages of growth. Genotypic variation in tillering capacity and unproductive tiller percentage exists in rice (S. Peng, unpublished data). The N and carbon of unproductive tillers can be mobilized to the productive tillers before they die (Thorne and Wood 1987), although the efficiency of such transport needs to be quantified. If the majority of N in unproductive tillers could be mobilized before they die, the negative impact of unproductive tillers on NUE_g can be minimized.

PLANT TRAITS RELATED TO NITROGEN USE EFFICIENCY

Although genotypic variation in NUE_g has been observed for a long time, improving NUE in rice has not been an objective in plant breeding (Samonte et al. 2006). This is partially because of the lack of simple and quick methods for estimating NUE_g , which could be used for screening large numbers of progenies in the breeding programme. The $G \times E$ interaction for NUE_g also makes the improvement of NUE more difficult. Furthermore, there is a danger of selecting for plants with low total N uptake and low grain yield if the selection is solely based on NUE_g . Rice breeders should develop new rice varieties that not only produce high yields but also use N efficiently. In order to achieve these objectives, plant traits that are associated with high grain yield and high NUE should be selected concomitantly, and breeders should be able to use these traits easily as selection criteria in the breeding programme.

Many plant traits have been studied to improve the mechanistic understanding of NUE_g . Genotypes with higher NUE_g had a lower percentage of straw N ($N_s\%$) at maturity (Tirol-Padre et al. 1996; Singh et al. 1998; Koutroubas and Ntanos 2003). Low grain N concentration ($N_g\%$) was also associated with high NUE_g (Tirol-Padre et al. 1996; Singh et al. 1998; Inthapanya et al. 2000; Koutroubas and Ntanos 2003). Grain N concentration decreases by about 0.1% as NUE_g increases by 7 to 10 kg kg^{-1} as grain N concentration decreases by about 0.1% (Tirol-Padre et al. 1996; Koutroubas and Ntanos 2003). Genotypes with high HI were more efficient in N use (Inthapanya et al. 2000).

Mathematically,

$$NUE_g = \frac{1}{\left(\frac{1}{HI} - 1\right) \times N_s\% + N_g\%} \tag{1}$$

This equation indicates that HI, $N_s\%$ and $N_g\%$ determine NUE_g . At $HI=0.5$, $N_s\%$ and $N_g\%$ contribute equally to NUE_g (Inthapanya et al. 2000). Rice generally has greater NUE_b and NUE_g than some other C_3 crops such as soybean and wheat, because of low $N_s\%$ and $N_g\%$. Further decreasing $N_g\%$ could contribute to efficient N utilization theoretically. Genotypic variation in $N_g\%$ is relatively small compared to the variation caused by management practices. Tirol-Padre et al. (1996) studied genotypic variation in $N_g\%$ of 180 lines grown without fertilizer-N input. About 93% of genotypes had $N_g\%$ of 0.95 to 1.20. It may not be feasible to improve NUE_g by reducing $N_g\%$ using conventional breeding because grain N concentration is affected more by environments than by genotypes (Ladha et al. 1998).

Koutroubas and Ntanos (2003) reported that difference in NHI explained genotypic variation in NUE_g . There was a significant positive correlation between NUE_g and N translocation ratio (NTR), which was calculated as the ratio of grain N content at maturity to plant N content at flowering (Samonte et al. 2006). Crop growth duration affects NUE_g through influencing crop yield and N uptake. Medium-duration genotypes had higher NUE_g than short-duration genotypes

(Broadbent et al. 1987; De Datta and Broadbent 1990). Longer duration could result in a decrease in NUE_g (Samonte et al. 2006).

Koutroubas and Ntanos (2003) argued that using single selection criteria for improving NUE may have negative implications on grain yield because of interaction among NUE-related traits. Broadbent et al. (1987) stated that the evaluation of NUE of different genotypes should be based on multiple parameters rather than just one parameter. The sum of Z-transformed values of grain yield, NUE_g , panicle weight, panicle weight/total N uptake and total dry matter/total N uptake, putting equal weights on each parameter, was used to rank genotypes (Broadbent et al. 1987; De Datta and Broadbent 1988; 1990). Singh et al. (1998) developed the N productivity index (NPI), which is the product of grain yield at zero N and NUE_g for evaluating NUE of genotypes. Quantifying and ranking N-efficient genotypes based on NPI was most consistent, whereas NUE_g , AE_N and RE_N had biases either toward soil N or fertilizer-N supply (Singh et al. 1998). However, determination of NPI requires field evaluation of genotypes at low N (or zero fertilizer-N input) and high N levels. The high N level should not be too high to induce lodging, pest and disease damages, which affect the crop N response and NUE (Tirol-Padre et al. 1996; Singh et al. 1998).

MOLECULAR APPROACHES TO IMPROVE NITROGEN USE EFFICIENCY

Recent developments in molecular biology provide a new opportunity to improve NUE through crop improvement. Transforming C_3 rice plants into C_4 rice plants has resulted in 10 to 35% increase in grain yield compared with control plants (Ku et al. 2000). The C_4 plant is assumed to have higher NUE than the C_3 plant (Ladha et al. 2005). Obara et al. (2001) used a backcross inbred-line population to detect putative quantitative-trait loci (QTLs) associated with the contents of cytosolic glutamine synthetase (GS1) and NADH-glutamate synthase (NADH-GOGAT). GS1 is a key enzyme in the mobilization of N from senescing leaves, and its activity in senescing leaves is positively related to yield. NADH-GOGAT is important in the utilization of N in grain filling, and its activity in developing grains is positively correlated with yield. Seven chromosomal QTL regions for GS1 and six for NADH-GOGAT were detected. Some of these QTLs were related to N recycling from senescing organs to developing organs. A structure gene for GS1 on chromosome 2 was co-located in the QTL region for seed weight. A structure gene for NADH-GOGAT on chromosome 1 was co-located in the QTL region for soluble protein in developing leaves. Yamaya et al. (2002) developed transgenic lines overproducing NADH-GOGAT, and two of the transgenic lines showed an increase in grain weight. These studies suggest that genotypes, obtained from genetically manipulated populations or genetic resources, with high GS1 in senescing leaves and high NADH-GOGAT in developing grains should promote N remobilization from straw to grain and consequently improve NUE_g (Andrews et al. 2004).

SUMMARY

The emphasis on increasing rice grain yield of irrigated lowland rice when water and N are amply supplied will gradually diminish in importance as concerns mount about reduced water availability for irrigated rice and the environmental impact from N losses. The new challenge is to sustain the needed increase in rice yields while reducing the requirements for water and N per unit of grain production. Newly developed crop management strategies have been very effective in maintaining rice yield with reduced input of water and N, resulting in great WUE and NUE. However, it is always more difficult for farmers to adopt a new crop management technology than planting new varieties. Research on genetic improvement of rice varieties for high WUE and NUE should receive more attention in the near future. For water, new varieties that produce high grain yields under water-saving technologies such as AWD and the aerobic rice systems should be developed. Small yield penalty is acceptable when they are grown under water-saving technologies compared to flooded conditions. For N, genotypic variation in NUE has been reported in many studies. Plant traits that are associated with high grain yield and high NUE should be identified so that breeders are able to use these traits easily as selection criteria in the breeding programme to develop N-efficient varieties without sacrificing rice yield potential. New breeding techniques such as development of F₁ hybrids, marker-aided selection, transformation and genetic engineering should be combined effectively with the empirical breeding method in order to increase rice grain yield with less water and N.

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