CrossMark

Maturity groups and growing seasons as key sources of variation to consider within breeding programs for high yielding rice in the tropics

Crisanta S. Bueno · Tanguy Lafarge

Abstract Differences in crop performance between seasons has raised concerns on whether or not contrasting rice varieties should be grown in each season in the tropics. Solving this question requires evaluation if key plant traits subtending grain yield are expressed similarly across seasons. Within each dry season (DS) and wet season (WS), one approach to address the issue was to group 32 high-yielding and contrasted cultivars with respect to crop duration, and to consider the crop cycle as two distinct phases: the first one from early vegetative to flowering (pre-flowering) and the second one from flowering to maturity (post-flowering). For each of these two phases, one key descriptive parameter was identified, the potential sink size (PSS) at flowering for the pre-flowering phase, and the grain filling rate (FR) for the post-flowering phase. Significant correlations were observed for grain yield with both PSS and FR within maturity groups in both seasons, indicating the strong effect of both phases in grain yield establishment. Finally, relevant traits in the DS were those favoring light capture along the whole crop cycle in both maturity groups. Traits for the WS differed among maturity groups. Traits for the early maturity group were also those favoring light capture, while the same traits were non desirable for the medium and late maturity groups, for which delayed leaf senescence and short plant height were identified. The difference between relevant traits highlights the need of developing distinct breeding programs respective of the growing seasons and maturity groups.

Keywords Grain filling rate · Maturity groups · Potential sink size · Rice · Season-based breeding traits · Traits for light capture · Traits for delayed leaf senescence

C. S. Bueno
Crop and Environmental Sciences Division, International Rice Research Institute, DAPO Box 7777, Metro Manila, Philippines

T. Lafarge (✉)
CIRAD, UMR-AGAP, 34398 Montpellier, France
e-mail: tanguy.lafarge@cirad.fr

Abbreviations
DS   Dry season
FR   Filling rate
GY   Grain yield
HI   Harvest index
LAI   Leaf area index
PSS   Potential sink size
SCL   Specific culm length
WS   Wet season

Introduction

Grain yield of high-yielding rice genotypes in irrigated paddy fields in the tropics, which has not gained much in the last 20 years, is regularly reported as significantly higher in the dry season (DS) than in the wet season (Yang et al. 2008b; Shahid et al. 2013). This large difference in crop performance between seasons raises the issue of whether or not contrasted varieties with different traits should be grown during each season. Solving this question requires investigation on whether key plant traits subtending grain yield are similar and expressed in the same way across contrasted seasons, or if higher yield is supported by different traits or traits expressed in a different way respective of the season. This may have important consequences on breeding programs which, in general, do not consider distinct seasons independently.

Sink size of a rice crop, defined as the total number of spikelets at flowering, is considered as the primary determinant of grain yield under favorable environments (Fischer 1983; Kropff et al. 1994): high yielding ability is well correlated with large sink size in temperate (Nagata 2006), subtropical (Wu et al. 2008; Li et al. 2009; Zhang et al. 2009; Xiong et al. 2013), and tropical (Ying et al. 1998; Yang et al. 2007) environments. This has been confirmed when sink size limitation due to higher temperature accelerated plant maturity despite maintenance of leaf photosynthesis activity (Kim et al. 2011). Accordingly, breeding programs for higher yield potential in rice have been mainly driven by increasing sink size (Yang et al. 2002). However, this strategy often reduced the breeding target to increasing one individual yield component without addressing any compensation phenomenon (Kovi et al. 2011; Fujita et al. 2013) or any relevance of subtending yield formation processes (Ying et al. 1998; Laza et al. 2004; Yang et al. 2007; Ohsumi et al. 2011). On one hand, compensation between yield components is widely expressed across genotypes through contrasted combinations of components (Huang et al. 2011; Dingkuhn et al. 2015). As examples, the breeding program for NPTs (Dingkuhn et al. 1991) and super hybrid rice (Yang et al. 2002) targeted bigger but fewer panicles; however, this was associated with lower filling capacity (Peng et al. 1999; Laza et al. 2003, for NPTs; Ao et al. 2008, for super hybrid rice). Similarly, introgression of a genetic segment driving the increase in one component, such

as the number of spikelets per panicle (Fujita et al. 2009, 2012), translated rarely into higher performance at the crop level, which was prone to G x E interaction (Ohsumi et al. 2011; Okami et al. 2015; Adriani et al. 2016a). On the other hand, as grain yield is well correlated with sink size (Liang et al. 2001; Kim et al. 2011), and sink size is already fixed at flowering, pre-flowering traits appear instrumental in determining grain yield in non-stressing conditions (Adriani et al. 2016b). In fact, sink size was already claimed (Lafarge and Bueno 2009; Bueno et al. 2010) as dimensioned in line with the supply capacity of the plant during the pre-flowering phase. Clearly, the method of improving plant types by focusing on yield components may bypass the likely identification of less integrated plant traits as possible means to explore genetic diversity and compare yield formation processes across genotypes and cropping seasons.

Higher crop growth rate (CGR) during the 14 days prior to heading has already been identified as a key early plant trait favoring panicle growth and sink size under temperate (Takai et al. 2006; Kamiji et al. 2011) and subtropical (Nagata 2006; Xiong et al. 2013) environments, and across environments (Ying et al. 1998). This was derived from higher radiation-use efficiency (Takai et al. 2006), inducing higher leaf area index (LAI) (Wu et al. 2008) with larger accumulation of non-structural carbohydrates (NSC) in the leaves, and higher translocation to the panicle (Takai et al. 2006; Xiong et al. 2013). Also under subtropical environments, longer crop (Zhang et al. 2009; Huang et al. 2013) and green leaf area (Ying et al. 1998; Wu et al. 2008) duration promoted biomass accumulation and yield. In the tropics, however, even if the possible occurrence of higher CGR (Sheehy et al. 2001; Yoshida et al. 2006; Bueno and Lafarge 2009) supported biomass growth as a target for higher yield (Peng et al. 1999), biomass allocation rather than biomass production was stated as a crucial trait for higher yield. This was the case in the DS, but also in the wet season despite a lower contrast in crop yield (Laza et al. 2003; Yang et al. 2007; Lafarge and Bueno 2009). Some traits at early stage have already been identified, such as specific leaf area, specific culm length, and earlier cessation of tiller production, whatever the cropping season (Bueno et al. 2010). Yet, these observations relative to tropical conditions were gathered without distinguishing between contrasted crop durations and without assessing whether desirable

plant type shall be different for wet and dry seasons. First, crop duration was mainly considered so far as a possible determinant for grain yield (Zhang et al. 2009; Huang et al. 2013), through the increase in grain filling duration under tropical conditions (Ying et al. 1998; Yang et al. 2008a). However, key traits subtending grain yield have not been evaluated with respect to crop duration, in a sense where crop duration might affect the weight of some of these traits in the process of grain yield formation. Second, despite the significant differences of crop performance widely reported between wet and dry seasons (Yang et al. 2008b; Bueno and Lafarge 2009), and the expected resulting differences between desired plant types, the same varieties are commonly grown in both conditions.

The objective of this study was to evaluate the grouping of genotypes with respect to crop duration as a comprehensive approach to identify relevant traits for high yield during each of the pre and post-flowering phases within each growing season. Here, potential sink size, as the product of total spikelet number at flowering and single filled-grain dry weight at maturity (Lubis et al. 2003), and filling rate, as the ratio of filled over total spikelet number, were evaluated as relevant integrated parameters to undergo such study: the principle was to evaluate their relevance in characterizing whether subtending plant traits instrumental in increasing yield potential can be revealed as accounting for distinct cropping seasons. Such a conclusion would have important implications within breeding programs on how they should consider distinct cropping seasons in their process. This study was conducted by comparing yield formation processes of a range of high-yielding rice genotypes between distinct growing seasons in the tropics (IRRI farm, Los Baños, Philippines). One strong component of this study was to take into account a large range of plant behaviour by considering 32 well-established high-yielding genotypes, either hybrids or inbreds, not only from the Philippines but also from India, Colombia, and China in the case of super hybrid rice.

Materials and methods

Site description and crop establishment

Field experiments were conducted at the research station of the International Rice Research Institute (IRRI), Los Baños, Laguna, Philippines (14°11′N, 121°15′E), from January to April for the 2010 dry season (DS), and from June to October for the 2010 wet season (WS). The soil was classified as Andaqueptic Haplaquolls with particle size distribution of 58% clay, 33% silt, and 9% sand. The topsoil contained 18.6 g organic C kg^{-1}, 1.90 g total N kg^{-1}, with pH (CaCl$_2$) of 6.5.

