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PHOSPHORUS DEFICIENCY IMPAIRS SHOOT REGROWTH OF SUGARCANE VARIETIES

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SUMMARY

The shoot regrowth vigour of sugarcane varieties having contrasting phosphorus (P) efficiency was evaluated under varying soil P availability. The P-inefficient (IAC91–1099 and IACSP94–2101) and -efficient (IACSP94–2094 and IACSP95–5000) sugarcane varieties were grown under low (25 mg P kg^{-1} soil) or high (400 mg P kg^{-1} soil) P supply at planting. After 90 days (first cycle of growth), the shoots were harvested and regrowth was studied 70–75 days later by evaluating photosynthesis, leaf area formation, biomass production and P uptake. The shoot dry matter (DM) of sugarcane regrowth subjected to a low P supply was genotype-dependent, with the P-efficient varieties exhibiting greater values than the inefficient ones. This result was explained by the greater efficiency of IACSP94–2094 and IACSP95–5000 in acquiring P rather than P utilization efficiency for shoot biomass production. The root P stored during the first cycle of growth would represent only a minor fraction (< 20%) of the total P content in the shoots at the end of the regrowth period. Thus, we argue that the improved shoot P uptake of the P-efficient varieties was related to their ability to sustain P acquisition after harvesting rather than to the remobilization of root P reserves. Moreover, our data revealed that net CO_2 assimilation per leaf area was not associated with differential performance among varieties under P deficiency, suggesting a more critical role of total leaf area in photosynthate supply for sugarcane regrowth. In conclusion, sugarcane regrowth is improved in P-efficient varieties under P deficiency conditions, a finding of practical relevance as such ability might benefit the productivity and the longevity of sugarcane ratoons in low P tropical soils.

INTRODUCTION

A more rational use of fertilizers corresponds to a critical component in determining the sustainability of ethanol production from sugarcane, as those products represent an important component of production costs (Karp and Shield, 2008). For instance, in the case of P, fertilizers rates around 180 kg P_2O_5 ha^{-1} should be placed in the furrow at planting to reach a stalk yield of 100–150 Mg ha^{-1} in low P soils (Raij *et al.*, 1997). Therefore, the selection of varieties more adapted to low P availability might

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contribute to a more sustainable feedstock production in P-deficient tropical soils, since such genotypes would maintain greater productivity when there is a reduction on fertilizers input. In fact, gains in the initial production of shoot biomass of sugarcane under low P supply during the first cycle of growth was already demonstrated to be attained with the use of varieties more adapted to the P deficiency condition (Zambrosi *et al.*, 2015). Although, it could be also proposed that the allocation of such varieties in low P soils would consequently improve the performance of ratoons, the interactive effects between soil P availability and sugarcane varieties with contrasting P efficiency on the vigour of sugarcane regrowth have not been investigated.

The understanding about the manner in which genotypes and nutrient supplies govern shoot regrowth vigour of sugarcane is critical for the management in farming systems because the ratoon corresponds to the major cultivated area and several cycles of growth should be obtained in the same area to save the cost of planting operations (Yadav *et al.*, 2002). In order to attain this, special attention should be given to the management of P fertilization, as the reduction of soil P availability over consecutive growth cycles is a critical factor behind the decline in stalk yield of those ratoons receiving a single dose of P at planting (Gopalasundaram *et al.*, 2011). Indeed, the occurrence of insufficient P supply to sugarcane regrowth is supported by evidence of gains in stalk yields and improvements in the P nutritional status of the plants with the reapplication of P fertilizers (Zambrosi, 2012). Despite such positive responses and the recommendation for P reapplication in low P soils (Raij *et al.*, 1997), the restricted P mobility in the soil solution and the strong interaction with the soil matrix (Fontes and Weed, 1996) limit the contact between plant roots and P applied at the soil surface, which, in turn, contributes to the impaired P fertilizer use efficiency of sugarcane ratoons (Singh *et al.*, 2013).

Accordingly, we aimed to study the interaction between soil P availability and sugarcane varieties with contrasting P efficiency taking into account the regrowth performance and evaluating photosynthetic parameters, DM production and P uptake by the plants. Furthermore, we also wanted to characterize the plants' traits favouring regrowth vigour under continuous P stress in order to contribute to the selection of varieties more suited to P deficient soils. For instance, we have recently demonstrated that both improved P acquisition efficiency and photosynthetic production capacity (measured as total leaf area and photosynthesis rate) should be combined in varieties recommended for low P soils (Zambrosi *et al.*, 2015). However, how these traits influence the performance of sugarcane regrowth under continuous limiting supply of P remains to be elucidated.

