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Macronutrient Uptake and Removal by Upland Rice Cultivars with Different Plant Architecture

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ABSTRACT: Modern high-yielding rice cultivars possibly take up and remove greater quantities of macronutrients than traditional and intermediate cultivars. This study was carried out with the aim of evaluating the extraction and removal of macronutrients by upland rice cultivars. These information are of utmost importance for the correct fertilizer management. The treatments consisted of three upland rice cultivars (Caiapó, a traditional type; BRS Primavera, an intermediate type; and Maravilha, a modern type). Macronutrient accumulation by rice cultivars up to the end of tillering (46 DAE) accounted for only 25 % of the total N and P, and between 35-45 % of the total K, Ca, Mg, and S; after that time, accumulation was intensified. In all of the cultivars, the period of greatest nutrient uptake occurred from 45 to 60 DAE for K, Ca, Mg, and S, and after 65 DAE for N. Phosphorus was taken up at greater rates at 70 DAE by the cultivar BRS Primavera and after 90 DAE by the cultivars Caiapó and Maravilha. The cultivars of the traditional (Caiapó) and intermediate (BRS Primavera) groups took up greater amounts of Ca (143 kg ha⁻¹), Mg (46-53 kg ha⁻¹), and S (45-52 kg ha⁻¹), but amounts of N (147-156 kg ha⁻¹) and P (18-19 kg ha⁻¹) were similar to those of the cultivar of the modern group (Maravilha). Caiapó cultivar took up more K (245 kg ha⁻¹) than other cultivars (204-207 kg ha⁻¹). The cultivars Caiapó and Maravilha showed similar grain yield (4,157 and 4,094 kg ha⁻¹); however, this was lower than the grain yield of cultivar BRS Primavera (6,010 kg ha⁻¹). Cultivars with greater yield levels did not necessarily exhibit a greater uptake and removal of nutrients per area, even if they had greater capacity for conversion of the nutrients taken up into the biomass.

Keywords: *Oryza sativa*, mineral nutrition, uptake rates, nutritional efficiency.

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INTRODUCTION

Rice is a staple food for a large part of the world's population, including Brazil. Brazil is currently the ninth largest producer of rice worldwide, with more than 70 % of the Brazilian production of this cereal crop coming from the flood irrigation growing system. However, due to the environmental risks associated with this growing system and because of the increase in rice consumption worldwide in recent years, the search for dryland or upland production systems has been encouraged, especially within the Brazilian *Cerrado* (tropical savanna) region, where this cereal crop is grown in no-tillage (NT) areas (Guimarães et al., 2006; Cazetta et al., 2008). In this system, in addition to the high yields that have been obtained by rice growers, integrating this cereal crop in rotation programs and/or crop successions has favored the performance of grain species grown in succession, such as soybean (Guimarães and Stone, 2004).

Nevertheless, inclusion of the rice crop in this growth environment has presented new challenges to the farmer, especially related to nutritional management of the crop, since this is a prevalent factor for economic viability of the crop (Alvarez et al., 2012). The rice plant is quite demanding of nutrients and, to avoid the limitation of grain yield, these nutrients need to be readily available at the times of greatest plant demand (Fidelis et al., 2012). The quantity of nutrients taken up and especially the time periods of greatest uptake are factors that must be considered in carrying out fertilization (Gargantini and Blanco, 1965). Studies indicate that the uptake and adequate use of nutrients by rice plants also depend on the physiological processes inherent to the cultivars used (Fageria et al., 1995a), which, depending on the type of plant, may exhibit expressive differences in biomass production and grain yield (Guimarães et al., 2008; Alvarez et al., 2012).

Cultivars of the traditional type, like Caiapó, have tall plants, long decumbent leaves, and long, transparent grains (Alvarez et al., 2012); these plants tolerate adverse soil fertility conditions better (Heinemann et al., 2011; Crusciol et al., 2012). Cultivars of the modern type, like Maravilha, have short plants, with long, fine grains, short, upright leaves, strong stems, and high tillering (Alvarez et al., 2012) and obtain high yields in amended soils with high fertility (Crusciol et al., 2012). Intermediate-type cultivars, like BRS Primavera, are the result of crosses between traditional and modern type cultivars; their main characteristics are reduced plant height and better grain quality (Pinheiro et al., 2006, Santos et al., 2006).

Since these cultivars have distinct characteristics and differ in relation to biomass production and yield (Guimarães et al., 2008; Alvarez et al., 2012), the demand of these cultivars for nutrients may also be different, because the traditional cultivars that were often used in the 1970s are considered rustic species that are tolerant to soil acidity (Crusciol et al., 2003a; Santos et al., 2006), whereas the development of modern cultivars is compromised in low fertility soils and soils with high Al toxicity (Crusciol et al., 2012). Furthermore, there are studies indicating greater removal of nutrients from the growing areas with the increase in rice grain yield (Crusciol et al., 2003a,b; 2007). We hypothesized that rice cultivars with different plant architectures, biomass production and grain yield may have a different dynamic of macronutrient accumulation throughout the cycle, with variation in the periods of greatest demand for these elements and in the total amounts taken up. However, there is no available information on the macronutrient uptake and removal by upland rice cultivars with these growth characteristics in a field production environment, which hinders the development of rational fertilization strategies to maximize grain yield in each cultivar type.

The aim of this study was to evaluate the dynamic of macronutrients uptake, and the extraction and removal of macronutrients by the upland rice cultivars with different plant architectures, such as Caiapó (traditional architecture), BRS Primavera (intermediate architecture), and Maravilha (modern architecture).

MATERIALS AND METHODS

Site description

The experiment was performed in Botucatu, São Paulo, in southeast Brazil (48° 23' W, 22° 51' S; 765 m above sea level) during the 2005/2006 growing seasons in a *Nitossolo Vermelho Distroférrico* (Santos et al., 2013) or Typic Rhodudalf (Soil Survey Staff, 2006). The climate, according to the Köppen classification, is Cwa, which is tropical with a dry winter and hot and rainy summer. Long-term annual (1956/2006) mean temperatures have a maximum of 26.1 °C, minimum of 15.3 °C, and average of 20.7 °C, and mean annual rainfall is 1,359 mm (Unicamp, 2012).

Prior to the experiment, a soil sample consisting of 20 subsamples was taken from the 0.00-0.20 m depth to determine soil chemical properties according the methods described by Raij et al. (2001). Soil pH was determined in a 0.01 mol L⁻¹ CaCl₂ suspension (1:2.5 soil:solution). Total acidity at pH 7.0 (H+Al) was extracted by 0.5 mol L⁻¹ calcium acetate at pH 7.0 and determined by titration with 0.025 mol L⁻¹ NaOH solution. Available P and exchangeable Ca, Mg, and K were extracted using ion exchange resin and determined by atomic absorption spectrophotometry. Cation exchange capacity (CEC) was calculated by the sum of the concentration of H+Al, K, Ca, and Mg cations. Base saturation (BS) values were calculated by dividing the sum of K, Mg, and Ca (bases) by the CEC and multiplying the result by 100 %. Soil S-SO₄ analyses were performed through extraction by calcium phosphate 0.01 mol L⁻¹ in a 1:2.5 soil:solution ratio and later determined by the turbidimetric method, using BaSO₄. The B extraction from soil was carried out using hot water and determined by atomic absorption spectrophotometry. The extraction of Cu, Fe, Mn, and Zn was performed using a 0.005 mol L⁻¹ solution of DTPA at pH 7.3, followed by determination by atomic absorption spectrophotometry. The determination of soluble Si concentration in the soil was performed with the extractant acetic acid (0.5 mol L⁻¹), according the method described by Korndörfer et al. (2004).

The results obtained were as follows: pH(CaCl₂) 5.0, organic matter 21 g dm⁻³, P (resin) 35 mg dm⁻³, K⁺ 2.5 mmol_c dm⁻³, Ca²⁺ 38 mmol_c dm⁻³, Mg²⁺ 17 mmol_c dm⁻³, H+Al 43 mmol_c dm⁻³, CEC 100.5 mmol_c dm⁻³, base saturation 57 %, S-SO₄ 20 mg dm⁻³; B 0.27 mg dm⁻³; Cu 6.5 mg dm⁻³; Fe 38 mg dm⁻³; Mn 6.2 mg dm⁻³; Zn 1.2 mg dm⁻³, and Si 8 mg dm⁻³.

Experimental design

The experiment was arranged in a randomized complete block design with split-plots and seven replications. Plots consisted of three cultivars of upland rice (Caiapó, a traditional type; BRS Primavera, an intermediate type; and Maravilha, a modern type). Subplots consisted of the plant samplings (assessments), which occurred at 39, 46, 55, 67, 75, 83, 92, 102, 111, 118, and 125 days after emergence (DAE). Each plot had eight 6-m long rows of upland rice, spaced at 0.30 m, and each subplot had three 0.75-m long rows of plants in the plot. Only the central row of the subplot was considered for evaluation, leaving 0.25 m on either side.