Experiments were laid out in a randomized complete block design (RCBD) with three replications. Thirty-two rice genotypes, 20 hybrids, and 12 high-yielding elite inbreds from a diverse genetic background and geographical origin (Philippines, India, China, Colombia) developed by distinct institution and companies, were grown under two contrasted seasons (Table 1). Seeds were soaked in water for 24 h, drained, wrapped in wet cloth, and incubated at room temperature for another 24 h. Pre-germinated seeds were sown in seedling trays at 3000 seeds m^{-2} to produce uniform seedlings. Then, 13-day-old seedlings in the DS and 11-day-old seedlings in the WS were manually pulled and transplanted in the field at a hill spacing of 20 × 20 cm with one seedling per hill. The plot size was 50 m^2 in both the DS and WS.

Crop management

Phosphorus (40 kg P ha^{-1} as single superphosphate), potassium (40 kg K ha^{-1} as muriate of potash), and zinc (5 kg Zn ha^{-1} as zinc sulfate heptahydrate) were applied and incorporated in all the plots a day before transplanting during both seasons. A total of 150 kg N ha^{-1} as urea was applied in four splits (40 kg N ha^{-1} a week after transplanting, 30 kg at mid-tillering, 40 kg at maximum tillering, and 40 kg two weeks before flowering), in all plots and in both seasons. The amount of N fertilizer applied in the WS was similar with that in the DS because of an additional application to compensate for fertilize lost due to a typhoon event. The field was flooded 3 days after transplanting and a floodwater depth of 3–5 cm was maintained until 10 days before physiological maturity. Weeds were controlled by applying Sofit (pretilachlor) at two days after transplanting. Subsequent weeding was done manually when required. Pests were intensively controlled using chemicals to avoid plant damage and yield loss. Bird watchers were hired to prevent birds from feeding and a 0.5-m-high plastic rat barrier was installed all around the plots to prevent rat damage.

Table 1 Genotypes code, characteristics (maximum tiller count during the dry season, crop duration during the dry and wet seasons), and country of origin

Code	Type	Maximum tiller count (dry season)	Crop duration (dry season)	Crop duration (wet season)	Country
H1	Hybrid	672	105	109	Philippines
H3	Hybrid	542	111	115	Philippines
H5	Hybrid	719	105	111	Philippines
H9	Hybrid	656	113	118	Philippines
H14	Hybrid	690	105	111	Philippines
H15	Hybrid	634	105	115	Philippines
H16	Hybrid	693	105	109	Philippines
H17	Hybrid	723	105	111	Philippines
H18	Hybrid	515	107	111	Philippines
H19	Hybrid	693	107	118	Philippines
H20	Hybrid	651	117	115	Philippines
H30	Hybrid	555	105	111	Columbia
H31	Hybrid	622	107	118	India
H32	Hybrid	695	113	118	India
H33	Hybrid	775	105	115	India
H34	Hybrid	640	113	118	India
H35	Hybrid	554	107	115	China
H36	Hybrid	481	111	115	China
H37	Hybrid	552	113	111	India
H39	Hybrid	723	117	118	India
I1	Inbred	795	111	111	Philippines
I2	Inbred	879	105	109	Philippines
I4	Inbred	590	111	111	Philippines
I7	Inbred	704	113	122	Philippines
I12	Inbred	560	111	115	Philippines
I40	Inbred	750	107	118	Philippines
I41	Inbred	668	107	115	Philippines
I42	Inbred	582	107	115	Philippines
I43	Inbred	513	117	122	Columbia
I44	Inbred	426	111	111	China
I45	Inbred	272	105	109	China
I46	Inbred	544	111	115	China

Climatic measurements and characterization of crop stage

Weather data were collected from the IRRI lowland agro-meteorological station within a 500-m radius from the experimental field. Solar radiation was measured by a Gunn-Bellani radiation-integrator (Baird & Tatlock, London, UK). Daily minimum and maximum temperature were measured by a standard ventilated psychrometer (no. 706, Wilh, Lambrecht KG, 34 Gottingen, Germany).

Panicle initiation (PI) was determined by dissecting and observing under a binocular microscope (Leica MZ 95, Leica Microsystems LTd., Heerbrugg, Switzerland) the main tillers of randomized collected plants from each plot every two days when PI was getting close. Panicle initiation was considered to have occurred when the first row of floral primordia was

visible on the shoot apex. Flowering (Fl) was determined from each plot when 50% of the spikelets per panicle had exerted their anthers. The crop reached maturity (Mat) when 95% of the spikelets in the whole plot had turned from green to yellow.

Crop measurements

At transplanting, 12 seedlings were randomly pulled from seedling trays for all the genotypes. For each subsequent sampling done in the field after transplanting, plants were randomly sampled every week from 0.32 m² that corresponded to eight hills for both the dry and wet seasons. The three external rows from the border of all plots were not considered for sampling. For each sampling date, plants were collected and placed in a plastic bag containing water and brought to the laboratory for cleaning and for subsequent processes. Plant samples were separated into green leaf blades, dead leaf blades, leaf sheaths, culms (internodes and nodes), and panicles (including juvenile ones) when present. The area of the green blades was measured with a leaf area meter (Li-3100C area meter, Li-Cor, Lincoln, NE, USA). Leaf area index (LAI) was calculated as leaf area (LA) of the sampled plants divided by the corresponding ground sampling area. For all sampling dates, dry matter of each entity previously listed was determined by drying the material for 72 h in an oven at 70 °C, and then weighing them. Specific leaf area (SLA, cm² g^{-1}) was calculated by dividing the leaf blade area by the corresponding leaf blade dry matter. Stem dry matter was calculated as the sum of the leaf sheath and culm dry matter. Shoot dry matter of the plants was calculated as the sum of the dry matter of leaf blades, stems, and panicles. Culm length of each tiller of four sub-sampled hills was measured at flowering. Specific culm length (SCL) was computed as the ratio of the stem length to its corresponding dry matter. To evaluate the spatial occupation of the leaves of one plant, the spreading of these leaves was estimated on a virtual horizontal plane, at higher collar level, by measuring the distance between the two extreme points of the plant, first on an axis within the row, and second on a perpendicular axis between rows. The ellipse area of the plant formed by the virtual 2D leaf area at highest collar level was then calculated as:

$$\text{Ellipse area} = \pi \times \text{radius } 1 \times \text{radius } 2$$

where radius 1 is half of the distance on the axis within the row and radius 2 is half of the distance of the perpendicular axis between rows.

Leaf angle between the leaf and its tiller culm was measured using the tiller as the reference (vertical).

At maturity, plants were randomly sampled from two 0.32-m² locations in each plot, and total tiller number and number of productive, non-productive, and dead tillers were determined. Dry matter of each plant organ as listed previously was measured. Grains were separated from the rachis and filled and unfilled grains were separated with respect to the flow rate of 4 m³ s^{-1} using a Seedburo blower (KL-1205, Seedburo, Chicago, IL, USA). The weight of total filled and unfilled grains and 1000 filled and unfilled grains and, by computation, the number of filled and unfilled grains per panicle were determined. Filling rate was computed as the ratio of filled grain number to the total grain number. Harvest index (HI) was computed as filled grain dry matter divided by shoot dry matter. Potential sink size was calculated as the product of the total number of spikelets (filled and unfilled) per panicle, the panicle number, and the individual grain size as calculated at maturity on the basis of 1000-grain dry weight. Potential sink size corresponded to the highest grain yield the plant could produce on the basis of the total number of spikelets it fully developed before flowering. Grain yield (GY) was determined by harvesting a 5-m² undisturbed sampling area (125 hills) at the center of each plot. Grains were separated from the rachis, filled and unfilled grains were also separated, and total filled grain dry matter was determined. Grain moisture content of the filled grains was measured with a digital moisture tester (DMC-700, Seedburo, Chicago, IL, USA) and grain yield was calculated at 14% moisture content.

Data analysis

Analysis of variance (ANOVA) was done using GLM procedure of SAS (2012) and mean separation tests were performed using LSD. Correlation test was done using the Pearson method.

Results

The 32 hybrids and elite inbreds differed with crop duration, from 105 to 117 days in the DS, and from

109 to 122 days in the WS (Table 1). Crop duration might have a strong effect on the interrelation of plant traits, with the assumption that key traits associated with a short-duration crop could be different from those associated with a long-duration crop. Considering the differences in climate between both seasons and in crop duration among genotypes, it is relevant to set up a methodology to evaluate traits of interest by grouping genotypes according to crop duration within each cropping season, so that the search for traits is done per group. Two maturity groups in the DS—short and medium duration—and three in the wet season—short, medium and long duration—were defined with average crop duration of 106 and 113 days, and 110, 115 and 119 days, respectively (Table 2).

