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Leaf gas exchange and yield of three upland rice cultivars

Rita de Cássia Félix Alvarez (1); Gustavo Habermann (2*); Carlos Alexandre Costa Crusciol (3); Adriano Stephan Nascente (3); João Domingos Rodrigues (4)

(1) Universidade Federal do Mato Grosso do Sul (UFMS), Departamento de Produção Vegetal, Caixa Postal 112, 79560-000 Chapadão do Sul (MS), Brasil.

(2) Universidade Estadual Paulista (UNESP), Instituto de Biociências, Departamento de Botânica, Avenida 24-A, 1515, 13506-900 Rio Claro (SP), Brasil.

(3) UNESP, Faculdade de Ciências Agronômicas (FCA), Departamento de Produção Vegetal, Caixa Postal 237, 18603-970 Botucatu (SP), Brasil.

(3) Embrapa Arroz e Feijão, Rod. GO-462, Km 12, 75375-000 Santo Antônio de Goiás (GO), Brasil.

(4) UNESP, Instituto de Biociências, Departamento de Botânica, Caixa Postal 510, 18618-970 Botucatu (SP), Brasil.

(*) Corresponding author: ghaber@rc.unesp.br

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Abstract

Studies of physiological parameters associated with crop performance and growth in different groups of upland rice (*Oryza sativa* L.) may support plant breeding programs. We evaluated the role of gas exchange rates and dry matter accumulation (DMA) as traits responsible for yields in a traditional (cv. 'Caiapó'), intermediate (cv. 'Primavera') and modern (cv. 'Maravilha') upland rice cultivars. Leaf gas exchange rates, DMA, leaf area index (LAI), harvest indexes (HI) and yield components were measured on these genotypes in the field, under sprinkler irrigation. Panicles per m^2 and DMA at flowering (FL) and heading, as well as CO$_2$ assimilation rates (*A*) were similar across these cultivars. The highest yield was found in 'Primavera', which may be explained by (i) a two-fold higher HI compared to the other cultivars, (ii) greater rates of DMA during spikelet formation and grain-filling, as well as (iii) a slow natural decrease of *A* in this cultivar, at the end of the season (between FL and maturation).

Key words: *Oryza sativa*, net photosynthesis, harvest index, dry matter accumulation rates, crop growth rate.

1. INTRODUCTION

Rice (*Oryza sativa* L.) constitutes the diet of half of the world's population (Kumar & Ladha, 2011). Three-fourths of its production is grown on irrigated lands (Prasad, 2011). Upland rice, however, is cultivated in Asia, Africa, and the Americas (CGIAR, 2006); and because water availability for rice irrigation by flooding is decreasing in China and India, the use of upland rice systems has increased all over the world (Prasad, 2011).

Grain yields, including rice, depend on CO$_2$ assimilation rates (*A*) and how plants allocate photosynthetic products (Alvarez et al., 2012b; Ntanos & Koutroubas, 2002; Yoshida, 1972). In rice, this allocation depends on source/sink relationships, which change after flowering (Falqueto et al., 2009). Between flowering and panicle maturation, panicles may receive (i) products from leaf photosynthesis, (ii) starch and protein reserves from leaves, culms and sheaths, and (iii) directly-photosynthesized products from panicles (Machado et al., 1996).

The percentage ripe grains and the number of grains per area are positively correlated in tropical conditions (Yoshida, 1972), but negatively correlated in temperate regions (Matsushima, 1970). Artificial reductions in *A* during ripening limit rice yields, but after flowering, *A* is insufficient to fill the panicles (Machado et al., 1996).

Yields of modern and traditional cultivars of major cereal crops show significant relationships with harvest indexes (HI), rather than with biomass production (Evans et al., 1984). In rice, high yields can be achieved either by increasing biomass, HI or both (Yoshida, 1981). Among modern rice cultivars, however, biomass production is associated with high yields (Alvarez et al., 2012a), but the relationship between these traits is little understood.

The number of spikelets per unit land area, or sink size, is the primary determinant of crop grain yields (Yoshida, 1972); and in rice, the sink size can be increased either by increasing panicle number or panicle size, or both, but a strong trade-off exists between these two yield components (Ying et al., 1998). In this way, the number of spikelets per m^2 seems to be dependent on dry matter accumulation (DMA) occurring from panicle initiation (PI) to flowering (FL), whereas grain filling largely depends on DMA from FL to maturity (Yoshida, 1981).