Cultivar characteristics

The Caiapó cultivar is a traditional upland rice cultivar that is still widely grown by farmers in the *Cerrado* region. Caiapó was developed by Embrapa Arroz e Feijão (Brazilian Agricultural Research Corporation, Rice and Beans National Research Center). It is a cultivar with good grain quality and moderate resistance to grain spot and *Bipolaris oryzae*. The Caiapó cultivar has a life cycle of about 130 d, medium plant height (1.10-1.30 m), and moderate susceptibility to lodging (Santos et al., 2006).

The BRS Primavera cultivar has a short life cycle (from 95-105 d) and is recommended for rain-fed production throughout the state of Mato Grosso do Sul. It is an intermediate type upland rice cultivar that is widely grown by farmers in the *Cerrado* region. BRS Primavera

was developed by Embrapa Rice and Beans and has long grains and high drought tolerance (Santos et al., 2006). The cultivar shows good results in several management systems, including intercropping systems. It is a cultivar with excellent grain quality and moderate resistant to grain spot and *Diatraea saccharalis* (Fonseca et al., 2004).

The Maravilha cultivar has relatively high grain yield and excellent grain quality and is considered to be an economically attractive cultivar. It has low drought tolerance, a medium life cycle (from 125-132 d), medium plant height (0.80-1.00 m), and is very resistant to lodging. It is a modern-type upland rice cultivar that was developed by Embrapa Rice and Beans. Its initial growth is slow, which, together with its upright leaf architecture, makes it uncompetitive with weeds. Thus, this cultivar requires good herbicide management (Santos et al., 2006).

Irrigation management

Soil matric potential was monitored with 12 conventional mercury tensiometers (13-mm diameter, with a ceramic porous cup connected by tubing to a mercury manometer) inside the experimental area, which were constructed according to Richards (1941) and set up on the planting date at a 0.15 m depth. Irrigation was performed by a fixed conventional sprinkler system, with a discharge rate of 3.3 mm h⁻¹, when the mean matric potential in the soil reached -0.058 MPa (vegetative and maturity phenological phases) and -0.033 MPa (reproductive phenological phases), according to the recommendations of Stone et al. (1986), and calculated to increase tension values up to field capacity.

Crop management

The soil was tilled with moldboard plow and then two passes with a leveling disk were made, the first one soon after moldboard plow tillage and the second shortly before sowing. The cultivars were sown on November 17th at a row spacing of 0.30 m with 240 viable seeds m⁻². In addition, 1.5 kg active ingredient (a.i.) ha⁻¹ of carbofuran (2,3-dihydro-2,2-dimethyl-7-benzofuranol methylcarbamate) was added to the sowing furrow to control termites (*Syntermes molestus*, *Procornitermes striatus*, and *Cornitermes lespesii*) and the lesser cornstalk borer (*Elasmopalpus lignosellus*). Mineral fertilizer was applied in the sowing furrow using 20 kg ha⁻¹ N (in the form of urea), 120 kg ha⁻¹ P₂O₅ (superphosphate), and 20 kg ha⁻¹ K₂O (potassium chloride). No micronutrients or silicon were applied. The emergence of 50 % of the plants occurred 7 d after sowing. Nitrogen topdressing fertilization (in the form of urea) was applied at 30 and 60 DAE, at rates of 40 + 40 kg ha⁻¹ N. During the growing season, weeds were controlled using manual weeding.

Plant measurements and macronutrient accumulation

The sampled plants were separated into stems + sheaths, leaf blades, and panicles and were washed and dried to a constant weight in a forced-air oven at 65 °C. Based on dry matter (DM) data of sampled plants and on plant density, the amounts of DM accumulated in each plant part were calculated. The samples were ground in a Willey mill and the concentrations of N, P, K, Ca, Mg, and S were determined (Malavolta et al., 1997). Based on the nutrient concentrations and the amounts of DM accumulated, the amounts of macronutrients accumulated in each plant part were calculated. The amounts of macronutrients accumulated in each of the aforementioned plant parts were added up to obtain the amounts of macronutrients accumulated in the shoots. Accumulation rates of DM and macronutrients in panicles and shoot were obtained by the first derivative of the adjustment equations. The extraction of macronutrients per ton of grain was obtained dividing the maximum amounts of macronutrients accumulated in the shoot of rice cultivars by grain yield.

Grain yield and nutrient removal

Manual harvest was conducted when about 90 % of the panicles had grains of typical mature coloring. Panicles of plants from the central row of the subplot were collected,

dried in the sun for 1-2 d, and later underwent manual threshing. The grains were weighed and the data adjusted for the moisture content of 130 g kg⁻¹ (wet basis). Thus, the grain yield (kg ha⁻¹) was obtained considering the grain weight per plant sampled and the final plant population. A sample of grains from each plot was dried in a forced air oven at 65 °C for 72 h, and these grains were ground in a Willey mill. The macronutrient concentration in grains was determined according to Malavolta et al. (1997), and nutrient removal by the grain was derived from the grain yield data and the grain nutrient concentration. The relative removal was obtained by dividing the maximum amounts of accumulated macronutrients in the shoot by the amounts removed with grains, multiplied by 100.

Statistical analyses

The data were subjected to ANOVA. The mean values of the cultivars at each sampling time were separated by the LSD test at 0.05 probability. The effects of the plant samplings on the DM and nutrient accumulation variables were assessed by regression analysis using the SigmaPlot 10.0 software.

RESULTS AND DISCUSSION

The DM accumulation in the stem + sheath and in the leaf blades was approximately 1,550 and 1,355 kg ha⁻¹ from emergence up to 46 DAE, and did not differ between the cultivars (Figures 1a and 1b). This shows that the DM production of the cultivars Caiapó, BRS Primavera, and Maravilha in the first 46 days of development is slow and represented only 11 % of the total DM produced by the plant (Figures 1a, 1b, and 1d). After 46 DAE, the DM accumulations in the stem + sheath and in the leaf blades of all the cultivars increased to almost the end of the cycle, at which time the amounts of DM accumulated in these plant organs decreased by a maximum of 16 % (Figures 1a and 1b). These reductions in the amounts of DM accumulated in the stem + sheath and in the leaf blades in the final phase of the cycle occur because, in the maturation phase, vegetative organs such as the stem, sheath, and leaves become important sources of photoassimilates for the grains being filled (Kato et al., 2004).

The Caiapó cultivar had a high DM accumulation in the stem + sheath and in the leaf blades from 46 DAE up to 102 DAE, showing a maximum DM accumulation in these organs of 6,799 and 4,200 kg ha⁻¹, respectively, which were, on average, 16-34 % greater than in the other cultivars, especially between 83 to 102 DAE (Figures 1a and 1b). The BRS Primavera cultivar had a high DM accumulation in the stem + sheath at around 46 DAE, and the DM accumulation reduced in this organ and in the leaf blades as of 83 DAE. Growth of the stem + sheath in the Maravilha cultivar was 13-39 % lower than that of the other cultivars from 46 to 83 DAE; however, DM accumulation was 6,204 kg ha⁻¹ in this organ at 118 DAE, which overcame the other cultivars. The greater DM accumulations in the stem + sheath and in the leaf blades of the Caiapó and Maravilha cultivars at the end of the cycle is the result of greater DM accumulation in these organs as of 93 DAE, i.e., during the maturation phase. These cultivars (Caiapó and Maravilha) have greater partitioning of photoassimilates for growth of the stem + sheath (Crusciol et al., 2012), which is in agreement with the results obtained.

After flowering, there was intense DM accumulation in the panicles of all the cultivars, which led to intense translocation of reserve compounds from the vegetative structures (stems + sheath and leaf blades) to the reproductive organs (Figures 1a, 1b, and 1c). In the BRS Primavera cultivar, the DM accumulation in the panicles was, on average, 1.8-fold greater than in the cultivars Caiapó and Maravilha from flowering up to the end of the cycle. The greater development of the panicles of the BRS Primavera cultivar occurred due to the DM accumulation rates in this organ, which were 328 kg ha⁻¹ d⁻¹, i.e., double those observed in other cultivars (Figures 1c and 1e). Rice cultivars with greater growth rates during the reproductive period had greater grain yields because of the greater growth of the panicle in relation to the vegetative parts (Takai et al., 2006).