Average daily radiation received by the crop from sowing to maturity was higher in the DS (ranging from 15.6 to 19.7 MJ m^{-2}) than in the WS (15.0 to 15.7 MJ m^{-2}) (Table 2). Moreover, in the DS, the average daily radiation received during the grain filling stage was higher ranging from 19.1 to 19.7 MJ m^{-2}, than in the wet season, which ranged from 14.6 to 15.3 MJ m^{-2}, however, crop duration was longer in the wet season. The resulting difference in cumulative radiation was not that strong, ranging from 572 to 610 MJ m^{-2} in the DS, and from 452 to 535 MJ m^{-2} in the WS (Table 2). Average, minimum, and maximum temperatures during the DS were lower by 1 °C compared to those in the wet season. The average daily temperature in the DS during grain filling was higher than that during the vegetative and reproductive phases, whereas, in the wet season, the average daily temperature at all crop stages was similar (Fig. 1). Also, the WS under study was quite representative of the average of the wet seasons while radiation at tillering stage of the DS under study was appreciably higher than that of the average of the DSs (Supplementary Fig. 1). Genotype differences in grain yield were significant within each maturity group for each of the dry and the wet season. In the DS, grain yield ranged from 7.79 to 9.77 t ha^{-1}, and from 7.45 to 9.52 t ha^{-1}, in the early and medium maturity groups, respectively (Table 3). In the wet season, grain yield ranged from 5.80 to 8.73 t ha^{-1}, 4.77 to 7.86 t ha^{-1}, and 5.27 to 7.77 t ha^{-1}, in the early, medium, and late maturity groups, respectively (Table 4). Grain yield of each individual genotype was positively correlated to the associated cumulative daily radiation, with an r ($\rho < 0.05$) value of 0.57, measured during its grain

filling phase (between the flowering and the maturity dates of each individual), with radiation varying from 350 to 650 MJ m^{-2} (Fig. 2). This correlation emphasizes the importance of: (i) the incoming radiation when discriminating the dry from the WS in the Philippines, and (ii) the grain filling phase in the time-course to establish grain yield. The methodology for searching for key traits driving high yield was then set up by considering the crop cycle as two distinct phases: the first one from early vegetative to flowering and the second one from flowering to maturity. For each of these phases, one key variable was identified, the potential sink size at flowering and the filling rate between flowering and maturity. It was then necessary to check whether grain yield was correlated with each of these two key variables to use them as basis in the search for relevant traits.

Potential sink size was calculated as the product of grain number per unit area and single filled grain weight measured at maturity, assuming all grains get filled (Tables 3, 4). Grain yield was significantly correlated with potential sink size for each of the maturity groups in both seasons (Fig. 3a, b), with r values ranging from 0.52 to 0.71 in the DS, and from 0.52 to 0.81 in the WS. This shows how some traits at early stage can be revealed as strong indicators of yield potential based on their correlation with potential sink size. In this line, morphological and growth parameters of the pre-flowering phase, those with significant correlation with potential sink size, were identified and compared between maturity groups and seasons (Table 5). In the DS for both early and medium maturity groups, ellipse area, which represents the spread of tillers at the highest collar level; LAI, both measured at PI; and specific leaf area, leaf biomass, and stem biomass at maximum tillering, were positively correlated to potential sink size. In the WS for the early maturity group, LAI and leaf and stem biomass were also positively correlated with potential sink size. In contrast, in the medium and late maturity groups in the wet season, LAI and leaf biomass were negatively correlated with potential sink size. For all the three groups in the wet season, plant height at booting was negatively correlated to potential sink size (Table 5).

Grain yield formation was also strongly influenced by grain filling rate (Tables 3, 4) in line with the gap to 1 of the correlation coefficients associated with the relationship between grain yield and potential sink

Table 2 Average minimum temperature (T_{min}), average maximum temperature (T_{max}), average mean temperature (T_{mean}), average daily radiation, and cumulative solar radiation from sowing to panicle initiation (S–PI), panicle initiation to flowering (PI–Fl), and flowering to maturity (Fl–Mat) of the different duration groups during the 2010 dry and wet seasons

Season/Maturity	Average T_{min} (°C)	Average T_{max} (°C)	Average T_{mean} (°C)	Average daily radiation (MJ m^{-2})	Cumulative solar radiation (MJ m^{-2})
Dry/early (105–107 days)					
S–PI	22.6	29.2	25.9	15.6	717
PI–Fl	22.8	30.6	26.7	19.3	578
Fl–Mat	23.8	31.3	27.6	19.1	572
Dry/medium (111–117 days)					
S–PI	22.6	29.3	25.9	16.1	822
PI–Fl	23.0	30.7	26.8	19.1	610
Fl–Mat	23.9	31.7	27.8	19.7	610
Wet/early (109–111 days)					
S–PI	24.8	32.1	28.5	15.5	697
PI–Fl	24.7	31.6	28.1	15.4	462
Fl–Mat	24.4	31.4	27.9	15.2	534
Wet/medium (115 days)					
S–PI	24.8	32.1	28.5	15.6	766
PI–Fl	24.6	31.4	28.0	15.0	464
Fl–Mat	24.6	31.6	28.1	15.3	535
Wet/long (118–122 days)					
S–PI	24.8	32.0	28.4	15.3	857
PI–Fl	24.5	31.6	28.0	15.7	502
Fl–Mat	24.7	31.3	28.0	14.6	452

size (Fig. 3). Indeed, in the DS in the early maturity group (Table 3), potential sink size was the same for H18 and I40; however, grain yield was significantly higher with H18 (9.50 t ha^{-1}) compared with I40 (8.44 t ha^{-1}). In the medium maturity group, potential sink size of I46 and H37 were similar, 1137 and 1149 g m^{-2}, respectively; however, grain yield of I46 was 11% higher than that of H37 (Table 3). In the wet season, potential sink size was the same for I4 and H37 in the early maturity group, I46 and I12 in the medium maturity group, and I40 and H39 in the late maturity group; however, grain yield of I4, I46, and I40 was 13, 22 and 32% higher than that of H37, I12 and H39, respectively (Table 4).

Filling rate ranged from 0.69 to 0.87 in the DS and from 0.59 to 0.87 in the WS (Tables 3, 4). In the WS, grain yield was correlated with filling rate, considering the whole set of genotypes within each maturity group, whereas no correlation was observed in the DS (Supplementary Table 1.). In this context, in order to

reveal key traits during grain filling, it was essential to select cultivars with same potential sink size but with contrasted filling rate. Accordingly, subgroups of genotypes with similar potential sink size within each maturity group were formed based on the highest number of genotypes whose potential sink size values were similar as indicated by the same letter of Tukey test at $P = 0.05$, and whose filling rate was the most contrasted as possible (Tables 3, 4). In the DS, the subgroups were formed with the genotypes whose potential sink size belonged to the statistical category 'f' in the early maturity group (8 genotypes) and 'c' in the medium maturity group (9 genotypes) (Table 3), whereas, in the wet season, the subgroups were formed with the genotypes whose potential sink size belonged to the statistical category 'f' in the early maturity group (5 genotypes), 'd' in the medium (4 genotypes), and 'a' in the late (3 genotypes) (Table 4). Correlation coefficients between grain yield and filling efficiency for each of these subgroups in the DS were 0.49 and
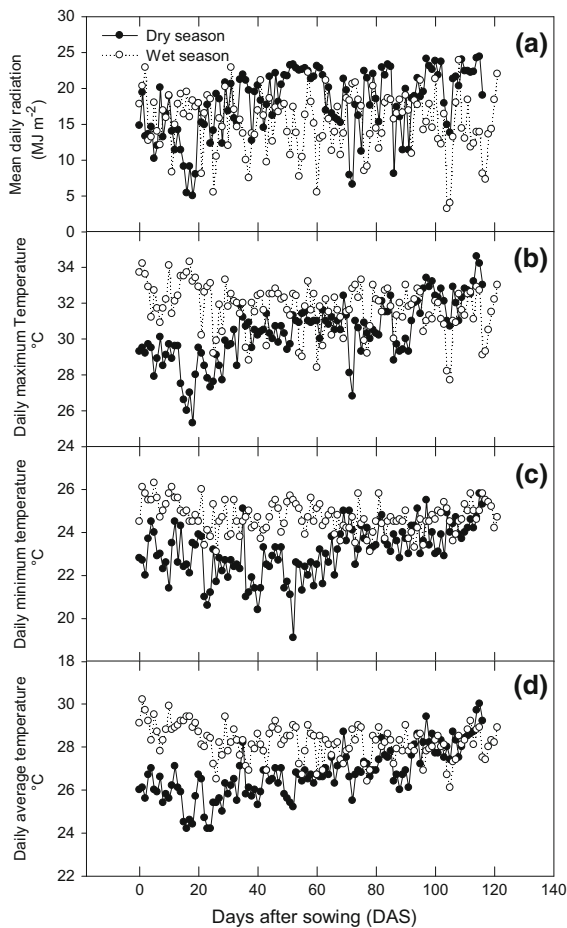
Fig. 1 Average daily radiation (**a**), daily maximum temperature (**b**), daily minimum temperature (**c**) and daily average temperature (**d**) at the experimental fields during the 2010 dry and wet seasons