MATERIALS AND METHODS

The experimental conditions for the first cycle of sugarcane growth have been reported previously (Zambrosi *et al.*, 2015). Briefly, the sugarcane varieties IAC91–1099, IACSP94–2101, IACSP94–2094 and IACSP95–5000 were grown under greenhouse conditions, either under low (application of 25 mg P kg^{-1} soil, P_{25}) or high (application of 400 mg P kg^{-1} soil, P_{400}) P supply to the soil at planting. The soil was a typical

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Oxisol with very low P availability (P-resin = 3 mg kg^{-1}) and P was supplied as soluble fertilizer sources, as previously described in Zambrosi *et al.* (2015).

The experiment was a complete factorial design and was arranged in randomized blocks with four replicates. Each replicate was composed of two plastic pots (25 cm diameter and 30 cm deep), with each pot containing 16.5 kg of soil and three uniform plants of the same variety. After 90 days under the two P treatments imposed at planting, the shoots were cut at the soil level, and the root system was also separated from the soil for evaluating DM production and P uptake by the plants during the first cycle of growth (Zambrosi *et al.*, 2015). Following this step, one group of 32 pots was maintained in the greenhouse, and the plants were allowed to regrow (second cycle of growth). According to our previous results (Zambrosi *et al.*, 2015), genotypes with contrasting responses to P deficiency were selected for evaluating shoot regrowth: P-inefficient (IAC91–1099 and IACSP94–2101) and -efficient (IACSP94–2094 and IACSP95–5000) sugarcane varieties.

At the end of the first cycle of growth, the average values across all treatments for soil P content (P-resin) were 10 and 212 mg P kg^{-1} in P_{25} and P_{400}, respectively. During the first 35 days of sugarcane regrowth, top-dress fertilization with N and K occurred every week in order to achieve a total amount of nutrients corresponding to 1.9 g N pot^{-1} and 1.6 g K pot^{-1}. The plants were watered daily to maintain soil moisture between 75% and 80% of the maximum soil water-holding capacity. The average air temperature inside the greenhouse was 31/15 ºC (day/night), and the relative humidity varied from 25% to 100%.

Leaf gas exchange was measured from 09:00 to 12:00 h using a portable photosynthesis system (LI-6400; LI-COR Inc., Lincoln, NE, USA) equipped with a modulated fluorometer (6400–40, LI-COR Inc., Lincoln, NE, USA) under 2000 μmol m^{-2} s^{-1} PAR and air CO_2 concentration of 380 μmol mol^{-1}. Measurements of net CO_2 assimilation, transpiration, stomatal conductance and intercellular CO_2 concentration were performed in fully expanded leaves 70 days after the first harvesting. The photosynthetic water use efficiency was calculated as the ratio between net CO_2 assimilation and transpiration. Chlorophyll fluorescence was evaluated simultaneously with gas exchange in light-exposed leaves. The effective quantum efficiency of photosystem II, the apparent electron transport rate and the photochemical quenching were estimated according to Roháček (2002) by applying a saturation pulse (λ = 630 nm, PAR ~ 8000 μmol m^{-2} s^{-1}, 0.8 sec). Minimum fluorescence was measured after photosystem I excitation with far-red light (λ = 740 nm, PAR ~5 μmol m^{-2} s^{-1}, 2.0 sec). The maximum quantum efficiency of photosystem II was evaluated in dark-adapted leaves (30 min).

Sugarcane regrowth was evaluated 75 days after the first harvesting. Following the cutting of shoots close to the soil surface, the leaves were separated from the stalks to estimate total leaf area using a digital planimeter (LI-3000, LI-COR Inc., Lincoln, NE, USA). Roots were collected by sieving the entire amount of soil from each pot. Leaves, stalks and roots were washed with tap water, rinsed with deionized water, dried for 72 h at 60ºC and weighed to quantify the production of DM. Dried leaves, stalks and roots were ground and digested in nitric-perchloric acid and P concentration was

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determined using an inductively coupled argon plasma emission spectrophotometer. Shoot P uptake at the end of the regrowth period were calculated as the product of the P concentration and shoot DM, and the shoot P utilization efficiency was calculated as the ratio between shoot DM and shoot P uptake.

The root DM production and root P uptake during the regrowth period for each sugarcane variety and P treatment were estimated by differences between the values of root DM and root P content obtained in the second cycle of growth (data reported herein) and those from the first cycle of growth (Zambrosi *et al.*, 2015).

The data were analysed using a two-way analysis of variance (ANOVA). If the interaction between sugarcane varieties and P treatments was significant ($p < 0.05$), sugarcane varieties in each P treatment and P treatments within each variety were compared using a Duncan's multiple range test and the F test ($p < 0.05$), respectively. If an interaction between factors was non-significant ($p > 0.05$), a Duncan's multiple range test and the F test were used to study the effects of main factors.