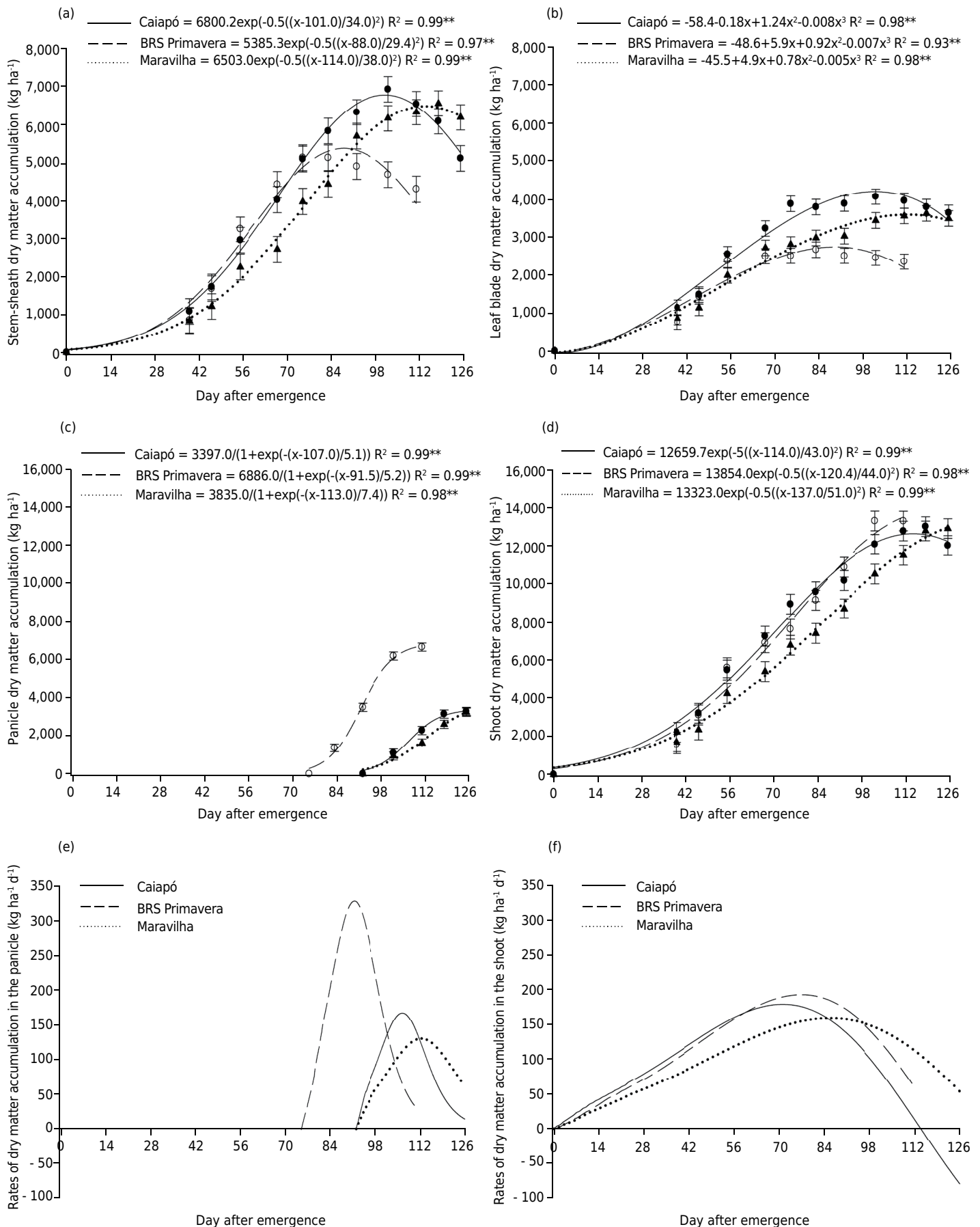


Figure 1. Dry matter (DM) accumulation in the stems + sheath (a), leaf blades (b), panicles (c), shoots (d), and DM accumulation rates in the panicles (e) and in the shoots (f) of rice cultivars throughout their cycle. **: significant at 1 % by the F test. Vertical bars indicate the LSD value by the t test (LSD) at 5 %.

In the cultivars Caiapó and Maravilha, the DM accumulation in the panicles was less and did not differ from that of the cultivar BRS Primavera, due to the similar rates of DM accumulation in this organ. The lower DM accumulation in the panicles of these cultivars occurred because, even after flowering, these cultivars had higher growth of the stem + sheath and of the leaf blades, whereas the BRS Primavera cultivar practically stopped the growth of shoots and even directed a large part of the photoassimilates accumulated in the vegetative part to the growth of panicles (Figures 1a, 1b, 1c, and 1e). These results are in agreement with those obtained by Alvarez et al. (2012) and indicate that rice cultivars such as BRS Primavera are more efficient in the partitioning of photoassimilates to the growth of panicles since they showed the growth of panicles during the final reproductive period was much greater than that of the vegetative parts (Sheehy et al., 2004; Takai et al., 2006).

In all of the cultivars, DM accumulation in the shoots fit the sigmoid regression model (Figure 1d), as also observed by Alvarez et al. (2006). From 67 to 111 DAE, the Maravilha cultivar had DM accumulation in the shoots of 10-25 % lower than that of the other cultivars because of the lower rates of DM accumulation in the shoots emerging up to around 90 DAE, when it reached $158 \text{ kg ha}^{-1} \text{ d}^{-1}$ of DM (Figures 1d and 1f). Nevertheless, at the end of the cycle, the DM accumulation in the shoots of the cultivars under study did not differ and it was approximately $13,099 \text{ kg ha}^{-1}$. This result was due to reduction in the DM accumulation rates in the shoots of the cultivars Caiapó and BRS Primavera and the maintenance of higher growth rates in the Maravilha cultivar.

In general, at the end of the cycle, the growth of the Maravilha cultivar was similar to that of the other cultivars, but the total growth of this cultivar was better characterized by the high production of stem + sheath ($6,204 \text{ kg ha}^{-1}$) and of leaf blades ($3,458 \text{ kg ha}^{-1}$), especially in the final phase of the cycle, than by panicle production ($3,024 \text{ kg ha}^{-1}$) (Figures 1a, 1b, 1c, and 1d), thus showing the high tillering capacity of this cultivar. Growth of the Caiapó cultivar, represented by DM accumulation in the shoots, was $12,655 \text{ kg ha}^{-1}$ and similar to that of the BRS Primavera cultivar, which was $13,328 \text{ kg ha}^{-1}$. However, the Caiapó cultivar had greater stem + sheath and leaf production and lower panicle production, whereas the opposite occurred in the BRS Primavera cultivar, where the panicle production was 1.8-fold greater than in the other cultivars. Cultivars of the traditional group (Caiapó) are characterized by greater growth, and cultivars of the intermediate and modern groups (Maravilha and BRS Primavera) have lesser growth (Alvarez et al., 2012). Nevertheless, from the results obtained, it can be observed that the growth of the cultivar of the traditional group is mainly characterized by greater development of the vegetative part (stem + sheath and leaf blades) and not of the reproductive structures (Figures 1a, 1b, 1c, and 1d).

With regard to nutrient uptake, it may be seen that the amounts of macronutrients accumulated in the stem + sheath of all the cultivars in the initial phases were only 7.4, 1.6, 41, 19, 5.5, and 8.7 kg ha^{-1} of N, P, K, Ca, Mg, and S, respectively (Figures 2a, 3a, 4a, 5a, 6a, and 7a). However, at 46 DAE, the accumulations of these nutrients were intensified. The small uptake of nutrients in the initial phase of the cycle is due to the slow initial growth of the crop (Guimarães et al., 2008), with low DM accumulation, but which increases at the beginning of tillering and of accelerated growth of the other parts of the plant (Figure 1). In the BRS Primavera cultivar, the maximum accumulations of macronutrients in the stem + sheath were earlier and occurred from 70 to 80 DAE (Figures 2a, 3a, 4a, 5a, 6a, and 7a). In the other cultivars, the maximum accumulations of macronutrients in these organs occurred after 80 DAE, but the maximum accumulation of macronutrients in the stem + sheath in the Maravilha cultivar was always later than in the Caiapó cultivar. This is because the Maravilha cultivar is characterized by a low growth rate throughout its development cycle (Guimarães et al., 2008; Alvarez et al., 2012), which was 8-29 % lower than in the other cultivars between 42 and 80 DAE, in this study and resulted in slower DM and nutrient accumulation in the stem + sheath.