Given expected relationships between carbon assimilation and yield components (panicles/m^2, spikelets/panicle, spikelet filling and 1000-grain mass), and the recent importance of upland rice cultivars, we measured these traits in three of these cultivars, considered traditional (tall plants with long and decumbent leaves, low ability for tillering, low response to high soil fertility and susceptible to lodging), such as 'Caiapó', modern (short plants with short and erect leaves, high ability for tillering, responsive to high soil fertility and great resistance to lodging), such as 'Maravilha', and intermediate (showing average characteristics between modern and traditional types), such as 'Primavera'. These definitions are in agreement with Santos et al. (2006). We checked whether *A* is associated with yield components, and if so, how such relationship can explain yields of rice groups that are consistently used in plant breeding programs.

2. MATERIAL AND METHOD

The field experiment was conducted on Lageado Experimental Farm (22°51' S, 48°26' W, 815 m of altitude), in the municipality of Botucatu, Sao Paulo State, Brazil, from January (peak of the wet season) to June (at the beginning of the winter) 2002. According to Köppen classification system, the climate at the experimental site is described as Cwa, with rainy summers and dry winters.

The plants grew on an ultisoil exhibiting pH 5.5 ($CaCl_2$), 21 g kg^{-1} soil organic matter, and 35.4 mg dm^{-3} P (resin). The concentration of K, Ca, and Mg in the soil was 2.5, 3.8, and 17.4 mmol$_c$ dm^{-3}, respectively, while H+Al stayed at 43 mmol$_c$ dm^{-3}. The base saturation was 57%, and CEC was 88 mmol$_c$ dm^{-3}.

The three upland rice cultivars were compared, so that their grain yield (kg ha^{-1}), yield components (panicles/m^2, spikelets/panicle, spikelet filling and 1000-grain mass), leaf gas exchange [CO_2 assimilation (*A*) and transpiration (*E*) rates, and stomatal conductance (*gs*)], as well as crop growth rate (g m^{-2} day^{-1}), dry matter accumulation between panicle initiation (PI) and flowering (FL), and between FL and maturation (MA) were also measured.

We used 'Caiapó' as a medium-maturity (128 days) traditional cultivar. It shows 110-130 cm in height, long grains and moderate resistance to lodging (Santos et al., 2006). As a modern cultivar, we used the highly recommended 'Maravilha', which is also a medium-maturity (125-132 days) but only 80-100 cm tall, with high resistance to lodging. The intermediate 'Primavera' cultivar was used because it has been recommended due to its early maturity (112 days), although moderately susceptible to lodging (Alvarez et al., 2012a).

As the study was conducted in the field, under uneven conditions, the three cultivars were cultivated in randomized blocks with seven replications, and each plot was 8 rows wide and 6 m long, with 0.30 m between rows. Plots were sowed on 1 Jan 2002, using 240 viable seeds per m^2, and emergence occurred on 24 Jan. Phenological events were described as days after emergence (DAE). The nutrient management was based on the common practices prescribed for upland rice cultivation systems (van Raij et al., 1997).

The experimental area was irrigated with a fixed sprinkler irrigation system (3.3 mm water h^{-1}). For irrigation management, three crop coefficients (Kc) were used. These were divided into four periods: for vegetative phase, Kc was 0.4; at the beginning of the reproductive phase it was 0.7, and 1.0 in the end. During the maturing phase, these values were reversed: Kc = 1.0 in the beginning and 0.7 in the end (Rodrigues et al., 2004).

PI was determined by dissecting four main stems from each experimental plot every other day, and when 90% examined main stems had a panicle primordium, PI was considered to be established. Flowering was considered to be established when 90% hills had one stem showing anthesis. The crop reached maturity when 95% spikelets had turned from green to yellow.

Leaf gas exchange rates were measured throughout the cycle of the three cultivars. A closed gas portable photosynthesis system (LI-6200, LI-COR, USA) with a transparent 0.25 L leaf chamber was used. Because the evaluation of gas exchange performance is best assessed during the highest photosynthetic photon flux density (PPFD) and before air temperature reaches limiting values for C_3 photosynthetic-mechanism plants (Feistler & Habermann, 2012), plants were assessed between 9:00 and 11:00 h. Two flag leaves per plant, randomly chosen in each plot, were assessed from booting to milk phase. Additionally, the water use efficiencies (*A*/*E*, WUE; *A*/*gs*, IWUE) were also computed. Six measurements were assessed for 'Primavera', at 41 (midtillering), 48 (panicle initiation), 57, 74 (flowering), 81 and 89 (maturation) DAE. Eight measurements were performed for 'Caiapó' and 'Maravilha', at 41, 48 (midtillering), 57 (end of tillering), 74 (7 days after PI), 81, 89 (4 days before FL), 108 and 121 DAE (MA). Measurements were taken on unclouded days, under natural fluctuation in PPFD, which oscillated between 700 and 1400 µmol m^{-2} s^{-1}. Within the leaf cuvette, air temperature varied between 30.9 and 31.9 °C, and air humidity between 60.7 and 62.6%. CO_2 and water vapor concentrations were determined by the LI-6200 infra red gas analyzers, and CO_2 assimilation (*A*) and transpiration rates (*E*), and stomatal conductance to water vapor (*gs*) were calculated by the LI-6200 data analysis program.