0.72 in the early and medium maturity groups, respectively, and, in the WS, 0.94 and 0.88 in the early and medium maturity groups, respectively (Fig. 4a, b). In the late maturity group in the wet season, the correlation coefficient was not calculated as the genotype number was too low. Within each subgroup, considering values of potential sink size were similar between genotypes, pairs of cultivars were selected based on the two most contrasted values of filling rate. These pairs were, for the first three, taken from the DS within the early (H18 vs. I40) and medium (H3 vs. H37, and I46 vs. H34) maturity groups, and, for the last three, from the WS within the early (I4 vs. H37), medium (I46 vs. I12) and late (I40 vs. H39) maturity groups. In all the six pairs, as designed, filling rate was significantly different

(Fig. 5a), and potential sink size similar (Fig. 5b), between the two considered genotypes. Filling efficiency and the associated grain yield were consistently higher with genotypes H18, H3 and I46 in the DS, and I4, I46 and I40 in the WS (Tables 3, 4). In the DS, HI (Fig. 5c), SCL at flowering (Fig. 5d), and ellipse area (Fig. 5e) and leaf angle (Fig. 5f) at 20 days after flowering, were identified as key traits associated with higher filling rate. Their values were significantly different for H18, H3 and I46 than for I40, H37 and H34. In contrast, in the wet season, no difference within each pair was observed for SCL at flowering, and a significant difference for HI and leaf angle was observed only within one and two pairs, respectively. In the WS, LAI at 20 days after flowering (Fig. 5g), delayed leaf senescence within the first 20 days after flowering (Fig. 5h), plant height (Fig. 5i) and panicle length (Fig. 5j) at flowering, were identified as key traits associated with higher filling rate in I4, I46 and I40 compared with that in H37, I12 and H39, respectively. In contrast, in the DS, no difference within each pair was observed for LAI, leaf loss rate and plant height, whereas, a significant difference in panicle length was observed only within two pairs.

Morphological parameters of the grain filling phase of all genotypes of the subgroup within each maturity group were then correlated against filling rate, and confronted to the results reported from the pairs analysis in Fig. 5. Harvest index, ranging from 0.45 to more than 0.6, was positively correlated with filling rate within both maturity groups in the DS, with r values of 0.41 (Fig. 6a), whereas this significant association was observed only for the medium maturity group in the WS (Table 6). SCL at flowering was negatively correlated with filling efficiency within the early maturity group in the DS, with r value of 0.47 (Fig. 6b), whereas, in the wet season, there was no correlation within both early and medium maturity groups, but a positive correlation was observed within the late maturity group (Table 6). In the WS within the three maturity groups, LAI at 20 days after flowering was positively correlated, and leaf loss rate and plant height were negatively correlated, with filling rate (Table 6), having r values as strong as 0.72–0.95 for plant height (Fig. 6d) and 0.53–0.74 for the ratio of leaf loss (Fig. 6e). In contrast, no correlation between filling rate and these three parameters was observed within each maturity group in the DS (Table 6). Ellipse area on one side and the leaf angle at 20 days

Table 3 Grain yield, potential sink size in decreasing sorted order and filling rate of the different genotypes in the 2010 dry season experiment

Maturity (day)	Genotype	Grain yield (t ha^{-1})	Potential sink size (g m^{-2})	Filling rate
Early (105–107)	H31	9.39ab	1326a	0.70c
	H1	9.38ab	1264ab	0.75bc
	H15	9.59a	1258ab	0.76bc
	H17	9.44a	1250abc	0.75bc
	H5	9.46a	1213abcd	0.77bc
	H30	9.77a	1204bcde	0.80abc
	H33	9.36a	1200bcde	0.77bc
	H19	9.38a	1190bcdef	0.79bc
	H14	9.63a	1144bcdef	0.83ab
	H16	9.46a	1128cdef	0.84ab
	H35	9.24abc	1119defg	0.82abc
	I42	8.52bcd	1092defg	0.79bc
	I40	8.44cd	1085efg	0.78bc
	H18	9.50a	1085efg	0.87a
	I41	8.30d	1068fg	0.78bc
	I2	8.53bcd	1001gh	0.85ab
	I45	7.79d	944h	0.85ab
Medium (111–117)	H39	9.04ab	1320a	0.70e
	H9	9.31a	1308a	0.71e
	H32	9.30a	1248ab	0.74cde
	H3	9.52a	1199bc	0.79bcd
	H34	8.22bc	1189bcd	0.69e
	I12	8.89ab	1164bcd	0.78bcd
	H36	8.56ab	1159bcd	0.74de
	H20	8.72ab	1152bcd	0.77bcd
	H37	8.15c	1149bcd	0.71e
	I46	9.06ab	1137cd	0.80abc
	I7	9.18a	1128cd	0.81ab
	I4	9.08ab	1127cd	0.81ab
	I44	8.81ab	1094de	0.81ab
	I1	8.89ab	1027e	0.86a
	I43	7.45c	1003e	0.74de

In a column, within each maturity, means followed by the same small letter are not significantly different at $\rho < 0.05$ using Tukey's test

after flowering on the other side (considering both the flag leaf and the second leaf to the last) were negatively correlated with filling rate for both seasons within all maturity groups, except for the late maturity group in the WS (Table 6). In the DS, with r values of 0.50 and 0.56, the range of the ellipse area was from 500 to 1500 cm^2 (Fig. 6c), whereas in the WS, with r values of 0.60 and 0.61, the range of the ellipse area

was only from 350 to 700 cm^2 (Fig. 6f). For the late maturity group in the WS, the relationships of filling rate with ellipse area and leaf angle were positive, with the ellipse area ranging from 500 to 700 cm^2 (Fig. 6f). Surprisingly, correlation between filling rate and biomass at flowering tended to be negative within all maturity groups, except for the medium one in the DS (Table 6). The correlation of filling rate with panicle

Table 4 Grain yield, potential sink size in decreasing sorted order and filling rate of the different genotypes in the 2010 wet season experiment

Maturity (day)	Genotype	Grain yield (t ha^{-1})	Potential sink size (g m^{-2})	Filling rate
Early (109–111)	H16	8.73a	1139a	0.75cde
	H5	7.63bc	1061b	0.71efg
	H14	7.38bc	1059bc	0.68fgh
	H30	7.25bcd	995cd	0.71def
	I44	8.18ab	981de	0.81a
	I4	7.15cd	947def	0.74de
	H37	6.34ef	934defg	0.66gh
	H18	6.89cde	926efg	0.72def
	H17	6.07ef	926efg	0.64h
	H1	7.06cd	906fg	0.76bcd
	I1	7.07cd	872gh	0.79abc
	I2	6.91cde	834hi	0.81ab
	I45	5.80f	794i	0.71def
Medium (115)	H15	6.50c	1068a	0.59d
	I41	7.40ab	1038ab	0.70bc
	I42	6.92bc	1036ab	0.65bcd
	H33	6.64c	1026ab	0.63cd
	H35	6.57c	969bc	0.66bcd
	H36	6.94bc	959cd	0.70bc
	H20	7.09bc	956cd	0.72b
	I12	6.43e	892d	0.70bc
	I46	7.86a	886d	0.87a
	H3	4.77d	759e	0.61a
Late (118–122)	H31	6.90b	980a	0.69bcd
	I40	7.77a	965a	0.78a
	H39	5.87cd	946ab	0.61f
	I7	6.76b	917b	0.72b
	H32	5.96c	859c	0.68cde
	H9	5.68cde	838cd	0.66de
	H34	5.27e	811de	0.64ef
	H19	5.57cde	773ef	0.70bc
	I43	5.39de	748f	0.70bc

In a column, within each maturity, means followed by the same small letter are not significantly different at $\rho < 0.05$ using Tukey's test

length was significant only within one group in each season, in the medium maturity group in the DS and the late maturity group in the WS (Table 6).