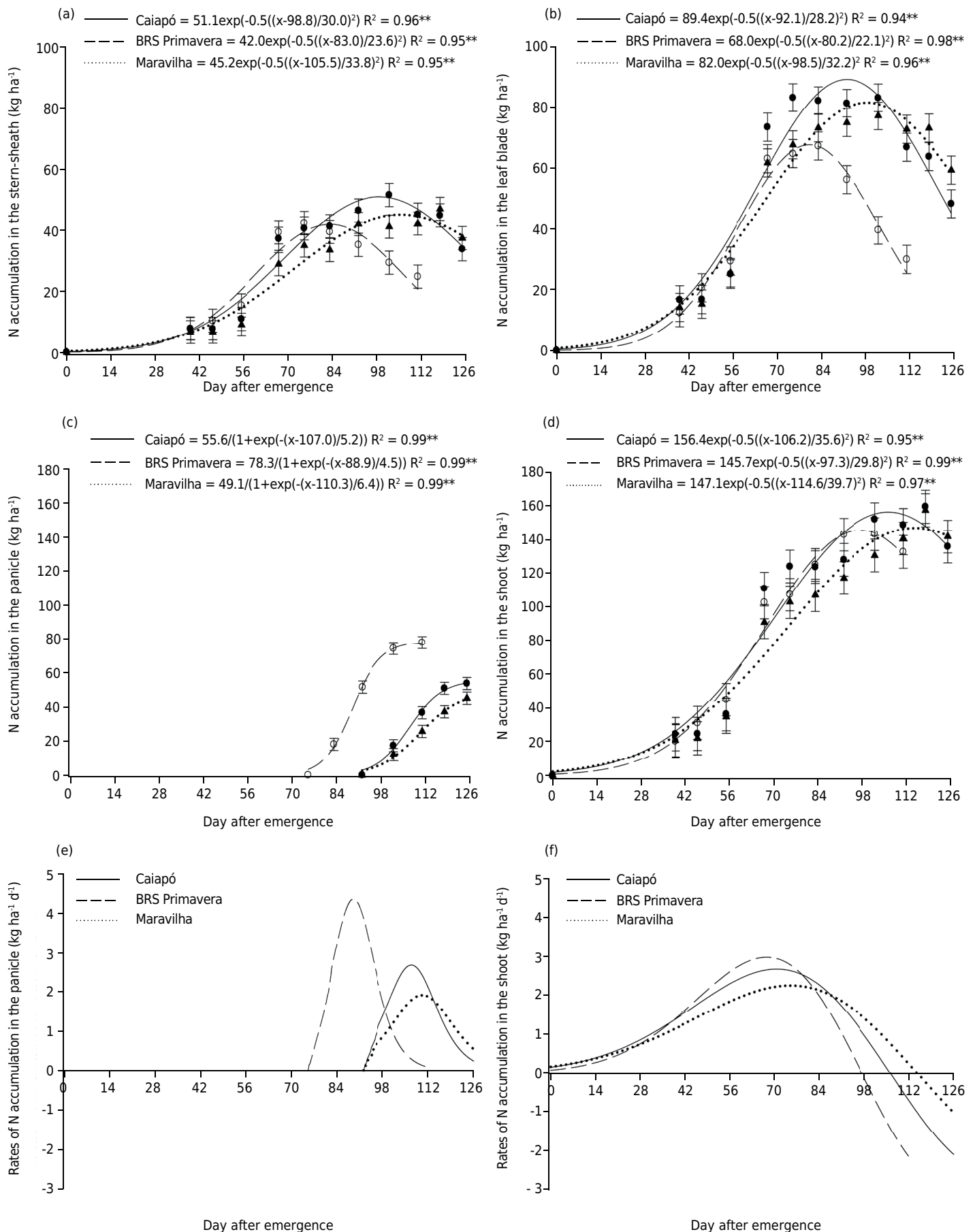


Figure 2. Nitrogen (N) accumulation in the stems + sheath (a), leaf blades (b), panicles (c), shoots (d), and N accumulation rates in the panicles (e) and in the shoots (f) of rice cultivars throughout their cycle. **: significant at 1 % by the F test. Vertical bars indicate the LSD value by the t test (LSD) at 5 %.

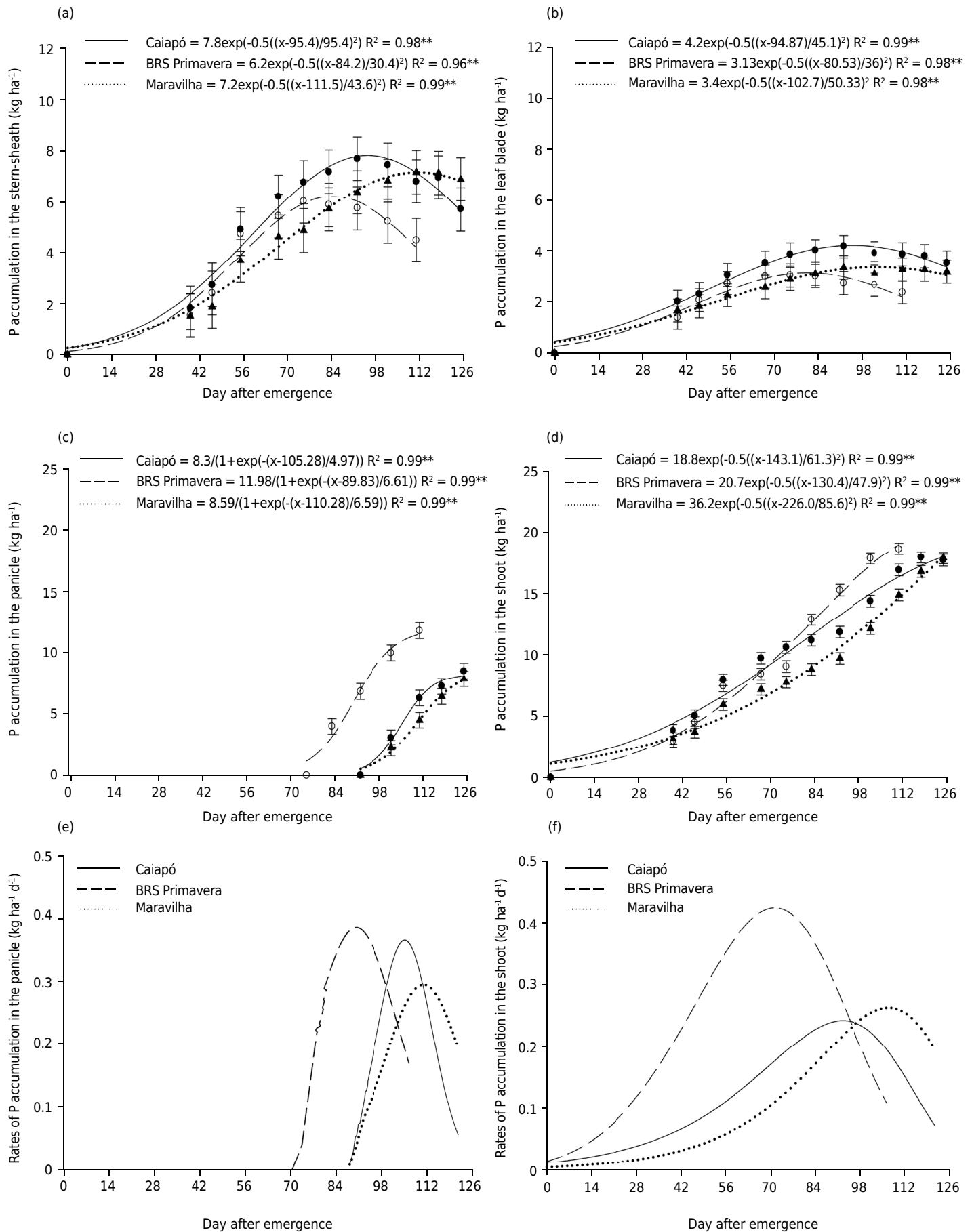


Figure 3. Phosphorus (P) accumulation in the stems + sheath (a), leaf blades (b), panicles (c), shoots (d), and P accumulation rates in the panicles (e) and in the shoots (f) of rice cultivars throughout their cycle. **: significant at 1 % by the F test. Vertical bars indicate the LSD value by the t test (LSD) at 5 %.