Sampling for the analysis of quantitative plant growth was done according to each cultivar's season length. Therefore, sampling was performed at 39, 46, 55, 67, 75, 83, 92, 102 and 111 DAE for 'Primavera' and at 39, 46, 55, 67, 75, 83, 92, 102, 111, 118 and 125 DAE for 'Caiapó' and 'Maravilha'. Samples consisted of 1.40 m of row per plot. Plant organs were separated into green leaf blades (leaf), culm plus sheath (stem), dead tissues, and panicles. Green leaf area of 20 leaves was measured with a leaf area meter (AAM-7, Hayashi, Denkoh, Japan), and their dry mass was determined. After measuring total leaf dry mass, total leaf area (cm^2) was calculated for each sample and expressed as leaf area index (LAI). Dry mass of each component was determined after oven-drying at 60 °C until constant mass. Plant dry mass was the sum of all the components except roots, and plant dry matter accumulation (DMA) was expressed per m^2. Crop growth rate (CGR) was calculated based on biomass accumulation per unit land area over a time interval.

Before harvesting, panicle number was recorded within 1 m of row in each plot and panicle number per m^2 was computed. Spikelets per panicle were determined from 20 panicles randomly taken from each plot. Panicles were hand-threshed and filled spikelets were manually separated using a sieve. Panicle mass was also measured after oven-drying at 60 °C to constant mass. Grain was separated from panicles and 1000-grain mass was measured. The grain fraction of the panicle dry mass was also weighted. Then, grain filling percentage and HI were calculated. The HI was obtained by the ratio of grain yield and total dry mass, and the values obtained were compared to the standards proposed by Yoshida (1981). Grain yield (kg ha^{-1}) was determined from 3.60 m^2 in each plot and adjusted to a moisture content of 0.13 g H_2O g^{-1} fresh mass.

Leaf gas exchange rates and DMA were plotted throughout plant cycles of each cultivar. CGR and LAI graphs do not show their standard deviation because they were calculated from adjusted curves of plant growth (Figure 1) obtained by the ANACRES® software (Portes & Castro, 1991). Mean values of panicles per m^2, spikelets per panicle, grain filling percentage, 1000-grain mass and grain yield were subjected to a one-way analysis of variance ($p \leq 0.01$ and $p \leq 0.05$) and mean values from the three cultivars were compared between each other by Tukey's test ($\alpha = 0.05$).

3. RESULTS AND DISCUSSION

The number of panicles per m^2 was the same for the three cultivars. 'Primavera' produced 25 and 40% more spikelets per panicle in relation to 'Caiapó' and 'Maravilha', respectively. This contributed to the highest HI in this cultivar, because the spikelet filling percentage was the same for the three cultivars. 'Caiapó' showed the highest 1000-grain weight, following 'Maravilha', and 'Primavera' exhibited intermediate values. The grain yield was approximately 30% higher in 'Primavera' as compared to the other two cultivars (Table 1).

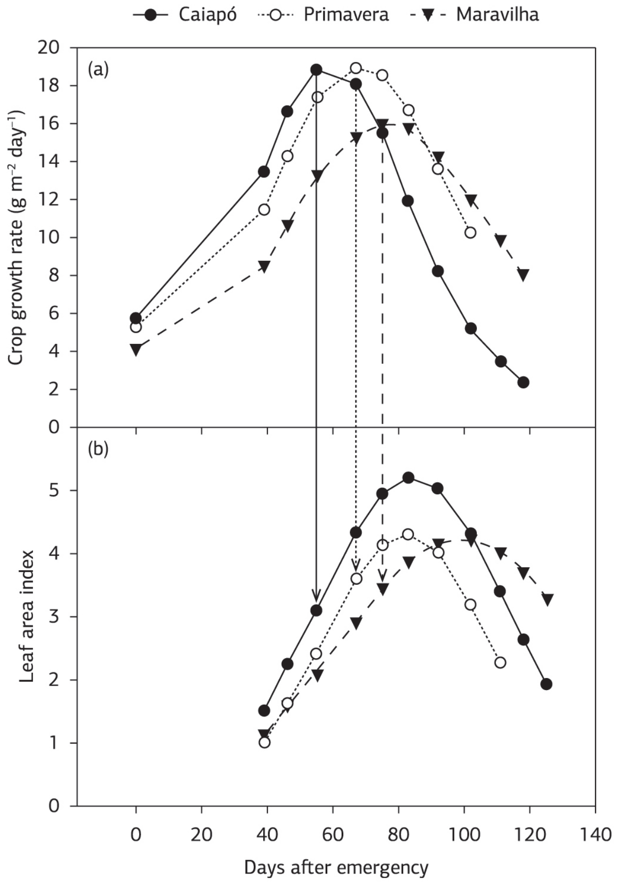

Figure 1. Crop growth rate (a) and leaf area index (b) in 'Caiapó', 'Primavera' and 'Maravilha' upland rice cultivars. Arrows indicate the maximum crop growth rate of each cultivar and its correspondent ideal LAI. Points are mean values calculated from the plant growth adjusted curve.