Filling rate was negatively correlated with potential sink size in the DS, with correlation coefficients of 0.81 and 0.63 for early and medium maturity groups, respectively (Fig. 7a), when considering all the genotypes within each maturity group. In contrast, no correlation was reported between filling rate and potential sink size in the wet season, for each of the three maturity groups (Fig. 7b).
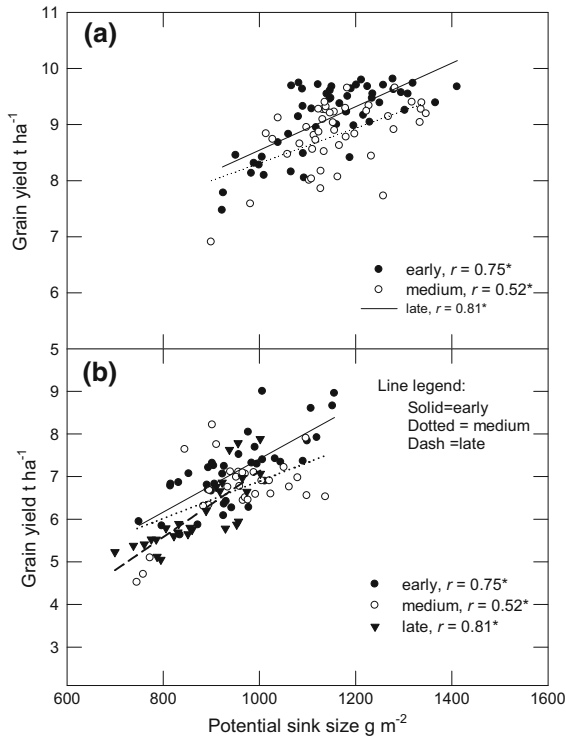
Discussion

The relevance of analysing genotype performance respective of season and crop duration

Grain yield was higher by 33% on average during the DS compared to the WS as expected by the associated higher radiation and lower temperature in the DS than in the wet season. This superiority of grain yield in the dry over the WS in tropical irrigated conditions was reported by several authors (Yang et al. 2007, 2008b),
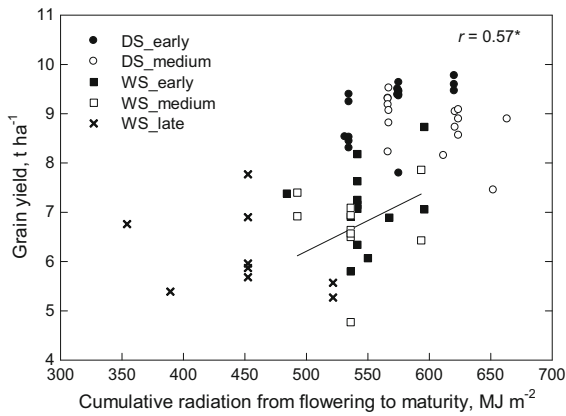
Fig. 2 Relationship between grain yield and cumulative radiation during grain filling of each of the 32 genotypes within both seasons (Ds and WS) grouped according to their maturity group
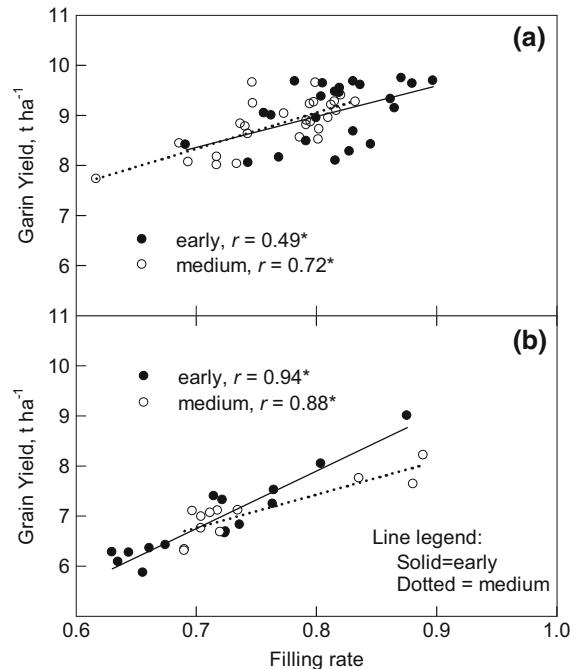
Table 5 List of significant growth parameters correlated with potential sink size ($\rho = 0.05$), and the correlation coefficient, r

Growth parameter	Dry season	
	Early	Medium
Ellipse area at panicle initiation	0.31*	0.36*
Leaf area index at panicle initiation	0.53*	0.61*
Specific leaf area at maximum tillering	0.27*	0.57*
Leaf dry weight at maximum tillering	0.41*	0.44*
Stem dry weight at maximum tillering	0.33*	0.28*

Growth parameter	Wet season		
	Early	Medium	Late
Leaf area index at maximum tillering	0.37*	−0.36*	−0.39*
Leaf dry weight at maximum tillering	0.31*	−0.41*	−0.39*
Stem dry weight at panicle initiation	0.35*	−0.51*	0.39*
Plant height at booting stage	−0.41*	−0.37*	−0.40*

* means significant at $\rho < 0.05$

Fig. 3 Relationship between grain yield and potential sink size during the dry (a) and wet (b) seasons. Potential sink size stands for the product of total spikelet number at flowering and single filled grain dry weight at maturity. The *symbol* indicates the maturity group the genotype belongs to (each data point represented an individual replication)
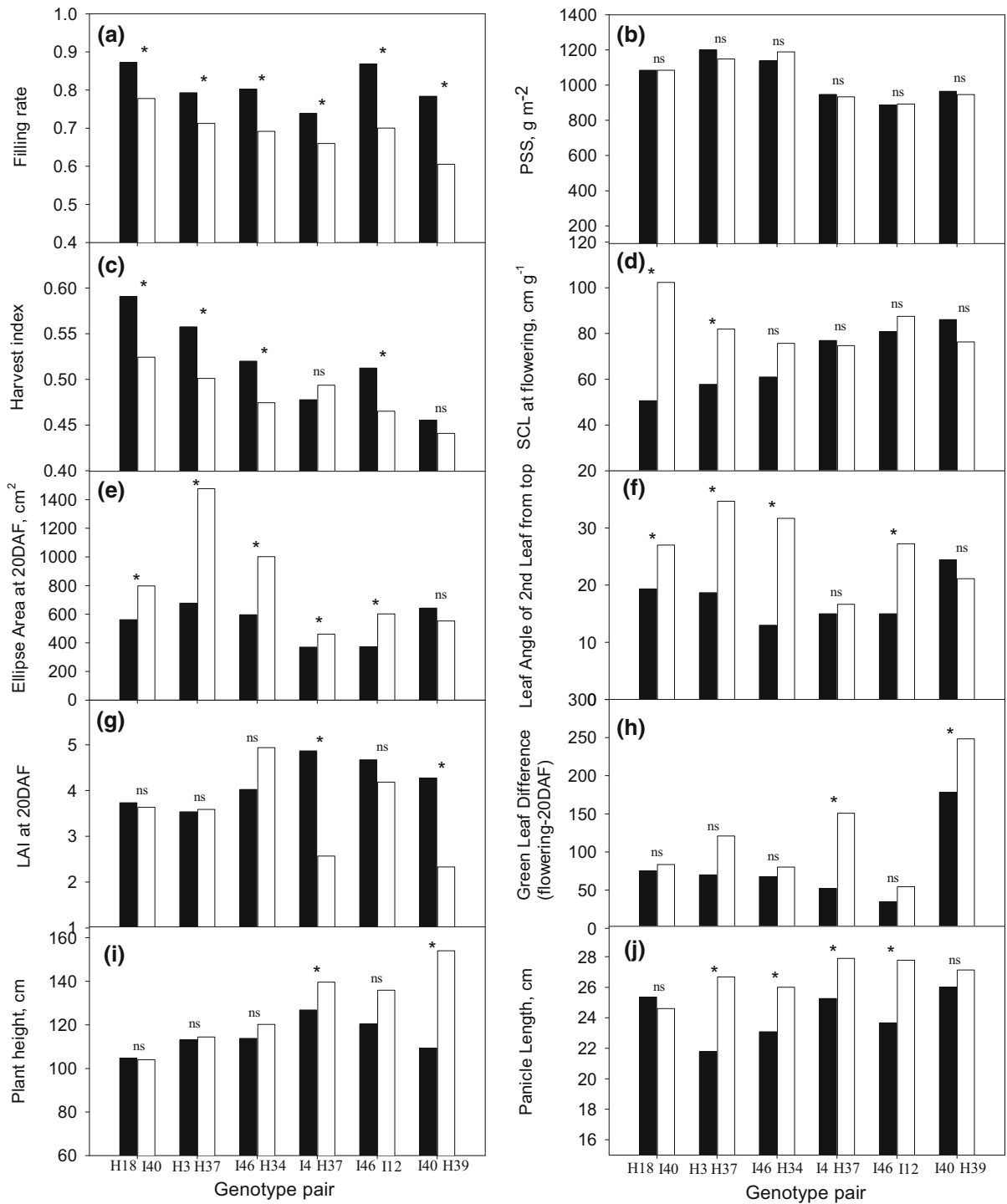