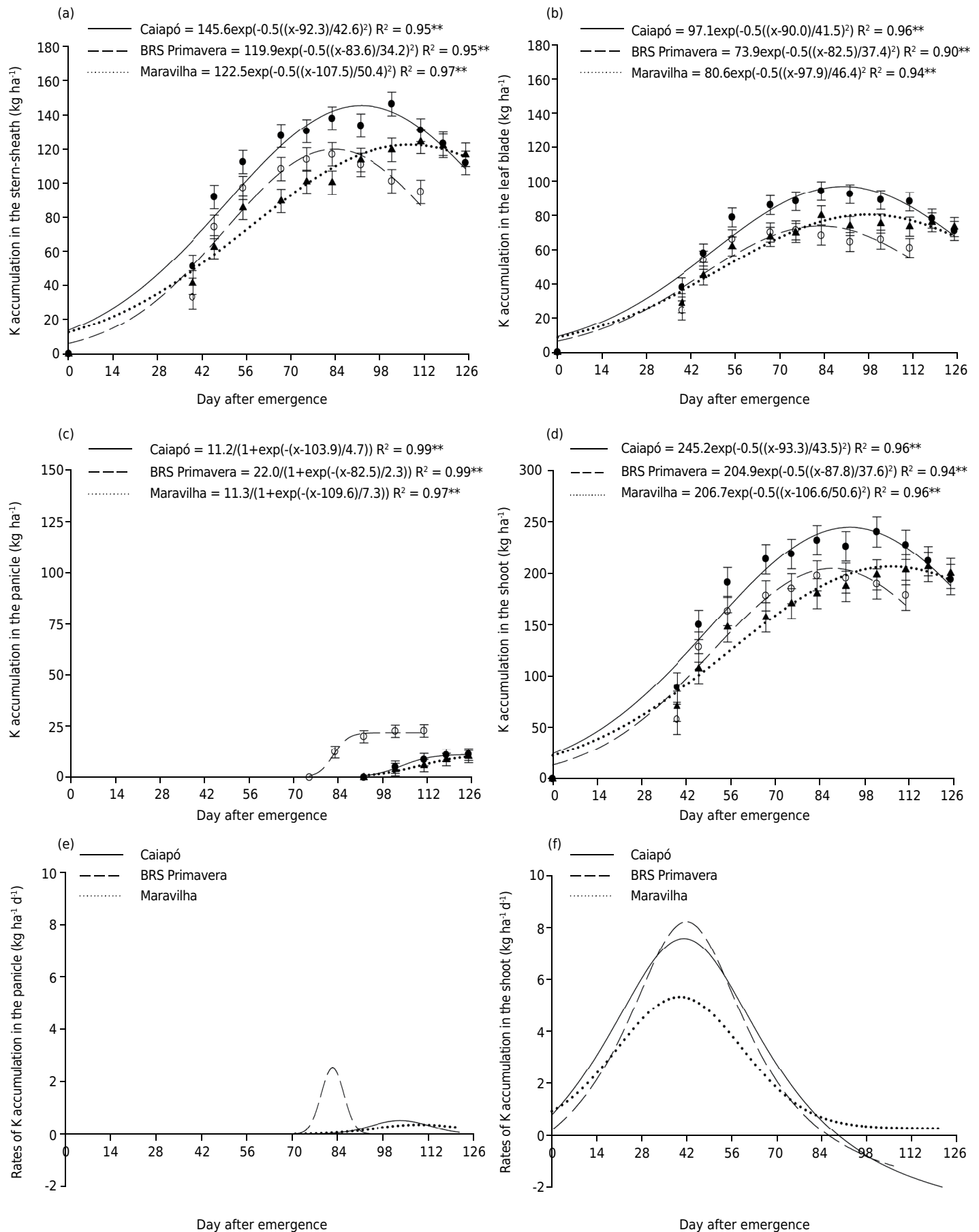


Figure 4. Potassium (K) accumulation in the stems + sheath (a), leaf blades (b), panicles (c), shoots (d), and K accumulation rates in the panicles (e) and in the shoots (f) of rice cultivars throughout their cycle. **: significant at 1 % by the F test. Vertical bars indicate the LSD value by the t test (LSD) at 5 %.

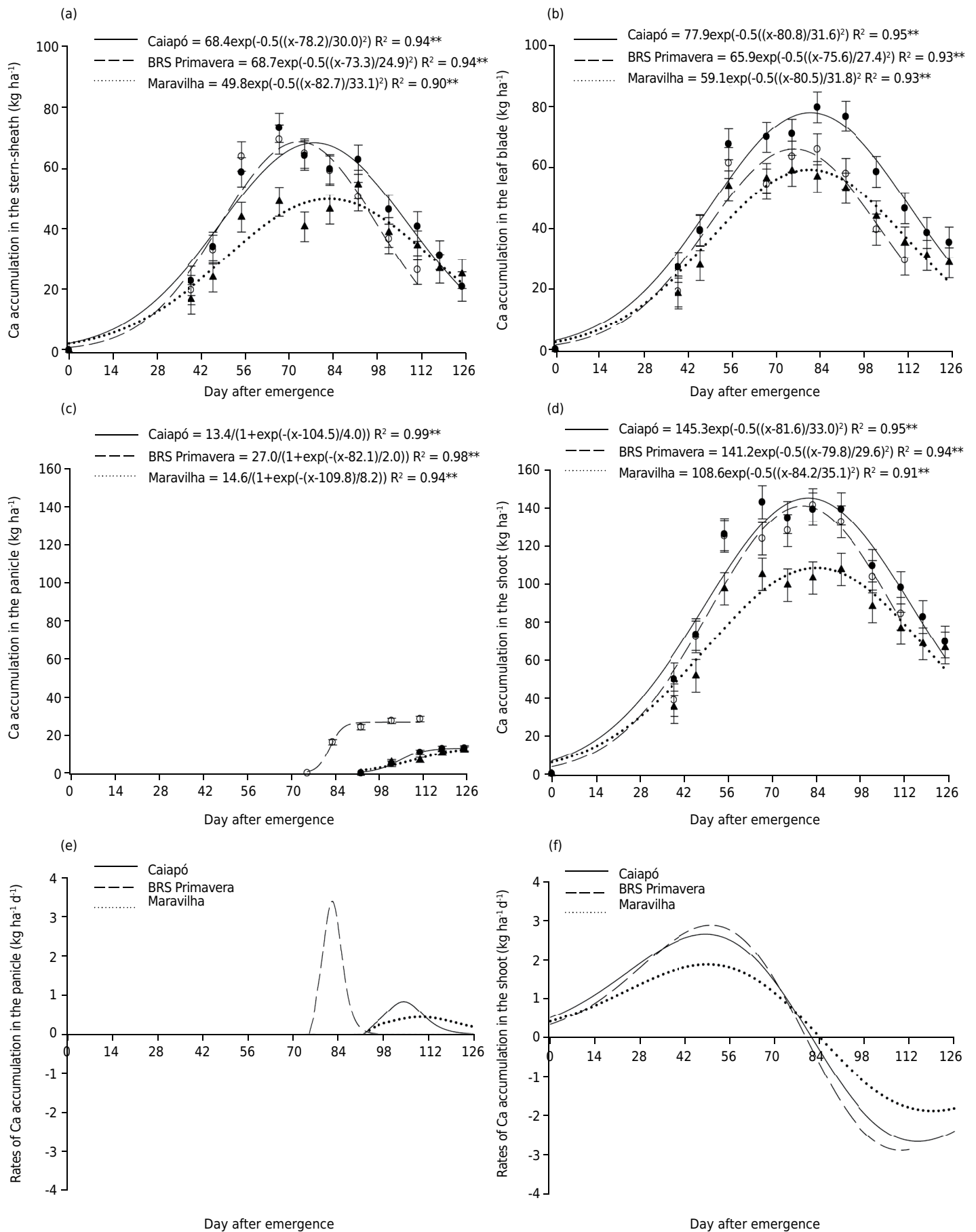


Figure 5. Calcium (Ca) accumulation in the stems + sheath (a), leaf blades (b), panicles (c), shoots (d), and Ca accumulation rates in the panicles (e) and in the shoots (f) of rice cultivars throughout their cycle. **: significant at 1 % by the F test. Vertical bars indicate the LSD value by the t test (LSD) at 5 %.