RESULTS

The results obtained for the first cycle of sugarcane growth have been presented elsewhere (Zambrosi *et al.*, 2015). In the present study, the treatment with low P supply at planting reduced the leaf area of sugarcane regrowth by 46% to 86% across varieties (Figure 1a). Under such stressful conditions, IACSP95–5000 and IACSP94–2094 exhibited higher leaf area than IACSP94–2101 and IAC91–1099. In the treatment with high P supply, all sugarcane varieties presented a similar leaf area (Figure 1a).

Shoot DM and root DM were 59% to 91% lower under P_{25} compared with P_{400}, and the highest differences were observed for IACSP94–2101 and IAC91–1099 (Figure 1b–c). We did not notice variation in shoot DM under P_{400}; however, the following ranking was obtained for this parameter under P deficiency: IACSP94–2094 = IACSP95–5000 > IAC91–1099 = IACSP94–2101 (Figure 1b). Concerning root DM, IACSP95–5000 and IACSP94–2094 also had higher values than IAC91–1099 and IACSP94–2101 under P_{25}, and IACSP94–2094 showed the lowest root DM under P_{400} (Figure 1c).

Compared with P_{400}, P_{25} reduced the leaf P concentration by 24% and 41% for IACSP95–5000 and IACSP94–2094 respectively, but such response was not found in IAC91–1099 and IACSP94–2101 (Figure 2a). Furthermore, IACSP94–2094 and IACSP95–5000 showed a lower leaf P concentration than the other varieties under P_{25} (Figure 2a). The root P concentration at low P supply was reduced from 39% to 57% compared to P_{400}, and the highest value was found in IAC91–1099 under the limiting P condition (Figure 2b). At high P availability, IACSP94–2094 exhibited the highest leaf P concentration, and IAC91–1099 and IACSP95–5000 had higher root P concentrations than IACSP94–2101 and IACSP94–2094 (Figure 2).

IACSP94–2094 and IACSP95–5000 showed higher both shoot and root P uptake than IAC91–1099 and IACSP94–2101 in the P deficiency condition (Figure 3). Under high P supply, shoot P uptake did not vary among the varieties (Figure 3a) and the highest root P uptake values were found in IAC91–1099 (Figure 3b). In

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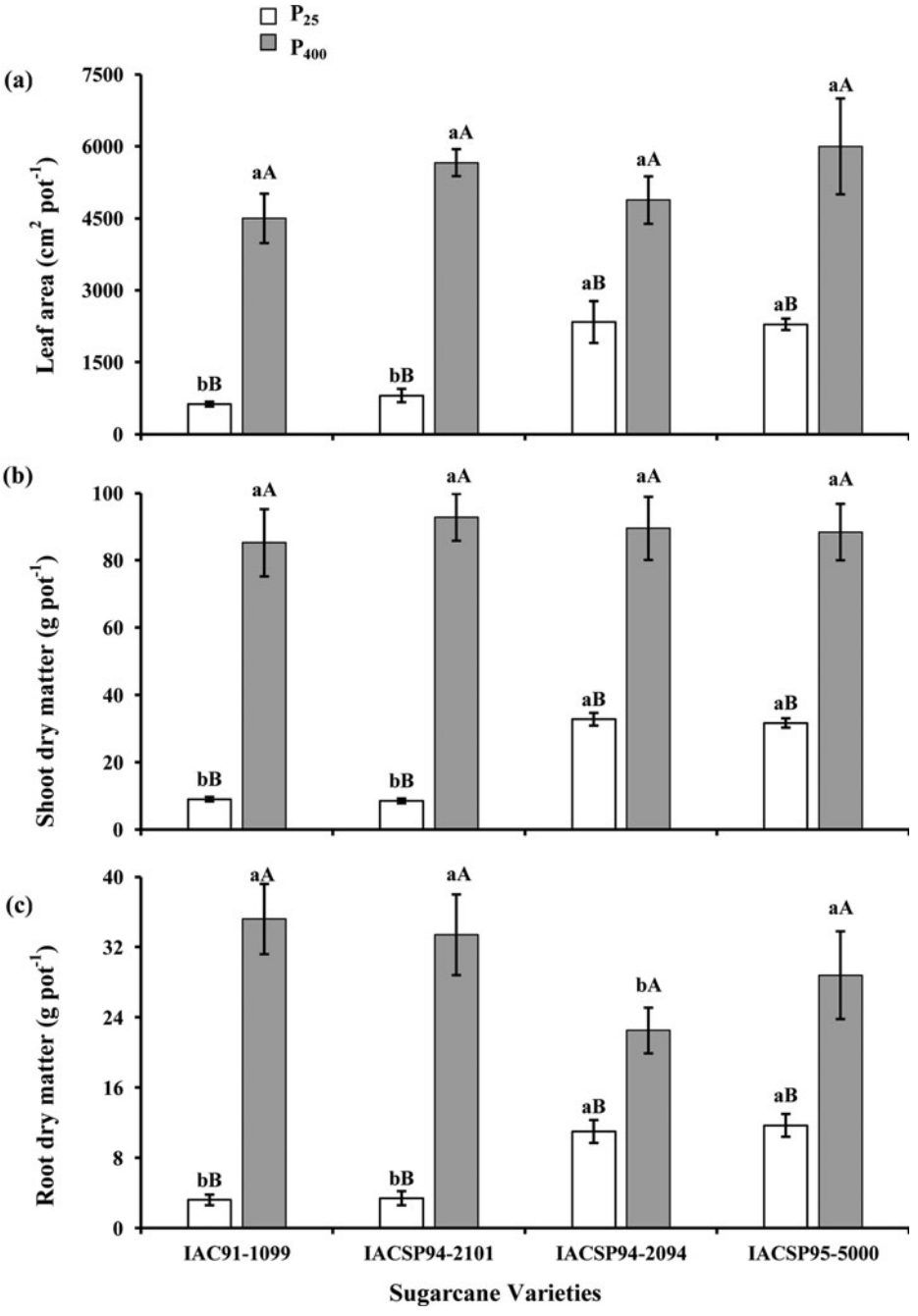

