Characteristics of nitrogen nutrition in hybrid rice

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Rice hybrids have a mean yield advantage of 10-15% over inbred varieties (Li 1981, Yang and Sun 1988). Growth and development processes associated with higher grain yields of rice hybrids include a more vigorous and extensive root system (Li 1981, Yang and Sun 1988), increased growth rate during vegetative growth (Yamauchi 1994), more efficient sink formation and greater sink size (Kabaki 1993), greater carbohydrate translocation from vegetative plant parts to the spikelets (Song et al 1990), and larger leaf area index (LAI) during the grain-filling period, but the physiological basis for heterosis remains unknown (Peng 1998). Specific characteristics of the uptake and physiology of N in hybrid rice appear to play a key role in this. In this paper, we reviewed the characteristics of N uptake and N use by hybrid rice, a proposed physiological basis for N efficiency, and the role of nitrate nutrition in hybrid rice. All cited papers are comparisons between hybrids and the best conventional cultivars, i.e., not comparisons between the hybrid and its parents.

Nitrogen uptake and use

The total N uptake by hybrid rice shoots is greater than that of conventional cultivars, especially from transplanting to tillering and from panicle emergence to grain-filling stages (Yang 1987). Hybrid rice takes up about 15-20% of the total amount of N accumulated in the plant after heading and responds well to late application of N at flowering. In the same studies, N uptake after heading of conventional varieties was only 6-7% of total N uptake (Yang 1987). In field experiments, hybrid rice had a greater N efficiency (defined as grain yield per unit N fertilizer applied) than conventional rice (Lin and Yuan 1980, Yang 1987). This increased N efficiency was not due to greater internal N use in dry matter production (defined as unit dry matter produced per unit N accumulated in the plant) (Yang 1987, Yang and Sun 1992). We propose that higher recovery efficiency of applied N (N uptake per unit N applied) because of greater root N absorption potential, greater shoot N-use capacity (N demand by the shoot, i.e., how much and how fast the shoot can use N), and greater N remobilization efficiency (N translocation to the grain, i.e., N harvest index) are the major factors that cause higher N efficiency in hybrid rice (Fig. 1).

Physiological basis for nitrogen efficiency in hybrid rice

Root growth and distribution density in soils, aerobic respiration, oxidizing power, and energy synthetic metabolism are the important traits responsible for higher N absorption potential in hybrid rice (Yang and Sun 1991c). Rice hybrids develop an extensive root system, which is essential for efficient N absorption from the soil and topdressed N fertilizer applications. Under field conditions, hybrids have greater root fresh and dry weights, root volume, and root length density than inbred varieties (Yang and Sun 1988, 1992). The activities of dehydrogenase and cytochrome oxidase, oxidizing power, and ATP content of hybrid roots were much greater than those of conventional cultivars at both early and late growth stages (Yang and Sun 1988). These root morphological and physiological characteristics were positively and significantly correlated with N uptake by rice shoots (Yang 1987).