Fig. 4 Relationship between grain yield and filling rate of genotypes during the dry (a) and wet (b) seasons. The *symbol* indicates the maturity group the genotype belongs to (each data point represented individual replication)

Fig. 5 Filling rate (**a**); potential sink size, PSS (**b**); HI (**c**); specific culm length, SCL at flowering (**d**); ellipse area at 20 days after flowering, DAF (**e**); leaf angle of 2nd leaf from top (**f**); leaf area index, LAI at 20 DAF (**g**); green leaf difference from flowering to 20 DAF (**h**); plant height (**i**) and panicle length (**j**) of 6 selected genotype pairs with same PSS and most contrasted filling rate; the first 3 pairs are issued from the DS and the last 3 pairs from the wet season

Fig. 6 Relationships between filling rate and HI (**a**), SCL at flowering (**b**), ellipse area at 20 days after flowering (**c**), plant height at 81 days after sowing (**d**), ratio of leaf loss from flowering to 20 days after flowering (**e**), and ellipse area at 20 days after flowering (**f**) of genotypes with the same potential sink size within each maturity group in the DS (**a–c**) and wet season (**d–f**) (each data point represented individual replication)
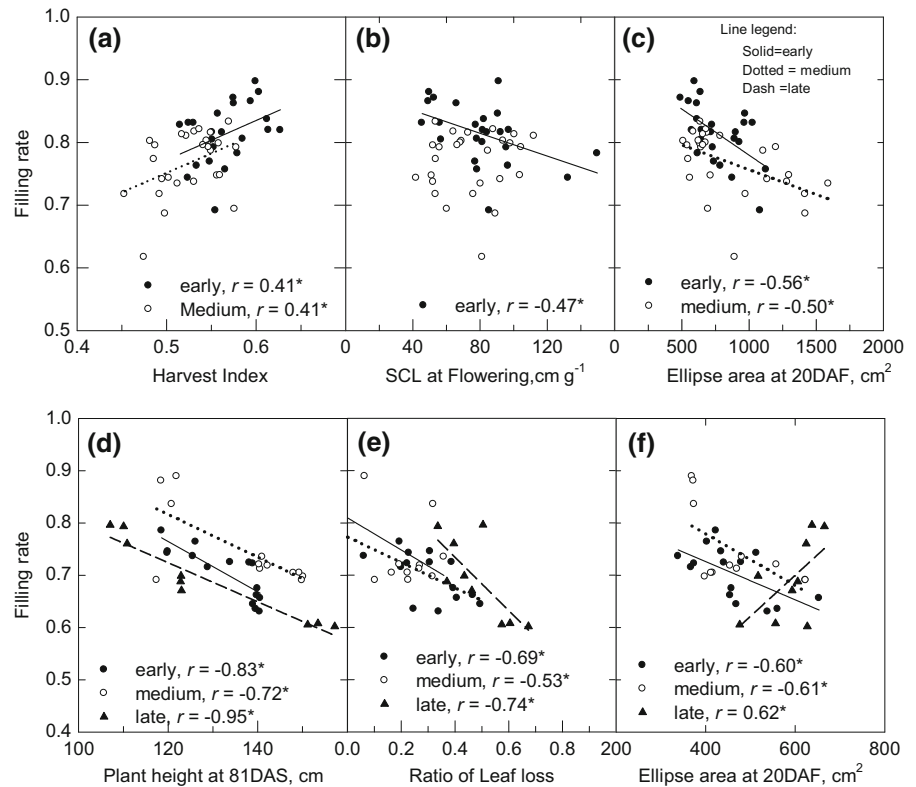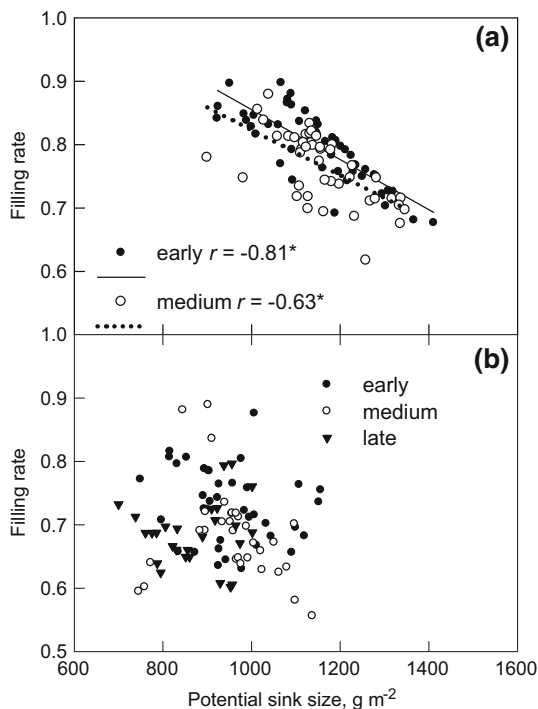

Table 6 Correlation between filling rate and grain yield; and between filling rate with growth parameters during the ripening phase of genotypes with similar potential sink size

Parameter	Dry season		Wet season		
	Early (n = 8)	Medium (n = 9)	Early (n = 5)	Medium (n = 4)	Late (n = 3)
Grain yield	0.49	0.72	0.84	0.88	0.97
Biomass at flowering	−0.38*	0.05 ns	−0.42 ns	−0.22 ns	−0.22 ns
Harvest index (HI)	0.41*	0.41*	0.13 ns	0.78*	0.11 ns
Specific culm length at flowering	−0.47*	0.10 ns	−0.13 ns	−0.02 ns	0.54*
Leaf area index at 20 days after flowering	−0.29 ns	−0.25 ns	0.58*	0.48 ns	0.75*
Ratio of leaf loss (flowering-20 days after flowering)	−0.31 ns	0.09 ns	−0.69*	−0.53*	−0.74*
Plant height at flowering	−0.03 ns	−0.34 ns	−0.83*	−0.72*	−0.95*
Ellipse area at 20 days after flowering	−0.56*	−0.50*	−0.60*	−0.61*	0.62*
Flag leaf angle at 20 days after flowering	−0.38*	−0.29 ns	−0.66*	−0.53*	−0.21 ns
Leaf angle of the leaf below the flag leaf at 20 days after flowering	−0.48*	−0.51*	−0.20 ns	−0.71*	0.53*
Panicle length	0.08 ns	−0.59*	0.32 ns	−0.86*	−0.46 ns

These genotypes were chosen from each maturity group based on statistically the same potential sink size having the highest number of genotypes and called subgroup (subgroups 'f' and 'c' in the DS early and medium; 'f', 'd' and 'a' in the WS early, medium and late, respectively)

* Significant at $\rho < 0.05$

ns means non-significant at $\rho < 0.05$

Fig. 7 Relationship between filling rate and potential sink size during the dry season (**a**) and wet season (**b**) (Each data point represented individual replication)

and was also attributed to higher radiation received after flowering, also confirmed from a survey of top yields done over different environments and countries (Dingkuhn et al. 2015). Interestingly, the classification of the 32 diverse high-yielding genotypes, differing in crop duration, maximum tiller number, and biomass at flowering, with respect to crop yield was different for both cropping seasons. Also, yield components are subjected to genotype x environment interactions (Adriani et al. 2016a). This suggests that an ideotype designed for the DS would be different from that for the wet season. This point was also highlighted under subtropical conditions by Wu et al. (2013). To confirm this assumption, the present analysis was thus conducted to check whether different traits would be revealed for each of the cropping seasons. It considered then the two growing seasons separately in order to set up a methodology to identify the relevant traits for adaptation. This was also the approach used under subtropical conditions by Li et al. (2009), Huang et al. (2013) and Wu et al. (2013). Furthermore, taking into account that genotypes with different crop duration have different growth dynamics, and that duration of

grain filling has a strong effect on grain yield (Yang et al. 2008a), the methodology distinguished between maturity groups within each cropping season, considering these groups as the entity for the analysis of trait discovery.

