Analysis and simulation of phenotypic plasticity for traits contributing to yield potential in twelve rice genotypes

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ABSTRACT

High-yielding rice varieties (HYV) show strong phenotypic plasticity, notably in compensatory tiller production and panicle size. In a precursor study on the high-tillering cv. IR72 we showed that the plasticity is adaptive by enabling yield stability across different stand densities, and we presented and validated the functional-structural crop model SAMARA, developed for the study of phenotypic plasticity. The present study analyses the phenotypic plasticity of high and low tillering plant types. Twelve contrasting, high-yielding irrigated rice genotypes were studied for the plasticity of traits contributing to grain yield under different season/site environments and stand densities in the Philippines. For the density factor, sequentially developing yield components along phenology, beginning with tillering, showed decreasing plasticity, indicating progressive adjustment to the initial stand density. For the site/season factor (climate), tillering was less plastic and panicle size and grain filling ratio provided for the strongest adjustments. Large plasticity was observed also for LAI and little plasticity for SLA and leaf morphology, particularly blade width. Genotypes differed strongly in organ size vs. number (leaves, panicles), representing organ "number" or "size" plant types. Up to 10 Mg ha^{-1} grain yield were observed for both extreme types. The plasticity of panicle size was caused by variation in spikelet number and not kernel weight. All genotypes were able to fully adjust yield components to differential plant stand density, resulting in unchanged yield. However, between environments, genotypes having greatest maximal yields and those having stable (but on average smaller) yields showed different patterns of phenotypic plasticity for yield component and plant morphology traits. The SAMARA model was calibrated for five genotypes showing contrasting morphology and plasticity. It was able to predict most of the genotypes' variation in morphological and yield component traits. Future opportunities to predict improved rice ideotypes for changing environments and cultural practices through combined field experimentation and modelling are discussed.

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1. Introduction

Crops use phenotypic plasticity (Schlichting, 1986, 2002) to adjust organ deployment and growth to variable resources, helping them to balance source-sink relationships (Donald, 1963, 1968; Bradshaw, 1965). Kumar et al. (2016) investigated orchestration of adjustment processes in IR72 rice if subjected to different stand density in different irrigated environments. Since rice yield components are formed sequentially (tillering, panicle initiation and subsequent tiller mortality, panicle differentiation, filling of fertile spikelets), each adjustment process impacts on the next (Agrama, 1996; Siband et al., 1999), ideally resulting in an optimal number of grains that are fully filled (Kumar et al., 2016). Other traits contributing to yield more indirectly also showed adaptive plasticity, such as variable phenology (setting the time available to capture and convert resources) and resource capture itself (e.g., traits for canopy and leaf morphology). Kumar et al. (2016) quantified the plasticity of such traits and demonstrated that the new crop model SAMARA can predict some of the adjustment processes using the concept of sink-sink competition for assimilates within the plant. The model was validated with independent data from 14 different combinations of year, site and season for the typical high-yielding, high-tillering, semidwarf, indica rice variety IR72.

Phenotypic plasticity in crops is a major mechanism to achieve yield stability in variable environments. For example, gap filling in canopies or compensation for defoliation relies on it (Rubia et al., 1996). Understanding phenotyping plasticity and the ability to predict it for specific crop environments trait genotypic combinations are important for crop improvement strategies through breeding. The recognized social and economic need to increase global rice production with finite land and water resources (Beddington et al., 2012; Brown, 2011), in the face of changing climatic conditions (Rötter et al., 2015) and crop culture systems, probably warrants innovative ideotype concepts for breeding. For example, future irrigated rice systems in the tropics will increasingly be direct seeded (as opposed to transplanted) to save labor and water, involving denser crop stands (Review: Farooq et al., 2011). Since the successful implementation of the Green Revolution rice ideotype in the 1960s and 70s (Peng et al., 1999, 2000) several new concepts emerged such as IRRI's New Plant Type (NPT) and China's Super Hybrid Rice (Peng et al., 2008). A rice ideotype was recently outlined to raise the yield ceiling, stagnating since the Green Revolution at about $10 \, t \, ha^{-1}$ (Dingkuhn et al., 2015). Beyond the challenge of raising the genetic and physiological yield ceiling, however, new varieties must also show the necessary adaptations to yield stably when challenged by climate variability and change, increased stand densities and inputs, and the increasing risks of lodging associated with these factors combined (Rötter et al., 2015). Theoretical blueprints for such crop varieties should thus not be based on a static ideotype vision but include phenotypic plasticity, in terms of adaptive, environment dependent expression of traits.

Conventional crop models are not well suited to test or improve such concepts because they lack detail and integration of physiological trait-trait and trait-environment interactions affecting the phenotype. The SAMARA model (Kumar et al., 2016; http://umr-agap.cirad.fr/en/equipes-scientifiques/modele-samara) was developed to simulate rice phenotypic plasticity and test ideotype concepts at the level of detail necessary to represent traits selected for by breeders, such as yield components. Proof of concept was thereby only provided for IR72, in terms of experimental analysis of phenotypic plasticity and its simulation. This analysis needs to be extended to rice genotypes representing different plant types and genetic backgrounds.