Figure 1. Leaf area (in a), shoot and root dry matter (in b, c) production of sugarcane regrowth as affected by varieties and phosphorus (P) rates applied to the soil at planting. Evaluations were taken 75 days after the first harvesting. Variety comparison: columns followed by different lowercase letters within the same P rate are significantly different by Duncan's multiple range test ($p < 0.05$). P rate comparison: columns followed by different uppercase letters for the same variety are significantly different by the F test ($p < 0.05$). P_{25} = application of 25 mg P kg^{-1} of soil; P_{400} = application of 400 mg P kg^{-1} of soil. Error bars indicate the standard error of the mean ($n = 4$).

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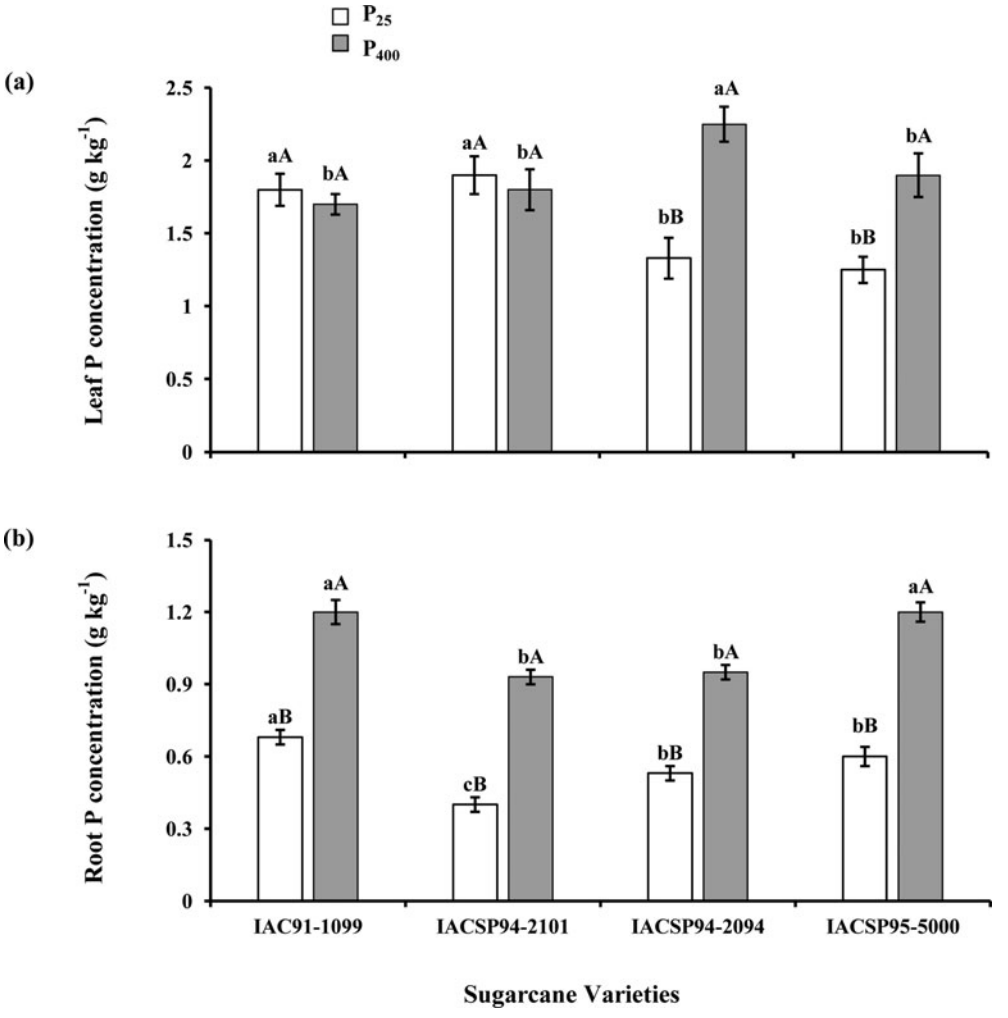

