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Improving yield potential of tropical rice: Achieved levels and perspectives through improved ideotypes

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ABSTRACT

Improving the genetic yield potential (YP) of tropical, irrigated rice varieties is a priority objective of rice breeding programs worldwide in the interest of achieving food security and maintaining political stability. But YP has stagnated at about 10 Mg ha^{-1} since the Green Revolution. We present a survey of researchers' current top yields across different environments and countries, experimentally investigate YP-related traits and radiation use efficiency (RUE) of 12 elite materials, and use a simple model to explore traits that would raise the yield ceiling. The survey indicated that maximal grain yield is between 5 and 12 Mg ha^{-1} depending on radiation during flowering and grain filling. The experiments conducted in several environments in the Philippines indicated that (1) different morphologies in terms of panicle number and size and leaf size lead to similar YP due to trait–trait compensation, and (2) differences in RUE are partly attributable to variation in terminal senescence which is strongly environment dependent. Simulations thus focused on post-floral physiological processes, namely dynamics of light interception, carbon assimilation and maintenance burden. Scenarios of different degree of stay-green indicated that terminal senescence is essential to limit N requirements and maintenance burden, but partial stay-green would strongly benefit RUE and YP, particularly if accompanied with increased leaf photosynthetic capacity. The need to increase pre-floral C and N reserves for grain filling is discussed, resulting in a concept to refine current ideotypes such as IRRI's New Plant Type and China's Super Hybrid Rice. In conclusion, current best tropical breeding products do not have higher YP than some varieties dating 30–40 years, and new concepts are needed in rice breeding. Breeding for such plants should be done under high N inputs.

1. Introduction

Irrigated, flooded rice is the most productive of all rice ecosystems and occupies the most valuable land particularly in Asia, located in densely populated areas where demand for land for other economic activities is high, while consuming vast amounts of fresh water (Beddington et al., 2012). Given the strategic role of rice as the world's second food crop after wheat (and the developing world's most important one), irrigated rice yields must increase further for the crop to remain economically sustainable and to justify the use of the prime land it occupies (Sheehy and Mitchell, 2011a,b), in the interest of world nutrition and even political stability (Brown, 2011).

The yield potential (YP) of irrigated rice cultivars took a quantum leap in the 1960's with the development of green revolution seed and agronomic technologies. Although little gain was since then achieved in genotypic YP, which stagnated at about 10 Mg ha^{-1} in tropical environments (Peng et al., 1999), mean global yields continued to increase due to improved practices and increased inputs.

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The growth in global yields, however, masks a stagnation occurring in important rice growing regions (Ray et al., 2012). As the gap between potential and actual farmers' yields narrows, research efforts to raise the apparent biological yield ceiling of the crop become more urgent. This is a challenge to breeders, molecular geneticists and physiologists.

The challenge has given rise to different conceptual approaches and multi-institutional thrusts. One approach is the improvement of the phenological and morphological plant type. With the metabolic functioning of a typical C_3-type plant taken as a givens, a modified morphological ideotype was conceived in the early 1990s at the International Rice Research Institute (IRRI) in the Philippines (New Plant Type, NPT; Dingkuhn et al., 1991; Peng et al., 1994) designed to improve light harvest for photosynthesis particularly during grain filling (large erect leaves located above the panicle stratum), and having sturdy stems storing additional non-structural carbohydrate (NSC) reserves for grain filling, large panicles, and tolerance to the inter-plant competition associated with increased stand density. Sturdy stems were also seen as important to improve lodging resistance, a structural biomass investment that may limit the harvest index (HI, generally about 0.5 in high-yielding varieties), but can be compensated with greater biomass production.

Results were initially disappointing on the basis of japonica-type germplasm alone, which offers many of the morphological traits, but shifting to indica x japonica NPT materials was more successful. Similar traits are being selected for at the Centro Internacional de Agricultura Tropical (CIAT) in Colombia. The NPT concept also inspired the development of Super Hybrid rices in China, which in addition to NPT-type traits are taller, have longer crop and grain filling durations, and maintain green leaves on the three uppermost positions until maturity (Peng et al., 2008; Li et al., 2014). Grain yields of ca. 15 Mg ha^{-1} are being envisaged and at times achieved in the sub-tropical summer season (Ying et al., 1998; Huang et al., 2013), but are not comparable with the lower environmental YP under warmer tropical conditions with shorter days. In fact, YP is a genotypic feature only in a given thermal and radiation environment.