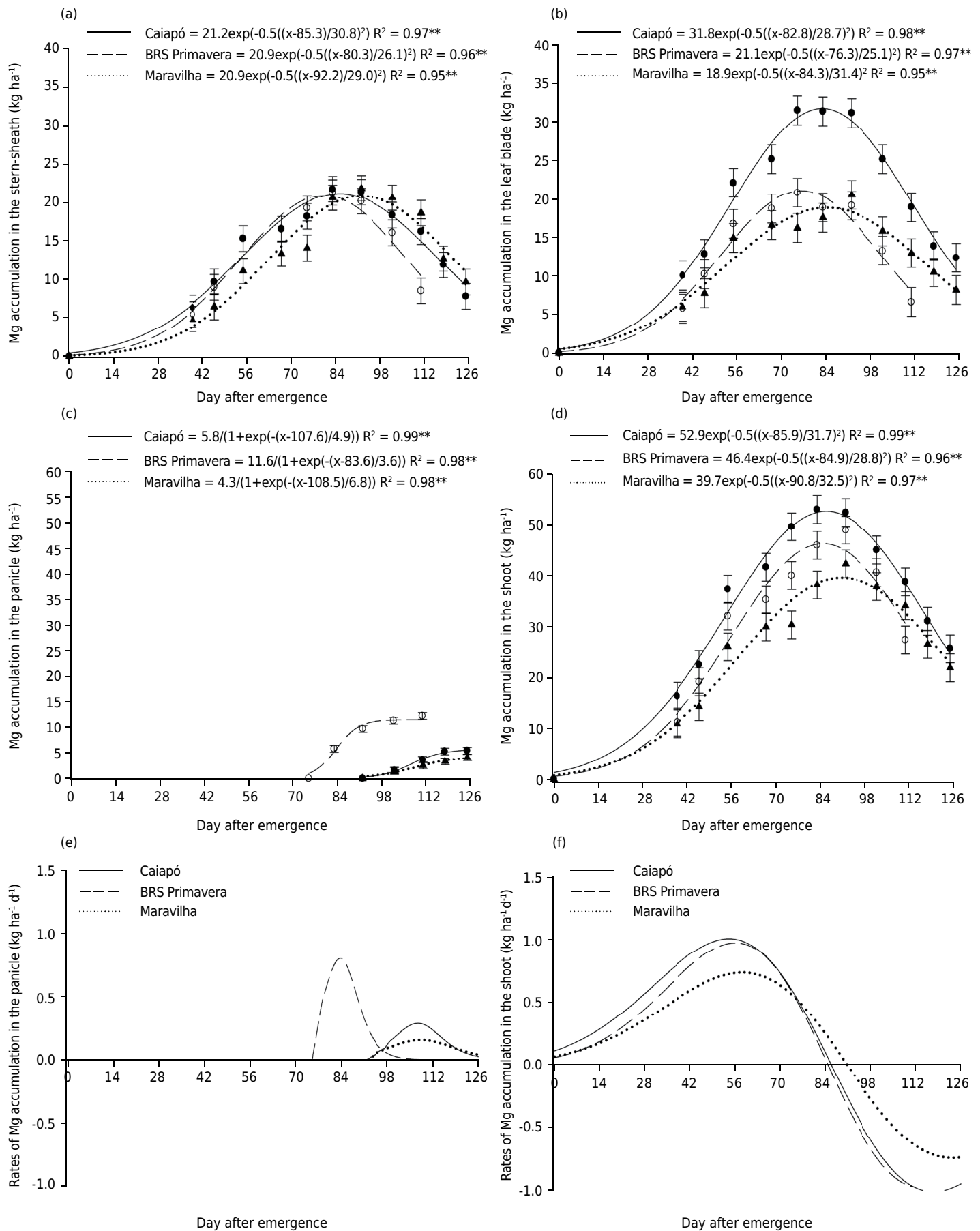


Figure 6. Magnesium (Mg) accumulation in the stems + sheath (a), leaf blades (b), panicles (c), shoots (d), and Mg accumulation rates in the panicles (e) and in the shoots (f) of rice cultivars throughout their cycle. **: significant at 1 % by the F test. Vertical bars indicate the LSD value by the t test (LSD) at 5 %.

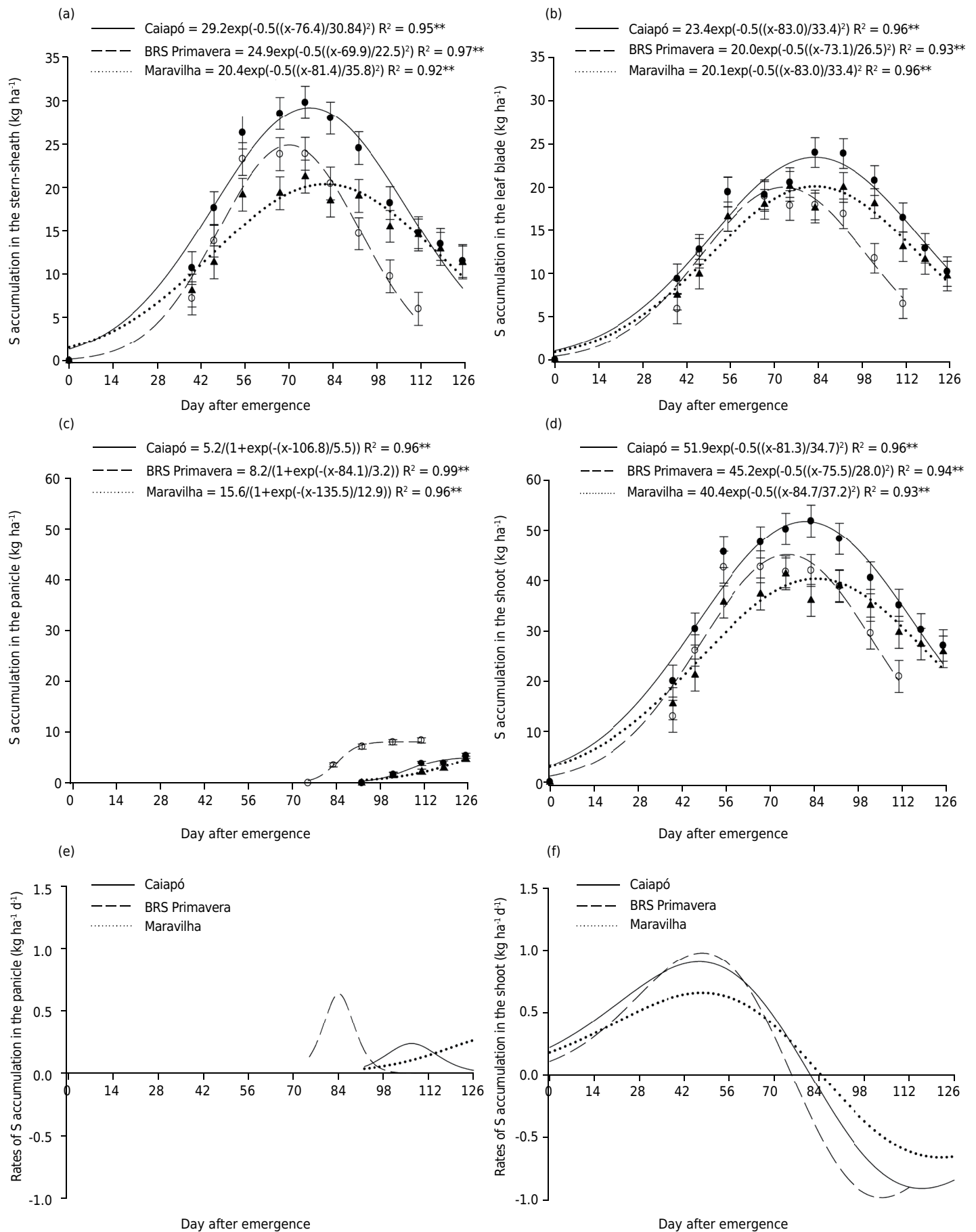


Figure 7. Sulfur (S) accumulation in the stems + sheath (a), leaf blades (b), panicles (c), shoots (d), and S accumulation rates in the panicles (e) and in the shoots (f) of rice cultivars throughout their cycle. **: significant at 1 % by the F test. Vertical bars indicate the LSD value by the t test (LSD) at 5 %.

In the final phase of the cycle, the amounts of macronutrients accumulated in the stems + sheath of all the cultivars decreased, but in a more expressive way in the BRS Primavera cultivar, which had a reduction between 1.3-4.0-fold in the amounts of accumulated nutrients in this plant organ (Figures 2a, 3a, 4a, 5a, 6a, and 7a). Reduction in the amount of macronutrients accumulated in this plant organ is the result of the decline in accumulated DM (Figure 1) and of the processes of remobilization of mobile nutrients in the tissues. Greater accumulations of N, P, and Ca in the stem + sheath occurred in the cultivars Caiapó and Maravilha, but the Maravilha cultivar had maximum accumulations of K and S less than those of the cultivars Caiapó and BRS Primavera (Figures 2a, 3a, 4a, 5a, and 7a). The maximum accumulations of Mg in the stem + sheath of all the cultivars were similar, with an average value of 21 kg ha⁻¹ (Figure 6a). The high accumulation of macronutrients in the stem + sheath of the Caiapó cultivar is related to the characteristics of this cultivar, such as a high number of tillers and greater plant height, with long and decumbent leaves, and high stem development (Fidelis et al., 2012; Alvarez et al., 2012).

In the leaf blades, the amounts of accumulated macronutrients did not differ among the cultivars up to 46 DAE, and were of 15, 2.0, 50, 34, 10, and 11 kg ha⁻¹ of N, P, K, Ca, Mg, and S, respectively (Figures 2b, 3b, 4b, 5b, 6b, and 7b). As of that time, the accumulations of macronutrients in the leaf blades of all the cultivars intensified, with maximum accumulations of macronutrients in the leaf blades of the BRS Primavera cultivar occurring at around 75 DAE and in the other cultivars from around one to two weeks after that. The Caiapó cultivar had macronutrient accumulation in the leaf blades greater than that of the other cultivars from 75 to 102 DAE, but after that period, the amounts of macronutrients accumulated in the leaf blades of this cultivar did not differ from the Maravilha cultivar.