Potential sink size and filling rate as key variables to identify correlations of component traits with grain yield

The crop cycle was analysed as two distinct phases within each group: first, from early vegetative to flowering (pre-flowering) with potential sink size as the key parameter, second, from flowering to maturity (post flowering) with filling rate as the key parameter. Potential sink size here was considered as the ceiling performance the crop could achieve based on what was already dimensioned at flowering from processes occurring during the vegetative and reproductive phases. Since grain yield was positively correlated with potential sink size within each maturity group, with the correlation coefficient varying from 0.52 to 0.71 in the DS, and from 0.52 to 0.81 in the WS, this clearly suggests how early plant traits detected during the pre-flowering phase, those driving differences in potential sink size, have an impact on grain yield. To detect if grain yield was also correlated with filling rate, and to avoid bias by comparing genotypes that are already different at flowering, a representative sub-group was statistically defined within each maturity group, based on the highest number of genotypes characterized with the same potential sink size. Grain yield was then found to be positively correlated with filling rate in each situation, with the correlation coefficient varying from 0.49 to 0.72 in the DS, and from 0.88 to 0.94 in the wet season. This confirms that post-flowering traits, those driving filling rate, have also an impact on grain yield. However, when the whole set of genotypes was considered within each maturity group in the DS, and not only those with similar potential sink size, (i) there was no correlation between grain yield and filling rate and (ii) there was a negative correlation between filling rate and potential sink size with the correlation coefficient varying from −0.63 to −0.81 depending on the maturity group. This last observation confirms the necessity to focus on genotypes with the same potential sink size when searching for relevant traits during the filling phase, particularly in the DS. In contrast, in the wet season, a

positive correlation was reported between grain yield and filling rate even if the whole set of genotypes within each maturity group was considered, and no correlation was identified between filling rate and potential sink size. This suggests the higher weight in the establishment of grain yield of traits related (i) to the pre-flowering phase under favorable radiation (mean daily value of 19.3 MJ m^{-2}), and (ii) to the post-flowering phase under limited radiation (mean daily value of 15.2 MJ m^{-2}).

Traits respective of seasons and crop durations can be revealed by this framework of analysis

Plant traits relevant to higher yield at the early tillering stage for the DS under study were those enhancing light interception directly or indirectly, such as large ellipse area, high LAI and high specific leaf area: indeed, by analysing the effect of transient shading, tiller production was reported as a main priority for high yield (Lafarge et al. 2010). As already published by Bueno and Lafarge (2009), early and rapid biomass accumulation is important for high yield as long as it occurs in favorable growing conditions. This is in agreement with traits at early stage reported under subtropical conditions, such as rapid ground cover through high LAI and tiller number around PI (Li et al. 2009; Huang et al. 2013; Wu et al. 2013) to the detriment of organ vigor, such as leaf or stem thickness for example. However, getting nearer to flowering and during the post-flowering phase in this DS, traits corresponding to greater erectness of the crop, such as low ellipse area and leaf angles, and greater reserves storage, such as higher organ vigor, were highlighted. During this season, these traits were associated with higher HI, which emphasizes that biomass partitioning, through sink regulation, may be a key process to support higher yield under favourable light conditions. At earlier stage, better sink regulation was commonly associated with earlier cessation in tiller emergence (Lafarge and Bueno 2009; Adriani et al. 2016b). In the WS, however, plant traits relevant to higher yield differed with those from the DS and across maturity groups. During the pre-flowering phase, shorter stem length and plant height were identified within all maturity groups as a possible way to favor biomass investment into the leaves by limiting that into the stem. However, traits favoring early light capture as in the DS were reported as relevant to high

yield only within the early maturity group, whereas the same traits were non desirable in the medium and late maturity groups. Possible explanations are that: (i) a long duration of the pre-flowering phase implements per se large leaf area, and (ii) profuse leaf area under limited radiation would generate high proportion of shaded leaf area, likely inducing high biomass loss through respiration and senescence. During the post-flowering phase, in addition to short stem length and plant height as in the earlier phases, traits relevant to high yield for all the three maturity groups in the WS under study included the delay in leaf senescence. This last trait was also identified as a crucial trait involved in yield potential through its environment-dependent contribution to higher radiation use efficiency (Ding-kuhn et al. 2015). In the case of the late maturity group, the low stem vigor with short stem length favoured high filling efficiency probably by reducing single stem demand for biomass. In the same maturity group, the shorter stem associated with planophile morphology (high ellipse area and leaf angle) were identified as favourable, with these traits likely contributing to a higher resistance to lodging. The same traits were unfavorable within the early and medium maturity groups as in the earlier stages.

Justification of the relevance of this framework of analysis

The main purpose of this study was to set up a framework of analysis that can address whether breeding traits of contrasted growing seasons within the same site are distinct or not. This framework was successful as it highlighted that potential sink size and grain filling rate were two relevant parameters to work with. In this study, it revealed that plant traits for high yield were distinct with respect to the growing season, so that it supports the need of establishing one breeding program devoted to each cultural season within the same site. This distinction in-between growing seasons is well aligned with the concept of Target Population of Environments which aims at grouping sites (or seasons) with respect to environmental similarities, and identifying a representative site for each group where a dedicated breeding program would be conducted (Windhausen et al. 2012; Heinemann et al. 2015). The consideration of only two field trials here, one in the dry and one in the WS, would have been an issue (i) if the purpose of the

study would have been the validation of phenotypic markers relative to breeding programs and (ii) if the weather data of the seasons under study would have been considerably different from the average weather data measured at the same location. Indeed, the weather data of the year under study were close to those of the 10-year average, even though radiation at tillering stage in the DS was appreciably higher. Moreover, the purpose of this study was rather to validate that phenotypic markers may be different across growing seasons within the same site, which is sufficient to argue for the setup of distinct breeding programs with respect to growing conditions.

Conclusion

The framework of analysis presented in this study highlights that distinct traits, depending on the cropping season and, in some cases, of the maturity groups within a season, are revealed as key component traits of crop performance. This distinction was possible by analysing genotypes within maturity groups and by using potential sink size and grain filling rate as two complex traits directly associated with crop performance and closely related to subtending component traits of each of the pre and post-flowering phases. In the present study in the WS for example, traits favouring rapid biomass accumulation were highlighted within the early maturity group until about flag leaf emergence, whereas they were not relevant within late maturity groups. Surprisingly in both seasons in this study, high HI and low panicle length were favourable traits within the medium maturity group only, and some traits were even having an opposite effect with respect to the growing conditions. It is noteworthy that no reference on favourable traits for the WS in the tropics could be found in the literature: (i) none of the concerned studies in the tropics (Yang et al. 2008a) did consider separately the wet from the DS and, (ii) if separated, no trait could be revealed in the WS (Yang et al. 2007). In that study, the genotypes were not classified with respect to their maturity groups, whereas this is proved to be of relevance in the present study. This also may explain why Yuan et al. (2011) reported that selection on plant traits was not successful in comparison with direct selection for yield: the impact in terms of yield of the traits used by these authors was not analysed separately with respect

to the growing seasons and maturity groups. Considering also in this study that some genotypes of the early and the medium maturity groups were high yielders in the wet season, but not in the dry, indicates that phenotypic plasticity is not large enough to account for the differences in growing conditions and to consider that a single genotype could be the highest yielder in both seasons. These observations suggest that DS high-yielding genotypes should be different from WS genotypes to maximize crop production during both seasons and highlights the need of developing distinct breeding programs depending on the growing seasons and maturity groups.

References

Adriani DE, Dingkuhn M, Dardou A, Adam H, Luquet D, Lafarge T (2016a) Rice panicle plasticity in near isogenic lines carrying a QTL for larger panicle is genotype and environment dependent. Rice 9:8. doi:10.1186/s12284-016-0101-x

Adriani DE, Lafarge T, Dardou A, Fabro A, Clément-Vidal A, Yahya S, Dingkuhn M, Luquet D (2016b) The qTSN positive effect on panicle and flag leaf size of rice is associated with an early down-regulation of tillering. Front Plant Sci 6:1197. doi:10.3389/fpls.2015.01197

Ao HJ, Wang SH, Zou YB (2008) Study on yield stability and dry matter characteristics of super hybrid rice. Sci Agric Sin 41:1927–1936

Bueno CS, Lafarge T (2009) Higher crop performance of rice hybrids than elite inbreds in the tropics. 1. Hybrids accumulate more biomass during each phenological phase. Field Crops Res 112:229–237

Bueno C, Pasuquin E, Tubaña B, Lafarge T (2010) Improving sink regulation and searching for promising traits associated with hybrids, as key avenue to increase yield potential in the tropics. Field Crops Res 118:199–207

Dingkuhn M, Penning de Vries FWT, De Datta SK, van Laar HH (1991) Concepts for a new plant type for direct seeded flooded tropical rice. In: Direct seeded flooded rice in the tropics, proceedings of the international rice research conference, 27–31 August 1990, Seoul, Korea, pp 17–38

Dingkuhn M, Laza MRC, Kumar U, Mendez KS, Collard B, Jagadish K, Singh RK, Padolina T, Malabayabas M, Torres E, Rebolledo MC, Manneh B, Sow A (2015) Improving yield potential of tropical rice: achieved levels and perspectives through improved ideotypes. Field Crops Res 182:43–59