Figure 2. Concentration of phosphorus (P) in leaves (in a) and roots (in b) of sugarcane regrowth as affected by varieties and phosphorus (P) rates applied to the soil at planting. Evaluations were taken 75 days after the first harvesting. Variety comparison: columns followed by different lowercase letters within the same P rate are significantly different by Duncan's multiple range test ($p < 0.05$). P rate comparison: columns followed by different uppercase letters for the same variety are significantly different by the F test ($p < 0.05$). P_{25} = application of 25 mg P kg^{-1} of soil; P_{400} = application of 400 mg P kg^{-1} of soil. Error bars indicate the standard error of the mean ($n = 4$).

the treatment with low P supply, IACSP94–2094 and IACSP95–5000 exhibited higher shoot P utilization efficiency than the other varieties (Figure 4). While shoot P utilization efficiency of IACSP94–2094 and IACSP95–5000 was lower under P_{400} than under P_{25}, non-significant variation due to P supply was found in IAC91–1099 and IACSP94–2101 (Figure 4).

Leaf CO_2 assimilation, stomatal conductance, leaf transpiration, the photochemical quenching and the apparent electron transport rate of sugarcane regrowth were genotype-dependent but not affected by P supply (Table 1). Regardless of P availability

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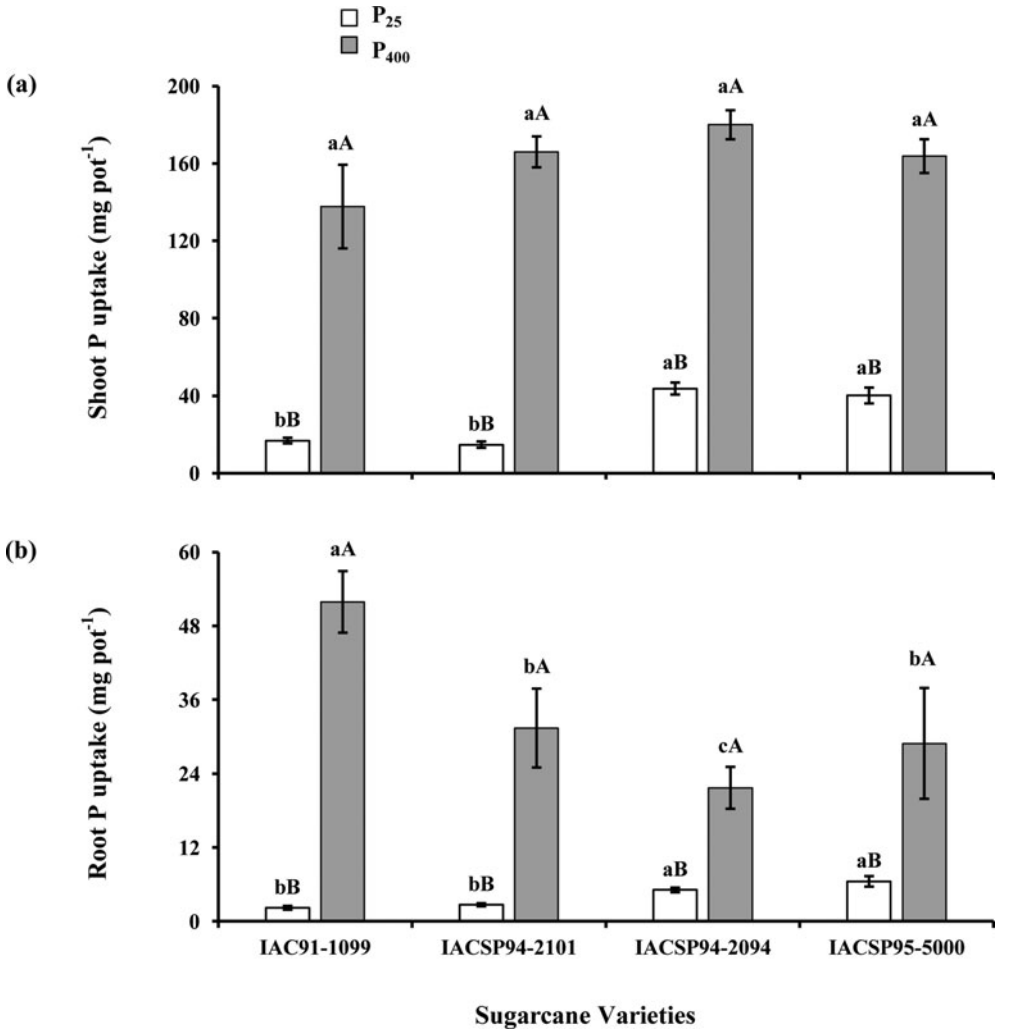