Traits that are frequently proposed for improved irrigated-rice plant types concern phenology, crop geometry (e.g., leaf angle or extinction coefficient), organ size and number (tillers, leaves, stems, panicles, spikelets, grains), and the dynamics of terminal senescence and partitioning, including reserves (Dingkuhn et al., 1991; Peng et al., 2008; Dingkuhn et al., 2015). The tropical Green Revolution rice varieties, such as IR72, owe their semidwarf morphology to a genetic gibberellin deficiency (loss of function of SD1 gene; Ashikari et al., 2002), a physiological stunting that is associated with smaller, more erect and more rapidly appearing leaves, greater tillering ability and smaller but numerous panicles. The varieties originally were generally indica materials, but increasingly breeders also introgressed traits from the japonica subspecies as they sought to develop modified plant types, such as the NPT (Peng et al., 2008). In a comparative study on the yield potential of 12 diverse elite genotypes, Dingkuhn et al. (2015) described NSIC-Rc 240, an indica-japonica inbred line from PRRI (Philippines) that out-yielded several elite indica semidwarfs while having fewer but larger panicles, larger leaves, slightly delayed terminal senescence and taller, sturdy stems. Although this observation cannot be generalized, it shows that different high-yielding plant types, with possibly different plasticity and adaptability, can be bred for tropical irrigated rice systems.

This study builds on Kumar et al. (2016) on the modelling of adaptive, phenotypic plasticity of IR72 rice and extends the analytical framework to 12 diverse genotypes previously characterized for yield potential (Dingkuhn et al., 2015). The objectives of the study are (1) to characterize yield component and crop morphological traits for the 12 genotypes when exposed to different stand density and climatic conditions; (2) analyze the phenotypic plasticity of these traits in response to two factors, stand density and season; and (3) model with SAMARA the behavior of the most contrasting five contrasting cultivars. The broader aim is to contribute to the development of knowledge and tools needed to predict rice ideotypes with improved yield potential and adaptability for tropical irrigated rice ecosystems.

2. Materials and methods

The experiments having generated the data used in this study were previously described by Dingkuhn et al. (2015), where they served to assess current levels of rice yield potential in conjunction with survey data. The present study uses the published grain yield information and relates it to detailed, unpublished trait observations from the same experiments with focus on their phenotypic plasticity.

2.1. Experimental study—design and statistical tools

A field experiment was conducted in four environments (combinations of sites and season): The 2012 dry season (DS) and wet season (WS) at the at the experimental farm of the International Rice Research Institute (IRRI), Los Baños, Philippines (14°11′N, 121°15′E, 21 m asl); and the 2012 DS and 2013 DS at the Philippine Rice Research Institute (PRRI), Muñoz, Nueva Ecija, Philippines (15°40.3′N, 120°53.5′E, 48 m asl). Each experiment had a split plot in a randomized complete block design with two factors and four replications (blocks). Factor 1 (sub-plot) consisted of two stand densities (recommended density: 25 hills m^{-2} at $0.2 \times 0.2 \, m$ spacing; high density: 100 hills m^{-2} at $0.1 \times 0.1 \, m$ spacing). Factor 2 (sub-sub plot) was genotype (12 accessions).

Elemental plot size was $4 \, m \times 6 \, m$ ($24 \, m^2$) including a $0.4 \, m$ planted border not used for sampling. Sowing dates were 29 Dec 2011 in the DS 2012 and 07 June 2012 in the WS 2012 at IRRI; and 28 January 2012 in the DS 2012 and 25 December 2012 in the DS 2013 at PRRI. Seeds were sown on seedling trays to obtain uniform seedlings. Fourteen-day-old seedlings were transplanted at 4 seedlings per hill onto water saturated, puddled soil. Total N applied was 160 kg ha^{-1} in the DS and 90 kg ha^{-1} in the WS applied in 3 splits as prilled urea. Potassium chloride (40 [20] kg K ha^{-1} in DS [WS]), triple super phosphate (30 [15] kg P ha^{-1} in DS [WS]) and Zn sulphate heptahydrate (5.0 [2.5] kg K ha^{-1} in DS [WS]) were applied basally. Pests and weeds were controlled using recommended chemicals as needed. Fields were kept flooded at 5–10 cm depth except after one week after flowering, when surface water was drained off.

Some stem borer damage was observed in the PRRI 2012 DS due to late planting, and lodging damage was observed during mid grain filling in the IRRI 2012 DS experiment due to a freak rain storm. These experiments were thus disregarded for grain yield but morphological observations at and before flowering and agdw at maturity were considered. The IRRI 2012 WS and PRRI 2013 DS experiments represented potential conditions and the analyses relating grain yield to morphological traits focused on them.

Data was analyzed using Statistical Tool for Agricultural Research (STAR Version 2.0.1, PBGB Biometrics and Breeding Informatics Unit, 2014). Analysis by ANOVA has been presented elsewhere (Dingkuhn et al., 2015). Means of all observations ±SE for IRRI 2012 WS and PRRI 2013 DS experiments are presented in Table S1 (annexe).