At 48 DAE, 'Primavera' had already reached the PI phenophase (46 DAE), while the other two late-maturity cultivars were still tillering. Gas exchange rates were the same across the three cultivars (Figure 2). While 'Primavera' was the most productive cultivar ($p \leq 0.05$; Table 1), *A*, *E* and *gs* decreased after 57 DAE in this cultivar. Such decreases in 'Caiapó' and 'Maravilha' occurred after 89 DAE, four days before FL or 36 days before these two cultivars were harvested (125 DAE). There was a great decay in *A* in the late-maturity cultivars, whereas 'Primavera' maintained *A* values around 17 µmol m^{-2} s^{-1} between FL and MA (Figure 2a).

There were no differences in WUE (Figure 3c) and IWUE (Figure 3d) between the cultivars. Stomatal aperture of the three cultivars seemed to control *A* in a similar manner (Figure 3b), and the relationship between *A* and *E* was also the same for the three genotypes (Figure 3a). Absolute values of *A*, *gs* and *E* are in the same range of those

Table 1. Grain yield and yield components of 'Caiapó', 'Primavera' and 'Maravilha' upland rice cultivars, cultivated in Botucatu-SP, Brazil, from January to June 2002

Cultivars	Panicles m^{-2}	Spikelets panicle^{-1}	Spikelet filling (%)	1000-grain weight (g)	Harvest index	Grain yield (kg ha^{-1})
Caiapó	241±34 a[†]	114±21 b	77±6 a	27.0±3.1 a	0.27±0.06 b	4157±797 b
Primavera	253±38 a	151±22 a	76±5 a	24.7±0.6 ab	0.50±0.01 a	6010±1493 a
Maravilha	260±44 a	92±11 c	77±7 a	22.3±1.2 b	0.26±0.05 b	4094±1279 b
CV (%)[‡]	15.7	3.5	8.1	7.3	10.3	19.9

[†] Mean ± standard deviation. The same letters in columns are not significantly different from each other by Tukey's test ($p \leq 0.05$). [‡] Coefficient of variation.