Figure 3. Shoot (in a) and root (in b) phosphorus (P) uptake of sugarcane regrowth as affected by varieties and P rates applied to the soil at planting. Evaluations were taken 75 days after the first harvesting. Variety comparison: columns followed by different lowercase letters within the same P rate are significantly different by Duncan's multiple range test ($p < 0.05$). P rate comparison: columns followed by different uppercase letters for the same variety are significantly different by the F test ($p < 0.05$). P_{25} = application of 25 mg P kg^{-1} of soil; P_{400} = application of 400 mg P kg^{-1} of soil. Error bars indicate the standard error of the mean ($n = 4$).

in the soil, IACSP95–5000 presented the highest leaf CO_2 assimilation and stomatal conductance. This variety also showed higher leaf transpiration than IAC91–1099 and IACSP94–2094, as well as higher photochemical quenching and apparent electron transport rate than IACSP94–2101. Intercellular CO_2 concentration, photosynthetic water use efficiency, potential and effective quantum efficiency of photosystem II were not affected ($p > 0.05$) by either variety or P rate, and the mean values across treatments were 64.0 μmol mol^{-1}, 4.49 μmol $mmol^{-1}$, 0.789 and 0.460, respectively.

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Table 1. Leaf CO_2 assimilation (A_N), stomatal conductance (g_s), transpiration (E), photochemical quenching (q_P) and the apparent electron transport rate (ETR) of sugarcane regrowth as affected by varieties and P rates applied to the soil at planting and evaluated 70 days after the first harvesting.

	Sugarcane varieties			
Variables	IAC91–1099	IACSP94–2101	IACSP94–2094	IACSP95–5000
A_N (μmol m^{-2} s^{-1})	$22.4^{\pm 2.9}$ b	$23.0^{\pm 2.8}$ b	$24.0^{\pm 1.5}$ b	$32.5^{\pm 1.6}$ a
g_s (mol m^{-2} s^{-1})	$0.110^{\pm 0.009}$ b	$0.120^{\pm 0.013}$ b	$0.111^{\pm 0.012}$ b	$0.153^{\pm 0.010}$ a
E (mmol m^{-2} s^{-1})	$2.9^{\pm 0.22}$ c	$3.4^{\pm 0.37}$ abc	$3.1^{\pm 0.34}$ bc	$3.9^{\pm 0.31}$ a
q_P	$0.307^{\pm 0.036}$ ab	$0.222^{\pm 0.040}$ b	$0.267^{\pm 0.032}$ ab	$0.348^{\pm 0.048}$ a
ETR (μmol m^{-2} s^{-1})	$103.0^{\pm 7.9}$ ab	$91.8^{\pm 8.8}$ b	$106.5^{\pm 10}$ ab	$128.3^{\pm 9.5}$ a

Varieties comparison: means ± standard error ($n = 8$) followed by different letters across paired columns are significantly different by the Duncan test ($p < 0.05$).