In the final phase of the cycle, the macronutrient accumulations in the leaf blades of the BRS Primavera cultivar were always less than those of the other cultivars, showing accumulated amounts of 29, 2.3, 61, 29, 6.6, and 6.5 kg ha⁻¹ of N, P, K, Ca, Mg, and S, respectively (Figures 2b, 3b, 4b, 5b, 6b, and 7b). The greater macronutrient accumulation in the leaf blades of the Caiapó cultivar is the result of the DM accumulation in leaf blades of this cultivar being 34 % greater than in the other cultivars (Figure 1b), and of its greater leaf area index (LAI) (Alvarez et al., 2012). The more drastic reduction in the amounts of nutrients accumulated in the leaf blades of the BRS Primavera cultivar in the final phase of the cycle may indicate the greater capacity of nutrient remobilization from the leaves to growth of the reproductive organs, since in the maturation phase, vegetative organs such as the stem, sheath, and leaves become important sources of photoassimilates for grain filling (Kato et al., 2004).

After flowering, the amounts of N and P accumulated in the panicle of all the cultivars increased up to the end of the cycle (Figures 2c and 3c). In the panicle of the cultivars Caiapó and Maravilha, the accumulations of K, Ca, Mg, and S also increased up to the end of the cycle, but in the BRS Primavera cultivar, the accumulation of these nutrients in the panicle stabilized as of 111 DAE (Figures 4c, 5c, 6c, and 7c). The accumulation of macronutrients in the panicle of the BRS Primavera cultivar was greater than in the other cultivars, and showed values of 78, 12, 23, 28, 12, and 8.4 kg ha⁻¹ of N, P, K, Ca, Mg, and S, respectively (Figures 2c, 3c, 4c, 5c, 6c, and 7c). This maximum nutrient accumulation in the panicles of the BRS Primavera cultivar occurred at an earlier phase of the cycle due to the early occurrence of high rates of accumulation of macronutrients in the panicles of this cultivar (Figures 2e, 3e, 4e, 5e, 6e, and 7e). In the panicle of the cultivars Caiapó and Maravilha, the accumulations of macronutrients did not differ because of a similarity in the rates of nutrient accumulation in this organ of these cultivars. These cultivars accumulated in the panicle, on average, 49, 8.2, 17, 13, 4.7, and 5.1 kg ha⁻¹ of N, P, K, Ca, Mg, and S, respectively.

The high nutrient accumulation in the panicles of the BRS Primavera cultivar, with accumulation rates nearly twice those in the other cultivars, occurred because this cultivar practically stopped growth of the stem and leaves after flowering, while the other cultivars still showed growth in these organs (Figures 1c, 1e, 2c, 2e, 3c, 3e, 4c, 4e, 5c, 5e, 6c,

6e, 7c, and 7e). In addition, after flowering, the BRS Primavera cultivar showed greater remobilization of carbohydrates (DM) and nutrients to panicle growth, which greatly increased the accumulation rates of DM and nutrients in this plant structure. Since they have a longer cycle, the cultivars Caiapó and Maravilha obtained peak demand for nutrients in the panicles, on average, 25 days after the period of maximum accumulation of macronutrients in the panicles of the BRS Primavera cultivar. This occurred due to the earlier accumulation of DM in the BRS Primavera cultivar, especially in the panicles (Figures 1c and 1e).

During the initial period of the vegetative phase, the macronutrient accumulations in the shoot were similar for all cultivars, and the rice crop took up, on average, less than 25 % of the total amounts of N and P, and between 35 and 45 % of the total amounts of the other nutrients (Figures 2d, 3d, 4d, 5d, 6d, and 7d). The amounts of macronutrients taken up in this phase were of 26, 4.4, 120, 60, 18, and 25 kg ha⁻¹ of N, P, K, Ca, Mg, and S, respectively. Nevertheless, after 46 DAE, the amounts of macronutrients accumulated in the shoots increased intensely, with maximum accumulations of nutrients occurring at different periods of the cycle. Regardless of the cultivar, the K, Ca, Mg, and S nutrients exhibited earlier maximum accumulation during the cycle, with the maximum uptake rates being concentrated from 40 to 60 DAE (Figures 4d, 4f, 5d, 5f, 6d, 6f, 7d, and 7f). The maximum accumulation of N in the shoots was later and occurred from 95 to 110 DAE, but with the maximum uptake rates occurring after 65 DAE (Figures 2d and 2f). Gargantini and Blanco (1965) also observed that the maximum accumulation of N in the rice shoots occurred at around 110 DAE. Phosphorus was the only nutrient to be accumulated at an increased rate in the shoots up to the end of the cycle, which shows that its uptake occurred practically throughout the crop cycle (Figure 3d), which was also observed by Gargantini and Blanco (1965). Nevertheless, there are periods in the cycle in which the cultivars take up P at higher rates, as may be seen in the high P uptake rates of the BRS Primavera cultivar at 70 DAE and of the cultivars Caiapó and Maravilha after 90 DAE (Figure 3f).

The maximum amounts of Ca and Mg accumulated in the shoots of the Maravilha cultivar were 108 and 40 kg ha⁻¹; i.e., values lower than those obtained in the other cultivars, mainly compared to BRS Primavera, which accumulated 141 and 46 kg ha⁻¹ of Ca and Mg, respectively (Figures 2d, 3d, 4d, 5d, 6d, and 7d). This result occurred, in part, due to the slower growth of the Maravilha cultivar (Guimarães et al., 2008). Although the maximum accumulations of N in the shoots of all the cultivars occurred at different periods of the cycle, they were practically the same and were from 147 to 156 kg ha⁻¹ of N (Figure 2d). In a study comparing a modern rice hybrid with two traditional cultivars in China, Katsura et al. (2007) did not observe any differences in the total amounts of N accumulated in the plant shoots, but other authors verified that two of newly developed cultivars in the same country accumulated 15-25 % more N than a traditional cultivar cultivated by farmers of that country (Chen et al., 2015). In a greenhouse study in Brazil, Crusciol et al. (2012) also observed differences among cultivars, in which the Maravilha cultivar was more able to accumulate N in the shoots than the Caiapó cultivar. The BRS Primavera cultivar (intermediate group), even with a shorter cycle, accumulated around 19 kg ha⁻¹ of P in the shoots, whereas the other cultivars (traditional and modern group) accumulated 18 kg ha⁻¹ of P (Figure 3d). This result does not necessarily indicate that modern cultivars (Maravilha) need greater levels of P to obtain high yields, as suggested by Fageria et al. (1995b). Similar accumulations of P in the shoots of the cultivars Caiapó and Maravilha were also observed by Crusciol et al. (2012). Environments with a high level of P positively favored the yield increase of the BRS Primavera cultivar of the intermediate group (Tonello et al., 2013), i.e., the one that took up more P in this study (Figure 3d). The Caiapó cultivar showed the greatest accumulations of K, Mg, and S in the shoots, with quantities that reached 245, 53, and 52 kg ha⁻¹, respectively (Figures 4d, 6d, and 7d). Yang et al. (2004) obtained K uptake by flooded rice in the range from 155-238 kg ha⁻¹. In the BRS Primavera cultivar, the accumulations of S in the shoots were intermediate, but in the Maravilha cultivar, they were lower and did not go beyond 40 kg ha⁻¹. The accumulation of K in the shoots of the cultivars BRS Primavera and Maravilha were 206 kg ha⁻¹, on average, but occurred

at different time periods. Calcium was accumulated in similar amounts in the shoots of the cultivars Caiapó and BRS Primavera (143 kg ha^{-1}), but at amounts greater than those obtained in the cultivar Maravilha (108 kg ha^{-1}) (Figure 5d). These results show that the cultivars of the traditional, intermediate, and modern groups take up very similar amounts of N and P. However, the cultivars of the traditional (Caiapó) and intermediate group (BRS Primavera) take up amounts of K, Ca, Mg, and S that are, on average, 1.2-fold greater than those of the cultivar of the modern group (Maravilha), which has a slower increase in growth (Guimarães et al., 2008) and in nutrient uptake during the cycle.

Grain yield in the BRS Primavera cultivar of the intermediate group was 45.7 % greater than the Caiapó (traditional group) and Maravilha (modern group) cultivars, which had similar yields (Table 1). The high yield of the BRS Primavera cultivar ($6,010 \text{ kg ha}^{-1}$) is a result of the greater efficiency of its assimilation system involved in dry matter production (Alvarez et al., 2012), which resulted in high rates of DM accumulation in the panicles (over $300 \text{ kg ha}^{-1} \text{ d}^{-1}$) and was reflected in greater DM accumulations in this organ ($6,660 \text{ kg ha}^{-1}$) (Figures 1c and 1e). These results confirm that DM accumulation in the reproductive structures of rice plants is positively correlated with grain yield (Fageria et al., 2011).