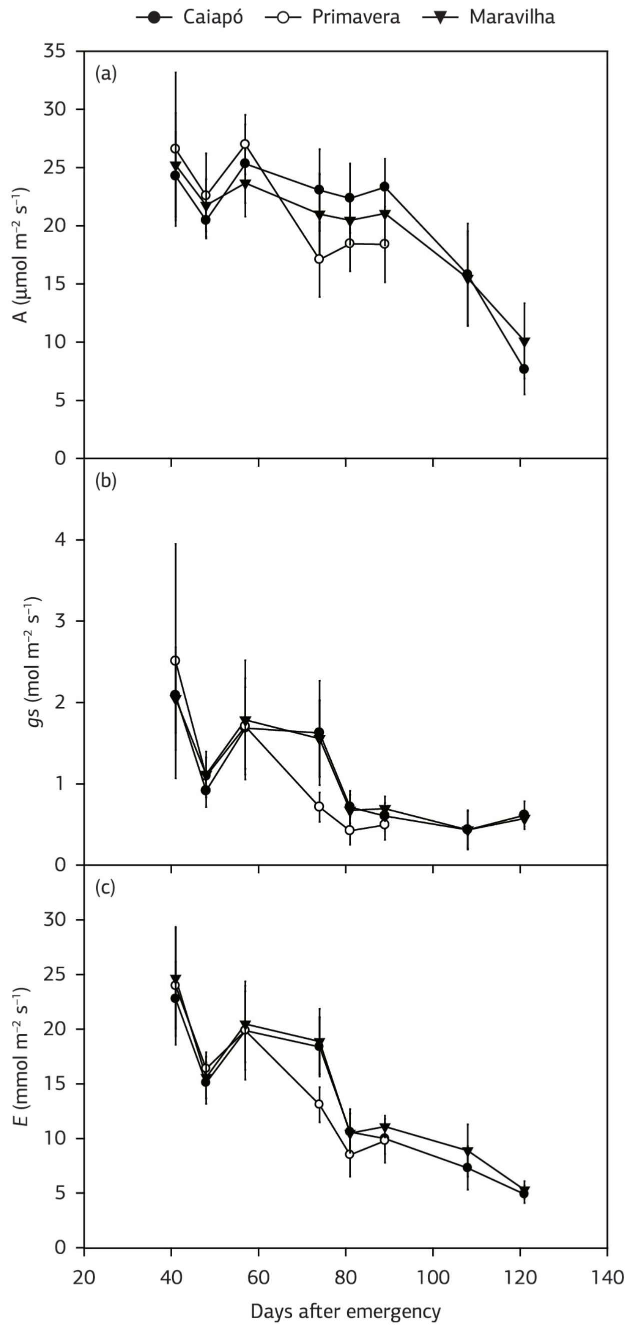

Figure 2. Mean values (n = 7 plants) of CO_2 assimilation rate (a), stomatal conductance (b) and transpiration rate (c) in 'Caiapó', 'Primavera' and 'Maravilha' upland rice cultivars. Vertical bars are S.D.

presented by Concenço et al. (2011), Gesch et al. (2003) and Machado et al. (1996). Therefore, gas exchange rates, *in general*, do not explain why 'Primavera' was the most productive cultivar ($p \leq 0.05$; Table 1). On the other hand, these rates, but especially *A*, suffered a great decay between FL (93 DAE) and MA (121 DAE) in 'Caiapó' and 'Maravilha', whereas for 'Primavera' it stayed unchanged between the same phenophases (FL/74 DAE and MA/89 DAE) (Figure 2).

CGR was similar for 'Primavera' and 'Caiapó' during the first 40 DAE. However, between 39 and 55 DAE, 'Primavera' showed lower CGR in relation to 'Caiapó'. During this vegetative period that was common for the three cultivars, 'Maravilha' showed the slowest rate of CGR, peaking at 75 DAE, almost 7 days after PI and 17 days before FL. For 'Primavera', the CGR peaked at 67 DAE, 7 days before FL; and for Caiapó, it peaked at 55 DAE, about 7 days after midtillering and 12 days before PI (Figure 1a). Thus, only 'Primavera' and 'Maravilha' had their CGR peaking during the reproductive period. The CGR started the decay at 67, 75 and 83 DAE for 'Caiapó', 'Primavera', and 'Maravilha', respectively, suggesting that such decay occurs during spikelet formation for the late-maturity cultivars, and during grain filling for 'Primavera' (Figure 1a).

The ideal LAI was very similar for 'Caiapó' and 'Maravilha' (≈ 3). For the former, it occurred at 55 DAE and the latter, at 75 DAE. For 'Primavera' (ideal LAI ≈ 3.5) it occurred at 67 DAE (Figure 1b). Considering that the ideal LAI occurs before the plant canopy starts self-shading (Kvet et al., 1971; Portes & Carvalho, 2009), then, it is noteworthy that for 'Primavera' (the most productive cultivar) it occurred before the grain-filling period, but for 'Maravilha' it occurred between PI and FL, and for 'Caiapó' it was observed even before the reproductive period. Additionally, the increase in LAI above the ideal point, up to the peak, was approximately 0.6 (m^2 m^{-2}) for 'Primavera', but 2.1 for 'Caiapó' and 1.0 for 'Maravilha' (Figure 1b). This indicates an excessive leaf area enlargement above the ideal LAI for the late-maturity cultivars as compared to 'Primavera'.

For the three cultivars, total DMA during the entire plant cycle was fitted with a sigmoid curve, and no significant differences between the three genotypes was observed (Figure 4c). However, between PI and FL, DMA rate for

'Primavera' was higher than for 'Caiapó' and 'Maravilha', suggesting that the sink strength in 'Primavera' is considerably higher than in the late-maturity cultivars (Figure 4a). In this same period (between PI and FL), 'Caiapó' showed a stable DMA rate, probably because of its late-maturity characteristics, and its biomass build up was almost zero between these phenophases.