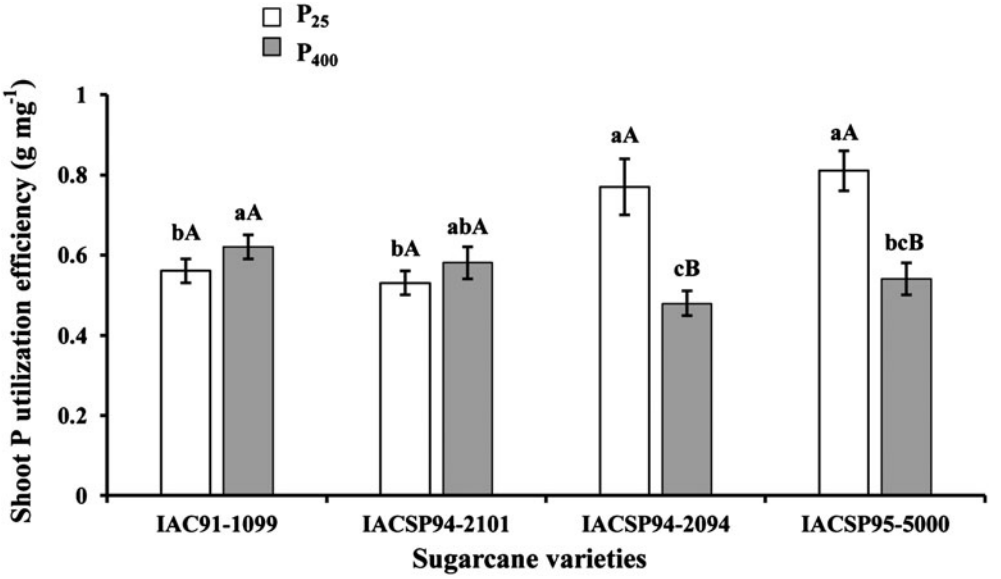

Figure 4. Shoot phosphorus (P) utilization efficiency of sugarcane regrowth as affected by varieties and P rates applied to the soil at planting. Evaluations were taken 75 days after the first harvesting. Variety comparison: columns followed by different lowercase letters within the same P rate are significantly different by Duncan's multiple range test ($p < 0.05$). P rate comparison: columns followed by different uppercase letters for the same variety are significantly different by the F test ($p < 0.05$). P_{25} = application of 25 mg P kg^{-1} of soil; P_{400} = application of 400 mg P kg^{-1} of soil. Error bars indicate the standard error of the mean ($n = 4$).

DISCUSSION

The treatment with low P supply at planting caused a pronounced reduction in the shoot biomass production of sugarcane regrowth compared with the P sufficiency condition (Figure 1b). However, there were differences for this parameter among the varieties under the low P availability, as already found in the first cycle of growth (Zambrosi *et al.*, 2015). IACSP94–2094 and IACSP95–5000 exhibited higher P efficiency (better performance under low P supply) than IAC91–1099 and

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IACSP94–2101. Thus, taken together, these results reveal interdependence between P efficiency of sugarcane varieties and the regrowth vigour under low P availability, which corresponds to a finding of practical relevance, as ratoon productivity is commonly impaired by P deficiency in tropical soils (Landell *et al.*, 2003; Zambrosi, 2012). Taking into account that the difference in shoot P uptake between IACSP94–2094 and IACSP95–5000 *vs.* IAC91–1099 and IACSP94–2101 was of a much higher magnitude than that observed for shoot P utilization efficiency (Figures 3a and 4), we might argue that P acquisition efficiency was the component of P efficiency that drove the improved shoot biomass of IACSP94–2094 and IACSP95–5000 in a P deficient soil during the regrowth period.

Although it is not possible to discriminate between the contribution of current P acquisition and that of internal P remobilization during sugarcane regrowth, there was a positive correlation between the values obtained for root P uptake during the first cycle of growth (Zambrosi *et al.*, 2015) and shoot DM of the regrowth under low P availability ($r = 0.81$; $p < 0.01$; $n = 16$). Accordingly, the shoot regrowth of sugarcane under P deficiency might be favoured by high amounts of P previously accumulated in plant tissues (i.e. root system). This argument is supported by the fact that initial shoot regrowth of defoliated or pruned plants is positively influenced by the remobilization of phloem-mobile nutrients (Thorton *et al.*, 1993; Zambrosi *et al.*, 2012). Considering that the P accumulated in roots during the first cycle of growth (Zambrosi *et al.*, 2015) in P-efficient varieties would represent only a minor fraction of shoot P uptake at the end of the regrowth period (15% for IACSP94–2094 and 19% for IACSP95–5000), acquisition from the soil appeared to be the major source of P used to meet the nutrient demand. Our data also suggest that the higher shoot P uptake of IACSP94–2094 and IACSP95–5000 (Figure 3a) might have been favoured by their improved ability to sustain root DM production during the regrowth period (Figure 1c), as a larger root system improves P acquisition efficiency (Lambers *et al.*, 2006). However, further studies are necessary to investigate differences among varieties regarding the maintenance of root activity (Smith *et al.*, 2005) and relate it to shoot P uptake of regrowth.

Accordingly, it is most likely that P remobilization was more critical to sugarcane regrowth immediately after shoot harvesting, when internal P reserves have a pronounced influence on new biomass production (Kim *et al.*, 2003). For instance, P uptake was found to be low just after defoliation, but an increasing amount of P was removed from the soil during the regrowth of ryegrass (Burkitt *et al.*, 2009). In addition, as sugar remobilization and translocation from roots is affected by P nutrition (Berg *et al.*, 2009), it could be argued that the compromised shoot regrowth of the P-inefficient varieties was also associated with impaired utilization of root sugar reserves under low P availability. However, our previous data on root P concentration for the first cycle of growth do not support this view (Zambrosi *et al.*, 2015), as no consistent variation for this parameter was found among varieties with distinct shoot regrowth. Indeed, it was demonstrated in other study that the root carbohydrate concentration increases in P-deficient plants (Wissuwa *et al.*, 2005).