Fischer RA (1983) Wheat. In: Smith WH, Banta SJ (eds) Potential productivity of field crops under different

environments. International Rice Research Institute, Los Baños, pp 129–154

Fujita D, Santos RE, Ebron LA, Telebanco-Yanoria MJ, Kato H, Kobayashi S, Uga Y, Araki E, Takai T, Tsunematsu H, Imbe T, Khush GS, Brar DS, Fukuta Y, Kobayashi N (2009) Development of introgression lines of an Indica-type rice variety, IR64, for unique agronomic traits and detection of the responsible chromosomal regions. Field Crops Res 114:244–254

Fujita D, Tagle AG, Ebron LA, Fukuta Y, Kobayashi N (2012) Characterization of near-isogenic lines carrying QTL for high spikelet number with the genetic background of an indica rice variety IR64 (*Oryza sativa* L.). Breed Sci 62:18–26

Fujita D, Trijatmiko KR, Tagle AG, Sapasap MV, Koide Y, Sasaki K, Tsakirpaloglou N, Gannaban RB, Nishimura T, Yanagihara S, Fukuta Y, Koshiba T, Slamet-Loedin IH, Ishimaru T, Kobayashi N (2013) NAL1 allele from a rice landrace greatly increases yield in modern indica cultivars. PNAS 110:20431–20436

Heinemann AB, Barrios-Perez C, Ramirez-Villegas J, Arango-Londoño D, Bonilla-Findii O, Medeiros JC, Jarvis A (2015) Variation and impact of drought-stress patterns across upland rice target population of environments in Brazil. J Exp Bot 66(12):3625–3638. doi:10.1093/jxb/erv126

Huang M, Zou Y, Jiang P, Xia B, Ibrahim Md, Ao H (2011) Relationship between grain yield and yield components in super hybrid rice. Agric Sci China 10:1537–1544

Huang M, Jiang L, Xia B, Zou Y, Jiang P, Ao H (2013) Yield gap analysis of super hybrid rice between two subtropical environments. Aust J Crop Sci 7:600–608

Kamiji Y, Yoshida H, Palta JA, Sakuratani T, Shiraiwa T (2011) N applications that increase plant N during panicle development are highly effective in increasing spikelet number in rice. Field Crops Res 122:242–247

Kim J, Shon J, Lee C, Yang W, Yoon Y, Yang W, Kim Y, Lee B (2011) Relationship between grain filling duration and leaf senescence of temperate rice under high temperature. Field Crops Res 122:207–213

Kovi MR, Bai X, Mao D, Xing Y (2011) Impact of seasonal changes on spikelets per panicle, panicle length and plant height in rice (*Oryza sativa* L.). Euphytica 179:319–331

Kropff MJ, Cassman KG, Peng S, Matthews RB, Setter TL (1994) Quantitative understanding of yield potential. In: Cassman KG (ed) Breaking the yield barrier. International Rice Research Institute, Los Baños, pp 21–38

Lafarge T, Bueno CS (2009) Higher crop performance of rice hybrids than elite inbreds in the tropics. 2. Does sink regulation, rather than sink size, play a major role? Field Crops Res 114:434–440

Lafarge T, Seassau C, Martin M, Bueno C, Clément-Vidal A, Schreck E, Luquet D (2010) Regulation and recovery of sink strength in rice plants grown under changes in light intensity. Funct Plant Biol 37:413–428

Laza RC, Peng S, Akita S, Saka H (2003) Contribution of biomass partitioning and translocation to grain yield under sub-optimum growing conditions in irrigated rice. Plant Prod Sci 6:28–35

Laza RC, Peng S, Akita S, Saka H (2004) Effect of panicle size on grain yield of IRRI-released indica rice cultivars in the wet season. Plant Prod Sci 7:271–276

Li G, Xue L, Gu W, Yang C, Wang S, Ling Q, Qin X, Ding Y (2009) Comparison of yield components and plant type characteristics of high-yield rice between Taoyuan, a 'special eco-site' and Nanjing, China. Field Crops Res 112:214–221

Liang J, Zhang J, Cao X (2001) Grain sink strength maybe related to the poor grain filling of indica-japonica rice (*Oryza sativa*) hybrids. Physiol Plant 112:470–477

Lubis I, Shiraiwa T, Onishi M, Horie T, Inoue N (2003) Contribution of sink and source sizes to yield variation among rice cultivars. Plant Prod Sci 6:119–125

Nagata K (2006) Ecophysiological traits and genetic analysis of yield and ripening in high-yielding semi-dwarf indica rice varieties. JARQ 40:307–316

Ohsumi A, Takai I, Ida M, Yamamoto T, Arai-Sanoh Y, Yano M, Ando T, Kondo M (2011) Evaluation of yield performance in rice near-isogenic lines with increased spikelet number. Field Crops Res 120:68–75

Okami M, Kato Y, Kobayashi N, Yamagishi J (2015) Morphological traits associated with vegetative growth of rice (*Oryza sativa* L.) during the recovery phase after early-season drought. Eur J Agron 64:58–66

Peng S, Cassman KG, Virmani SS, Sheehy J, Khush GC (1999) Yield potential trends of tropical rice since the release of IR8 and the challenge of increasing rice yield potential. Crop Sci 39:1552–1559

Shahid MQ, Li Y, Saleem MF, Naeem M, Wei C, Liu X (2013) Yield and yield components in autotetraploid and diploid rice genotypes (indica and japonica) sown in early nad late seasons. 2013. Aust J Crop Sci 7:632–641

Sheehy JE, Dionora MJA, Mitchell PL (2001) Spikelet numbers, sink size and potential yield in rice. Field Crops Res 71:77–85

Takai T, Matsuura S, Nishio T, Ohsumi A, Shiraiwa T, Horie T (2006) Rice yield potential is closely related to crop growth rate during late reproductive period. Field Crops Res 96:328–335

Windhausen VS, Wagener S, Magorokosho C, Makumbi D, Vivek B, Piepho HP, Melchinger AE, Gary N, Atlin GN (2012) Strategies to subdivide a target population of environments: results from the CIMMYT-led maize hybrid testing programs in Africa. Crop Sci 52:2143–2152

Wu W, Zhang H, Qian Y, Cheng Y, Wu G, Zhai C, Dai Q (2008) Analysis on dry matter production characteristics of super hybrid rice. Rice Sci 15:110–118

Wu W, Nie L, Liao Y, Shah F, CuiK Wang Q, Lian Y, Huang J (2013) Toward yield improvement of early-season rice: other options under double rice-cropping system in central China. Eur J Agron 45:75–86

Xiong J, Ding CQ, Wei GB, Ding YF, Wang SH (2013) Characteristic of dry-matter accumulation and nitrogen-uptake of super-high-yielding early rice in China. Agron J 105:1142–1150

Yang J, Peng S, Zhang Z, Wang Z, Visperas RM, Zhu Q (2002) Grain and dry matter yields and partitioning of assimilates in japonica/indica hybrid rice. Crop Sci 42:766–772

Yang W, Peng S, Laza RC, Visperas RM, Dionisio-Sese ML (2007) Grain yield and yield attributes of new plant type and hybrid rice. Crop Sci 47:1393–1400

Yang W, Peng S, Dionisio-Sese ML, Laza RC, Visperas RM (2008a) Grain filling duration, a crucial determinant of genotypic variation of grain yield in field-grown tropical irrigated rice. Field Crops Res 105:221–227

Yang W, Peng S, Laza RC, Visperas RM, Dionisio-Sese ML (2008b) Yield gap analysis between dry and wet season rice crop grown under high-yielding management conditions. Agron J 100:1390–1395

Ying J, Peng S, He QR, Yang H, Yang CD, Visperas RM, Cassman KG (1998) Comparison of high-yield rice in tropical and subtropical environments. I. Determinants of grain and dry matter yields. Field Crops Res 57:71–84

Yoshida H, Horie T, Shiraiwa T (2006) A model explaining genotypic and environmental variation of rice spikelet number per unit area measured by cross-locational experiments in Asia. Field Crops Res 97:337–343

Yuan W, Peng S, Cao C, Virk P, Ying D, Zhang Y, Visperas RM, Laza RC (2011) Agronomic performance of rice breeding lines selected based on plant traits or grain yield. Field Crops Res 121:168–174

Zhang Y, Tang Q, Zou Y, Li D, Qin J, Yang S, Chen L, Xia B, Peng S (2009) Yield potential and radiation use efficiency of "super" hybrid rice grown under subtropical conditions. Field Crops Res 114:91–98