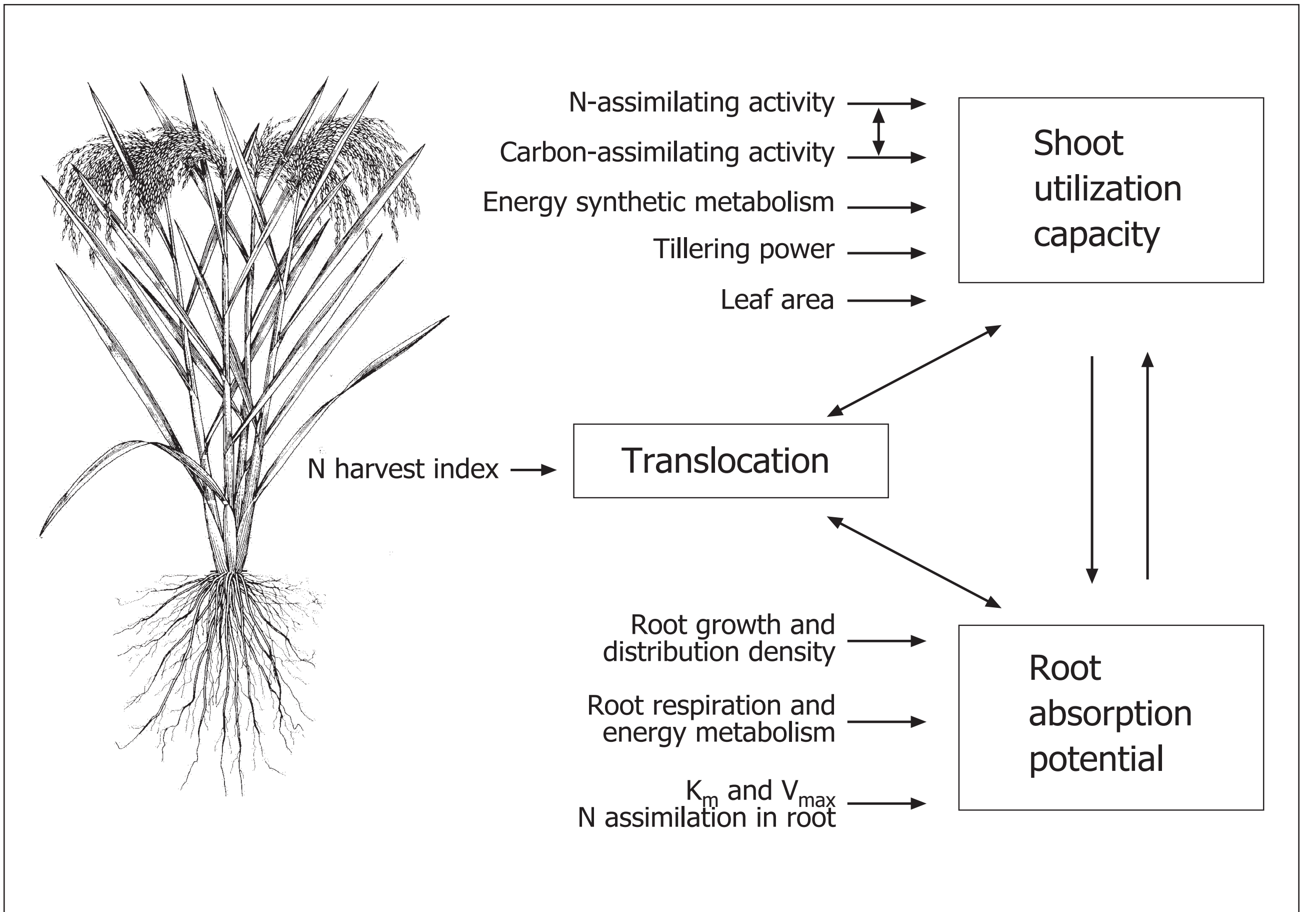

Fig. 1. Physiological parameters associated with N efficiency in hybrid rice. We hypothesized that the higher N efficiency in hybrid rice results from higher root absorption potential, greater shoot use capacity, and more efficient translocation of N and their positive interactions. The major related physiological traits for efficient absorption, use, and translocation of N by rice plants are listed.

The activities of nitrate reductase (NR, a rate-regulating enzyme in converting NO_3^--N to NH_3), glutamate synthase (Fd-GOGAT, a rate-regulating enzyme in processing NH_3 to glutamate), amino acid synthase (GPT and GOT), and CO_2-assimilating enzymes (Rubisco, a rate-regulating enzyme in photosynthesis and a key enzyme in N metabolism) in leaves at different growth stages differed considerably between hybrid rice and conventional cultivars (Yang and Sun 1989). The activities of NR and Fd-GOGAT in hybrid leaves were 40-60% greater than in leaves of conventional rice at the heading stage (Yang and Sun 1989, Yang and Sun 1992) and close correlations were observed between leaf N concentration and activities of these enzymes (Yang 1987). Compared with conventional cultivars, the activity and protein content of Rubisco were 25-40% higher at low N levels and twofold higher at adequate N levels in hybrid rice leaves (Yang and Sun 1991b, 1992). Apparently, the stimulation of activity and level of Rubisco by N is greater in hybrid rice than in inbred cultivars. Higher activities of Rubisco and of the N synthetic metabolism in hybrid leaves result from higher protein levels of the enzymes. Thus, the enhanced N- and C-assimilating metabolism of hybrid rice, combined with its greater tillering capacity and leaf area (Yang 1987), are possibly the major physiological causes of greater N-use capacity in hybrid rice shoots. The interaction between N and C synthetic metabolism further increases shoot N-use capacity in hybrid rice and, in turn, raises root absorption potential.