Among the more recent, large international breeding projects seeking to overcome the current yield ceiling is the Green Super Rice (GSR) project operating in many tropical countries and in China (Marcaida et al., 2014; http://thegsr.org/index.php/about-green-super-rice/). It uses conventional breeding, explicit plant type concepts and molecular marker assisted selection (MAS) to combine traits for high YP with tolerance to major biotic and abiotic stresses. But there are limits to increasing rice YP through the architectural and phenological organization of the plant alone, considering that the green revolution germplasm already built on the improvement of such traits. The C_4-Rice Project (Von Caemmerer et al., 2012; http://c4rice.irri.org) seeks to improve radiation use efficiency (RUE) through the molecular engineering of the more efficient C_4-type photosynthetic metabolism in rice. Genetic sources within *Oryza* for higher photosynthetic rates unrelated to leaf nitrogen (N) content, leaf thickness or stomatal conductance have so far not been identified. Maximal leaf photosynthetic rates of rice are about 32.5 μmol CO_2 m^{-2} s^{-1} (Peng, 2000), although values around 25 μmol m^{-2} s^{-1} at light saturation are more frequently observed on healthy field crops (e.g., Dingkuhn et al., 1992b; Shimono et al., 2009). Maximal observed canopy photosynthesis is about 50 μmol CO_2 m^{-2} s^{-1} (Dingkuhn et al., 1990), with a theoretical upper limit of about 55 μmol m^{-2} s^{-1} (Sheehy et al., 2000). The C_4-rice approach is promising but cannot be expected to yield utilizable seed technologies in the foreseeable future.

Existing rice cultivars assimilate only about 2.2 g dw per MJ intercepted photosynthetically active radiation (PAR) in the tropics, whereas the RUE of C_4-type crops is about 50% greater or more (Mitchell et al., 1998). Campbell et al. (2001), however, reported that RUE is developmental stage, biomass and leaf area dependent. The highest canopy photosynthetic rates and greatest RUE are observed during vegetative growth and start declining at mid season. Consequently, crop growth rates (CGR) tend to be low during grain filling and even negative towards maturity (Schnier et al., 1990a; Dingkuhn et al., 1990). This phenomenon has several causes: (1) the increasing burden of maintenance respiration (R_m) which depends on biomass and particularly, its N content (Penning de Vries et al., 1989); (2) terminal leaf senescence which reduces photosynthesis but is necessary to provide the panicle with the mobilized N to produce grain (Sinclair and Sheehy, 1999); and (3) the apparent inability of the crop to achieve substantial post-floral N uptake (Schnier et al., 1990a,b; Fu et al., 2009), or alternatively to store significant N reserves in organs other than leaves. Consequently, even additional N application late in the season does little to mitigate leaf area loss and sustain high canopy photosynthetic rates during grain filling (Dingkuhn et al., 1992a).

Since these growth-limiting phenomena concern chiefly the period during which grains are produced, they are as important to YP as the genotypic, primary photosynthetic potential. It is thus crucial to maintain maximal CGR without starving the grain filling process of N resources (Greenwood et al., 1990; Sheehy et al., 2004). This study aims at deriving a concept for increasing tropical, irrigated, rice YP from information on currently achieved yields, traits exhibited by best-performing genotypes and simple models predicting potential post-floral RUE and growth gains, involving stay-green, the associated N requirements and maintenance burden. Extensive published data on rice N uptake and canopy photosynthesis and respiration (Dingkuhn et al., 1990, 1992a,b; Ingram et al., 1990; Schnier et al., 1990a,b) are revisited, whereas analyses of RUE and YP traits are based on original experimental data on current best cultivars. We thereby focus on reproductive-stage growth and post-floral leaf senescence, while assuming that plants would adjust its sink potential in the panicles to the variable resource. Although some authors consider rice YP mainly as sink-limited, the strong yield increases observed under elevated ambient [CO_2] in FACE experiments (Shimono et al., 2009; Hasegawa et al., 2013; Zhang et al., 2013) indicates that high-yielding varieties are responsive to increased assimilate resources. It is generally observed that yield components adjust to resources, resulting in a stable HI if stresses are absent and management is appropriate. We included population density as a factor in the experiments to evaluate biomass production and the plasticity of yield components and HI under variable competition. A simplified approach to RUE was chosen, driven by green-leaf area dynamics because the germplasm considered had similar plant geometry.

The specific objectives of this study were to (1) assess the YP of current highest-yielding tropical, irrigated rice germplasm; (2) assess key YP traits and RUE for a subset of elite materials experimentally, and (3) conduct a simple crop modeling exercise highlighting potential strategies to enhance YP through higher post-floral growth rates.

2. Materials and methods

2.1. Yield survey

A survey was conducted in 2014 among breeders and physiologists from four research centers to collect recent grain yield and final aboveground dry weight (agdw) data for elite breeding lines and high-yielding check varieties. The centers/sites were the Philippine Rice Research Institute (PRRI) with site Muñoz, Nueva Ecija, Philippines (15°40.3′ N, 120° 53.5′, 48 m asl); the International Rice Research Institute (IRRI) with site Los Baños, Philippines (14°11′ N,