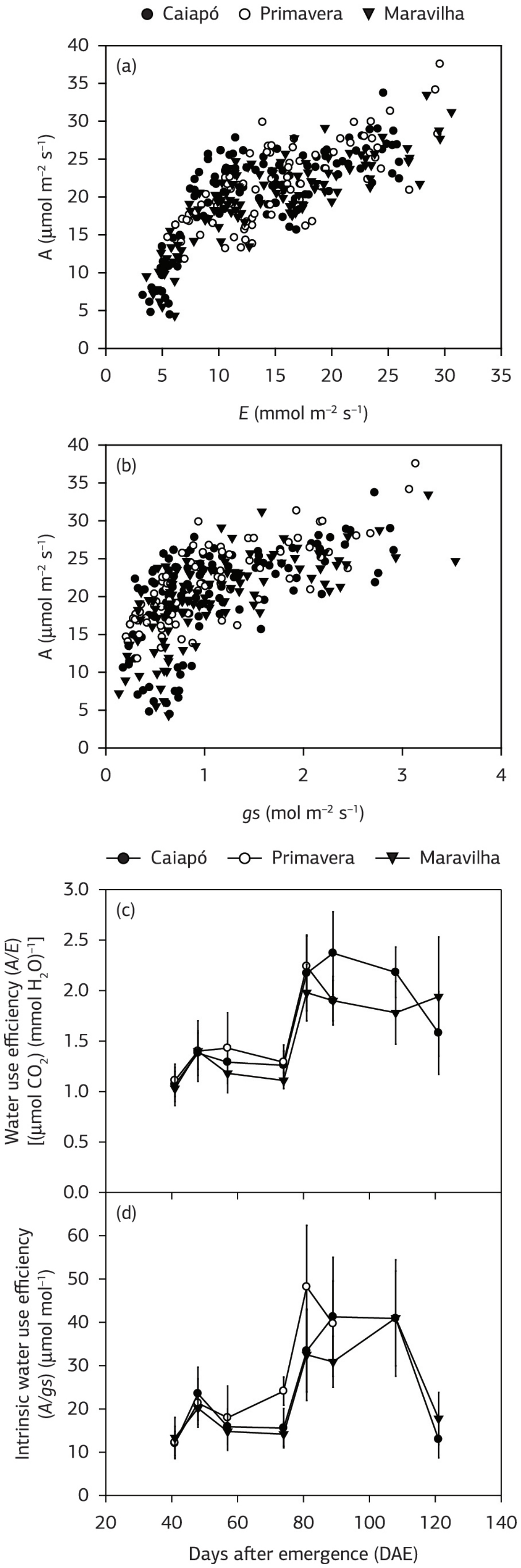

Figure 3. Replicates (readings) of CO_2 assimilation rate in response to transpiration rate (a) and stomatal conductance (b), and mean values (n = 7 plants) of the water use efficiency (*A*/*E*) (c) and intrinsic water use efficiency (*A*/*gs*) (d) in 'Caiapó', 'Primavera' and 'Maravilha' upland rice cultivars. Vertical bars are S.D.

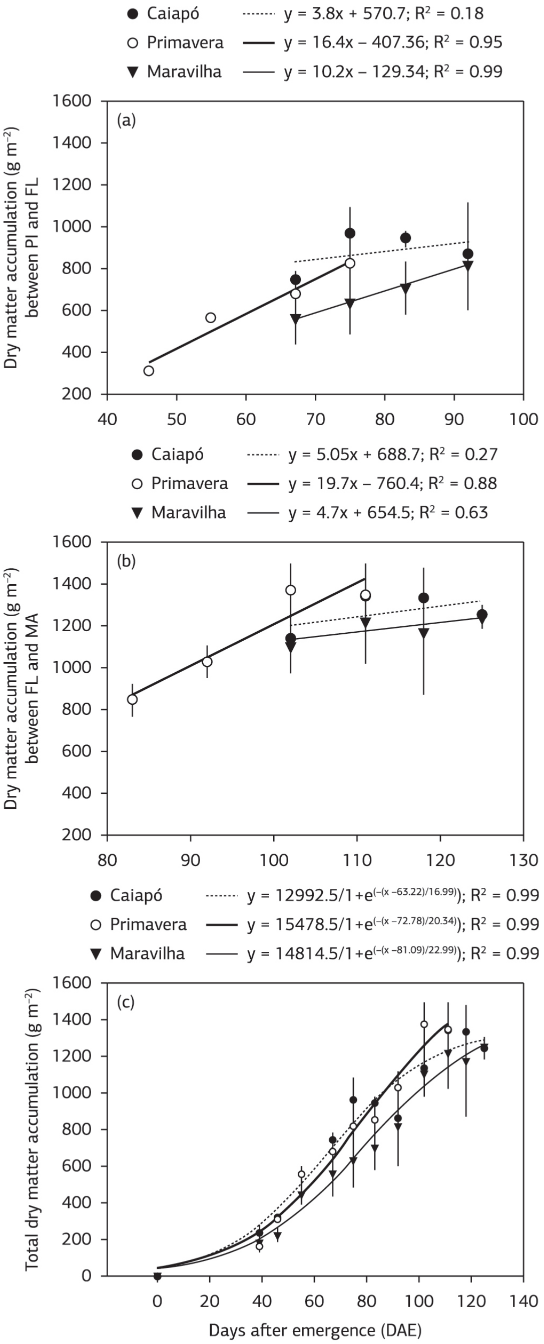

Figure 4. Mean values (n = 7 plants) of total dry matter accumulation in 'Caiapó', 'Primavera' and 'Maravilha' upland rice cultivars, between PI and FL (a), between FL and MA (b) and throughout the plant cycle of each cultivar (c). Vertical bars are S.D.