Hybrids tend to have a higher N harvest index than conventional cultivars. After flowering, more N is translocated into hybrid rice panicles than into those of conventional cultivars (Yang and Sun 1990). This higher N translocation efficiency could be one of the major factors responsible for increased N efficiency in hybrid rice.

Nitrate vs ammonium nutrition during reproductive growth

Research conducted during the past 10 yr has provided evidence that hybrid rice roots are more efficient in absorbing NO_3^- than inbred varieties and that a preferential uptake of NO_3^- during reproductive growth may be one of the causes of the higher yields observed (Yang and Sun 1990, 1991a, 1992). Although NH_4^+ is the major available N form in flooded soils, nitrate exists in the oxidized surface soil layer, in the irrigation water, and, probably, in the oxidized rhizosphere surrounding rice roots. Rhizosphere oxidation and acidification in hybrid rice exceed those of conventional rice (Yang et al 1997), but there is no information available about the distribution of nitrate in the rhizosphere. A special feature of hybrid rice is the much greater development of fine, dense, superficial roots. These are mainly distributed in the oxidized surface soil layer (Yang and Sun 1988) and appear to (1) enhance surface soil and rhizosphere oxidation and (2) be capable of absorbing NO_3^- efficiently, particularly after panicle initiation.

In nutrient solution experiments, hybrid roots had higher affinity for NO_3^-, especially at the reproductive growth stages, than conventional cultivars. The uptake of NO_3^--N by roots of hybrid rice increased linearly with increasing NH_4NO_3 concentrations in nutrient solution, but did not in the conventional cultivar (Luo et al 1993). At high supply levels (80-120 mg N L^{-1}), the hybrid absorbed more NO_3^- than NH_4^+, whereas the conventional cultivar did not, implying that preference for NO_3^- is genetically controlled and dependent on N supply levels. Studies on NO_3^- uptake kinetics showed that K_m values of NO_3^- uptake by hybrid roots were 27% lower for 22-d-old seedlings and 62% lower for 63-d-old seedlings than those by roots of conventional cultivars (Yang and Sun 1991c).