Table 1. Grain yield, macronutrient extraction per Mg of grain, macronutrient concentration in the grain, macronutrient removal per area and per Mg of grain, and relative removal of macronutrient by rice cultivars

Cultivar	Grain yield	N	P	K	Ca	Mg	S
	kg ha^{-1}	Macronutrient extraction (kg Mg^{-1} of grain produced) ⁽¹⁾					
Caiapó	4,157 b	38 a	4.6 a	59 a	34 a	12.7 a	12.5 a
Primavera	6,010 a	24 b	3.0 b	34 c	24 b	7.7 c	7.5 c
Maravilha	4,094 b	36 a	4.4 a	51 b	26 b	9.5 b	9.8 b
CV (%)	26.5	18.5	17.0	10.4	15.0	16.2	15.7
		Macronutrient concentration in the grain (g kg^{-1})					
Caiapó	-	16.7 a	3.6 a	3.6 b	4.1 b	1.7 a	1.7 a
Primavera	-	12.4 b	2.7 b	4.0 a	4.3 a	1.8 a	1.3 b
Maravilha	-	14.0 b	2.9 b	4.0 a	3.9 c	1.2 b	1.5 ab
CV (%)	-	10.0	10.3	16.1	2.6	11.0	16.1
		Macronutrient removal per area (kg ha^{-1})					
Caiapó	-	69 a	15 a	15 b	17 b	7.1 b	7.1 a
Primavera	-	75 a	16 a	24 a	26 a	10.8 a	7.8 a
Maravilha	-	57 b	12 b	16 b	16 b	4.9 c	6.1 a
CV (%)	-	20.0	17.5	13.7	16.3	9.8	13.2
		Macronutrient removal (kg Mg^{-1} of grain produced)					
Caiapó	-	17 a	3.6 a	3.6 b	4.1 b	1.7 a	1.7 a
Primavera	-	12 b	2.7 b	4.0 a	4.3 a	1.8 a	1.3 b
Maravilha	-	14 b	2.9 b	4.0 a	3.9 c	1.2 b	1.5 ab
CV (%)	-	10.1	10.3	16.6	2.6	11.0	16.1
		Relative removal of macronutrient ⁽²⁾ (%)					
Caiapó	-	45	79	6.1	12	13	14
Primavera	-	51	90	11.7	18	24	17
Maravilha	-	39	66	7.9	15	13	15
Mean	-	45	78	8.6	15	16	15

Values followed by the same letter in the column are not significantly different at $p \leq 0.05$ according to the LSD test. ⁽¹⁾ Data based on grain yield and on the values of maximum macronutrient accumulated in the shoot, shown in figures 2, 3, 4, 5, 6, and 7. ⁽²⁾ Proportional macronutrient removal in relation to the maximum quantities of macronutrient taken up by rice crop, shown in figures 2, 3, 4, 5, 6, and 7.

The amounts of nutrients extracted for each ton of grains produced were always lower in the BRS Primavera cultivar of the intermediate group, i.e., in the cultivar that had the greatest grain yield (Table 1). This shows that higher-yielding cultivars are not necessarily more demanding of nutrients, because they are able to obtain greater yields, taking up the same amounts of nutrients as other cultivars, which is an indication of greater efficiency in the use of the nutrients taken up for grain production. These results also show that cultivars of the modern group (Maravilha) are not more demanding of nutrients than cultivars of the traditional group (Caiapó), because both cultivars obtained values of 36-38 and 4.4-4.6 kg of N and P taken up per Mg of grain produced, which were very similar. In addition, the Maravilha cultivar required less K, Ca, Mg and S to produce 1.0 Mg of grains, showing values of 51, 26, 9.5, and 9.8 kg, respectively. In China, a study showed that to produce 1.0 Mg of grain, the rice crop requirements of N, P, and K were on average 18.5, 3.9 and 21.5 kg, respectively (Xu et al., 2015), i.e., values lower than those of this study (Table 1).

In the BRS Primavera cultivar (intermediate group), the N, P, and S concentration in the grains were 34, 33, and 30 % lower than observed in traditional cultivars, respectively, possibly due to the dilution effect brought about by the high grain yield of the BRS Primavera cultivar (Table 1). Nevertheless, the K and Ca concentration in the grains of the BRS Primavera cultivar were 4.7-10.0 % greater than those of the traditional cultivar (Caiapó).

The N and P nutrient removal per area by Maravilha cultivar was 17.4-25 % lower than that of the other cultivars, due to the lower concentration of these nutrients in the grains, since the grain yield in this cultivar did not differ from the Caiapó cultivar (Table 1). The removal of S per area did not differ between cultivars, but the removal per ton of grain of N, P, and S in the Caiapó was always at least 1.3-fold higher than in the BRS Primavera. This result shows that cultivars with a higher yield, such as the BRS Primavera cultivar, do not necessarily remove greater amounts of all nutrients. In spite of that, other authors observed that with the increase in grain yield, due to irrigation, there was a greater removal of nutrients from the area by the rice crop (Crusciol et al., 2003a,b), which led to the suggestion of an increase in phosphate and potassium fertilization of 50 and 30 %, respectively, in crops under irrigation (Stone and Pereira, 1994).

The greatest removal of K, Ca, and Mg per area was obtained from the BRS Primavera cultivar, but nutrient removal per ton of grain by this cultivar was only greater than that of other cultivars for Ca (4.3 kg Mg⁻¹ of grains produced) (Table 1). In general, the cultivars that exhibited greater nutrient content in the grains obtained greater values for nutrient removal per ton of grain produced; this shows that, in addition to yield, the nutrient concentration in the grain is a fundamental factor that determines the amount of nutrients removed. Thus, along with high yields, if there is an increase in the nutrient concentration in the grain, there will consequently be the greater removal of nutrients, and fertilization levels should be increased (Crusciol et al., 2007).

With regard to the relative removal of macronutrients, it may be observed that, on average, 78 % of the total of P taken up during the cycle was removed with the grain, whereas for the total of N taken up by the rice crop, only 45 % was removed with the grain (Table 1). Around 50 % of the N taken up by the rice crop are translocated to the grain, which are values similar to those obtained in the current study (Fageria, 1999). For the other nutrients, the amounts removed by the grain represented less than 20 % of the total taken up by the plant during the crop cycle. This shows that approximately half of the N, and most of the K, Ca, Mg, and S accumulated in plants during the cycle return to the soil with crop residues, reducing nutrient exhaustion; however, less than 30 % of the P taken up remains in the crop residues. Phosphorus is the nutrient that accumulates in the greatest proportions in the grains of the rice plant, whereas most of the N, K, Ca, and Mg return to the soil with the straw (Gargantini and Blanco, 1965). It should be noted that the BRS Primavera cultivar of the intermediate group removed

relatively greater proportions of nutrients than the other cultivars, since it is higher yielding and accumulates greater amounts of macronutrients in the panicles (Table 1).

CONCLUSIONS

Macronutrient accumulation by the rice cultivars up to the end of tillering (46 DAE) was only 25 % of the total N and P, and between 35-45 % of the total K, Ca, Mg, and S; however, the levels intensified after this period. In all cultivars, the period of greatest nutrient uptake occurred from 45 to 60 DAE for K, Ca, Mg, and S, and after 65 DAE for N. Phosphorus was taken up at greater rates at 70 DAE by the BRS Primavera cultivar and after 90 DAE by the cultivars Caiapó and Maravilha.

The cultivars of the traditional (Caiapó) and intermediate (BRS Primavera) groups took up greater amounts of Ca (143 kg ha^{-1}), Mg ($46\text{-}53 \text{ kg ha}^{-1}$), and S ($45\text{-}52 \text{ kg ha}^{-1}$), but amounts of N ($147\text{-}156 \text{ kg ha}^{-1}$) and P ($18\text{-}19 \text{ kg ha}^{-1}$) were similar to those of the cultivar from the modern group (Maravilha). Caiapó cultivar took up more K (245 kg ha^{-1}) than other cultivars ($204\text{-}207 \text{ kg ha}^{-1}$). The cultivars Caiapó and Maravilha showed similar grain yield ($4,157$ and $4,094 \text{ kg ha}^{-1}$), however this was lower than the grain yield of cultivar BRS Primavera ($6,010 \text{ kg ha}^{-1}$).

Cultivars with greater yields do not necessarily have greater uptake and removal of nutrients per area if they have greater capacity for conversion of the nutrients taken up into the biomass.

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