During the grain filling, there was a continuous biomass accumulation in 'Primavera', at the same rate observed during the previous period (between PI and FL), suggesting a high conversion efficiency of photosynthesized carbon into plant dry matter. These rates for 'Caiapó' and 'Maravilha' were lower (than 'Primavera') and exhibited moderate slopes when compared to the previous phase, showing, indeed, a decrease at the end of their plant cycles (Figure 4b).

Medium temperature varied between 20 and 25 °C from emergency until 90-95 DAE, when max and also min temperatures decreased considerably. After this, medium temperature kept around 20 °C up to the harvest of Primavera. Between FL (93 DAE) and maturation (121 DAE) of the late-maturity cultivars, the medium temperature was around 20 °C, and from 112 to 125 DAE these cultivars were exposed to medium temperatures even below 20 °C (Figure 5a). During the study, accumulated rainfall was 734 mm (Figure 5b), although water demand was supplemented by irrigation.

Grain yields of upland rice genotypes seem to be determined by *A*, tillering ability, and dry matter partitioning, which eventually affects HI (Falqueto et al., 2009). In our study, the number of spikelets per panicle seems to explain yield differences across the cultivars. Harvest indexes found in the

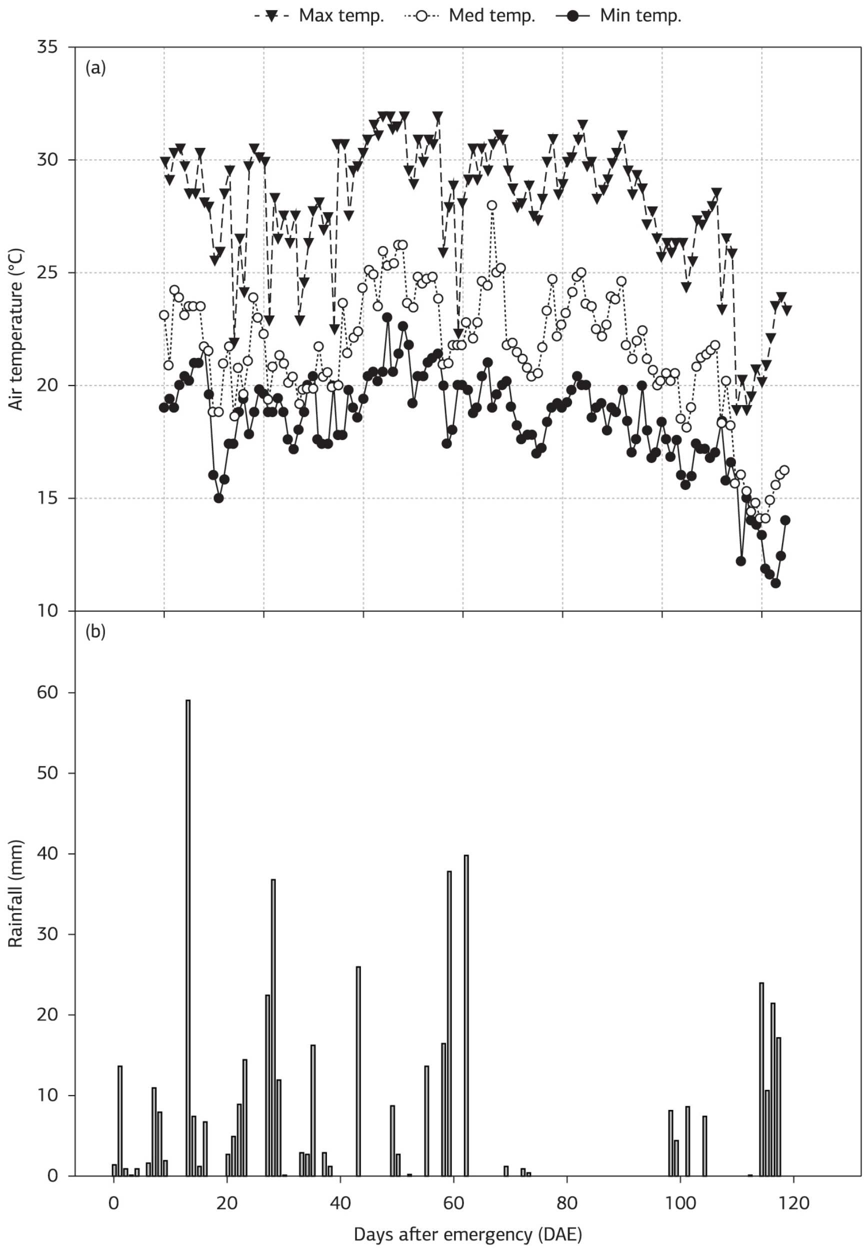

Figure 5. Minimum, medium and maximum air temperature (a), and daily rainfall (b) observed in the field, from emergency (0 DAE) up to the maturation in 'Caiapó', 'Primavera' and 'Maravilha' upland rice cultivars.