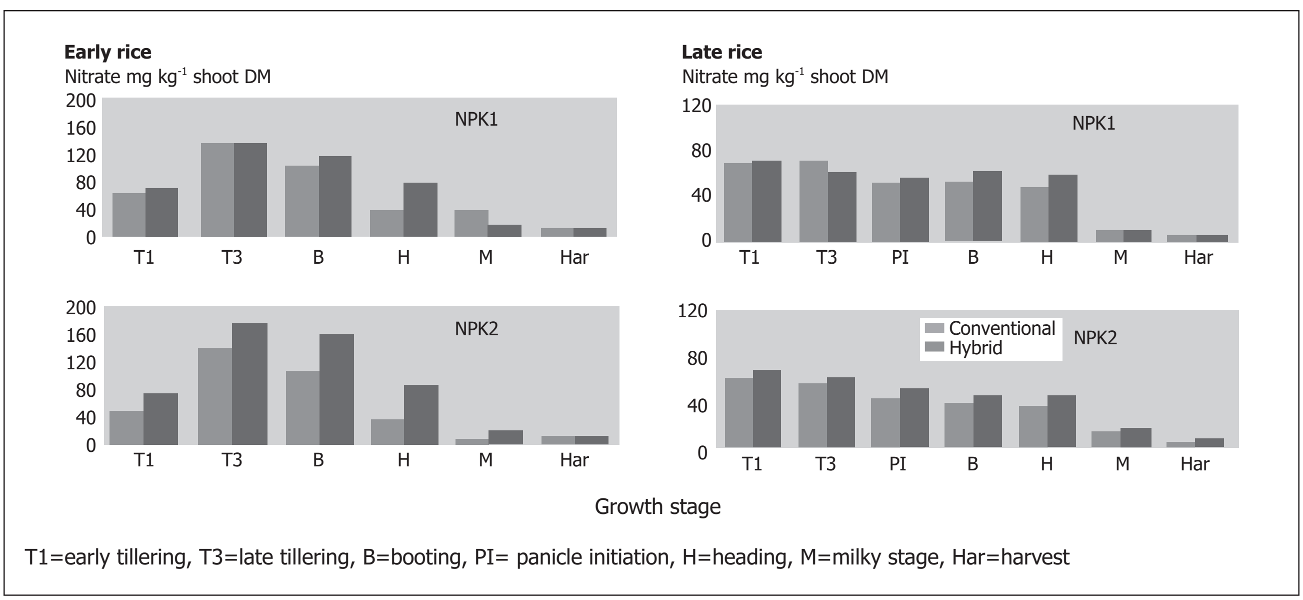

Fig. 2. Nitrate concentrations in the shoots of conventional and hybrid cultivars at different growth stages and different NPK levels. Field measurements conducted at Jinhua, China, 1998.

In pot experiments with topdressing of ^{15}N-labeled NO_3^--N and NH_4^+-N fertilizers during reproductive growth, NO_3^--N application stimulated the growth of superficial roots and increased grain yield more significantly in hybrid rice than in conventional rice, mainly because of improved grain filling (Yang and Sun 1990). Nitrate fertilizer use efficiency by hybrid rice after anthesis was 7.8% higher than that of conventional rice. NO_3^--N stimulated the vigorous growth of superficial roots, increased the synthesis of cytokinins (mainly zeatin) in roots, and delayed the appearance of the abscisic acid (ABA) peak in both leaves and filling grains. High ratios of zeatin/ABA enhanced the synthesis of RNA, which resulted in protein synthesis for carbon assimilation and transportation (Yang and Sun 1991a).

High nitrate reductase activities in both seedlings and functioning leaves of rice plants have been reported (Lin et al 1986, Yang and Sun 1989). Nitrate reductase activity at the seedling stage was negatively related to tolerance of a rice cultivar for high N supply, and was recommended as an indicator or parameter for screening high-N-tolerant cultivars (Lin et al 1986). Nitrate reductase activities were higher and more sensitive to N supply levels in hybrid rice leaves than in conventional rice (Yang and Sun 1989). Under field conditions, shoot NO_3^- concentrations of both hybrid and conventional rice varied with growth stages and NPK supply levels, but shoot NO_3^- concentrations in hybrid rice exceeded those of the inbred variety at most growth stages, especially with high amounts of N, P, and K applied (Fig. 2). Similarly, higher grain yields were obtained in hybrid rice than in the conventional rice cultivar, suggesting that NO_3^- accumulation and nutrition might be associated with high yield in rice.

Research needs

Our studies on the morphology and physiology of N nutrition in hybrid rice indicated that the greater N efficiency in hybrid rice mainly results from higher root absorption potential, greater shoot N-use capacity, and efficient N translocation, as well as their positive interactions (Fig. 1). More research is needed to understand (1) the influx and compartmentation of NO_3^- by rice roots, (2) strategies for hybrid rice to absorb more NO_3^- than an inbred variety, (3) the fate of NO_3^- from soil to leaves, and (4) the contribution of NO_3^- to N nutrition as well as to yield formation in rice. A quantitative linkage between form of N nutrition, cytokinin synthesis, delayed appearance of the ABA peak, and other physiological processes with grain yield remains to be established under field conditions to demonstrate the possible contribution of N nutrition to heterosis in rice. Only then will we be able to fine-tune water and N management practices in hybrid rice.

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