present study is in the same range found by Concenço et al. (2011); Kiniry et al. (2001); Wu et al. (1998); Ying et al. (1998), reinforcing the consistency of HI ranges observed for upland rice cultivars. The modern cultivar, 'Maravilha', and the traditional one, 'Caiapó', showed half of those HI values exhibited by 'Primavera', which was the most productive genotype (Table 1). Kiniry et al. (2001) suggest that high yielding rice cultivars are likely to come from increases in yield components contributing to large HI and not from increases in photosynthetic performances, such as radiation use efficiency (RUE).

In our study, *A* does not explain differences in yield across the cultivars. 'Maravilha' and 'Caiapó' showed higher DMA at PI (67 DAE) as compared to 'Primavera' (PI at 48 DAE), suggesting that the late-maturity cultivars tillered more during the vegetative phase (Figure 4a). On the other hand, between PI and FL and also during the grain filling, the *rate* of DMA was conspicuously higher in 'Primavera', in relation to the other two cultivars (Figures 4a, b).

In rice, the grain size is determined by the hull space, which is a stable varietal character (Matsushima, 1970; Peng et al., 2000; Santos et al., 2006), and grain filling is generally sink-limited (Mohapatra et al., 2004; Patel & Mohapatra, 1996), indicating that the sink size and the sink strength are more important than *A*. Our results indicate that in 'Primavera', matter accumulation in the grain seems to be dependent on post-flowering photosynthesis, as *A* was constant between 74 (FL) and 89 DAE (MA) (Figure 2a), when medium temperatures were as close as to 25 °C (Figure 5a). However, for 'Caiapó' and 'Maravilha', DMA did not steeply increase between PI and FL or FL and MA (Figures 4a, b). Moreover, in these cultivars, *A* started decreasing significantly after 89 DAE (4 days before FL) (Figure 2a), when temperatures were still around 25 °C (Figure 5a). This suggests that photoassimilates supply to grain filling in 'Caiapó' and 'Maravilha' might come from pre-flowering photosynthesis, when their *A* values remained between 20 and 25 μmol m^{-2} s^{-1} (Figure 2a). Carbon remobilization (from leaves, stems and possibly roots to grains) might also occur during the whole plant cycle. Therefore, abiotic constraints would be harmful for 'Primavera' if occurring after flowering, while for 'Caiapó' and 'Maravilha' it would be injurious if happening before flowering.

We cannot tell whether the decay in *A* for 'Caiapó' and 'Maravilha' during grain filling was due to low temperatures. However, it is the increase rather than the decrease in min air temperatures that has imposed drops in grain yields, aboveground biomasses and spikelets per m^2 of rice genotypes over the last 30 years in Asia (Peng et al., 2004).

Besides greater DMA rates between PI and FL, as well as during the grain filling period, 'Primavera' showed non-excessive leaf area enlargement above the ideal LAI, in relation to the late-maturity cultivars (Figure 1b). This might be related to the photosynthetic performance of the whole canopy, which is not commonly measured, mainly in rice plants. In fact, parameters that could be used to estimate canopy photosynthesis give good correlation with rice grain yield because canopy photosynthesis integrates the effects of leaf area, leaf angle, plant density, and shading effects of leaves, stems, and panicles (Evans et al., 1984; Scofield et al., 2002; Yang et al., 2002).

4. CONCLUSION

Panicle density is similar across upland rice cultivars, but more spikelets per panicle mostly contribute to greater sink sizes, leading to HI higher than 0.50.

The highest grain yields of upland rice cultivars, such as in 'Primavera', are not associated with high *A* values, but with slow decreases of *A* at the end of the plant cycle.

Excessive leaf area enlargement above the ideal LAI in late-maturity cultivars is harmful to the sink strength of upland rice cultivars, inducing non-competitive HI.

In 'Primavera', matter accumulation in the grain seems to come from post-flowering photosynthesis, and in 'Caiapó' and 'Maravilha', from pre-flowering photosynthesis.

Stresses would be harmful for 'Primavera' if occurring after flowering, while in 'Caiapó' and 'Maravilha' they would have impacts on yields if occurring before flowering.

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