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The maintenance of plant biomass production after shoot harvesting depends strongly on the current photosynthate production capacity of the new canopy being formed. Most (approximately 82%) of the carbon in the new shoot was derived from the photosynthetic activity of regrowing leaves in alfalfa, suggesting that limitations in the current CO_2 uptake would have detrimental effects on the vigour of plant regrowth (Avice *et al.*, 1996). Therefore, as P deficiency compromises both leaf area formation and photosynthesis rate (Fujita *et al.*, 2004), regrowth vigour might be impaired in a P deficient soil due to the insufficient production of photosynthate by plants. Herein, the impaired photosynthate production capacity of the P-inefficient varieties under low P supply was explained by lower leaf area rather than leaf CO_2 assimilation, as no variation in this latter parameter was found among IACSP94–2094, IAC91–1099 and IACSP94–2101 (Table 1). Indeed, a higher contribution of leaf area to the supply of photosynthate is consistent with the results obtained in the first cycle of growth (Zambrosi *et al.*, 2015). Additionally, low P supply did not impair leaf photochemistry and we did not find any consistent physiological pattern among the varieties (Table 1) that could explain the differential regrowth performance under P deficiency condition. This finding is most likely a consequence of high leaf P concentration (Figure 2a) caused by the concentration effect of reduced biomass production in the P-inefficient varieties.

In conclusion, the highest regrowth vigour of IACSP94–2094 and IACSP95–5000 was explained mostly by their improved capability of acquiring P from the soil and, at least in part, by the remobilization of P stored in their roots during the first cycle of growth. Our results also revealed that photosynthesis per unit leaf area does not explain (i) the reduced DM production at regrowth under low P supply or (ii) the contrasting performance among the varieties under the nutrient deficiency. Therefore, the differential ability of sugarcane varieties to sustain photosynthate supply for DM production during regrowth under low P supply was driven by the ability of the canopy to intercept solar radiation rather than photosynthesis per unit leaf area. Taking into account that in tropical soils, P deficiency is a widespread limitation on sugarcane ratoon productivity, we might argue that the use of P-efficient varieties is an important management practice for improving the performance of sugarcane regrowth under such limiting condition.

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REFERENCES

Avice, J. C., Ourry, A., Lemaire, C. and Boucaud, J. (1996). Nitrogen and carbon flows estimated by ^{15}N and ^{13}C pulse-chase labeling during regrowth of alfalfa. *Plant Physiology* 112:281–290.

Berg, W. K., Cunningham, S. M., Brouder, S. M., Joern, B. C., Johnson, K. D. and Volenec, J. J. (2009). Influence of phosphorus and potassium on alfalfa yield, taproot C and N pools, and transcript levels of key genes after defoliation. *Crop Science* 49:974–982.

Burkitt, L. L, Turner, L. T., Donaghy, D. J., Fulkerson, W. J., Smethurst, P. J. and Rochie, J. R. (2009). Characterization of phosphorus uptake by perennial ryegrass *(Lolium perenne* L.) during regrowth. *New Zealand Journal of Agriculture Research* 52:195–202.

Fontes, M. P. F. and Weed, S. B. (1996). Phosphate adsorption by clays from Brazilian Oxisols: relationships with specific surface area and mineralogy. *Geoderma* 72:37–51.

Fujita, K., Kai, Y., Takayanagi, M., El-Shemy, H., Adu-Gyamfi, J. J. and Mohapatra, P. K. (2004). Genotypic variability of pigeonpea in distribution of photosynthetic carbon at low phosphorus levels. *Plant Science* 166:641–649.

Gopalasundaram, P., Bhaskaran, A. and Rakkiyappan, P. (2011). Integrated nutrient management in sugarcane. *Sugar Tech* 14:3–20.

Karp, A. and Shield, I. (2008). Bioenergy from plants and the sustainable yield challenge. *New Phytologist* 179:15–32.

Kim, T., Jung, W., Lee, B., Yoneyama, T., Kim, H. and Kim, K. (2003). P effects on N uptake and remobilization during regrowth of Italian ryegrass (*Lolium multiflorum*). *Environmental and Experimental Botany* 50:233–242.

Lambers, H., Shane, M. W., Cramer, M. D., Pearse, S. J. and Veneklaas, E. J. (2006). Root structure and functioning for efficient acquisition of phosphorus: matching morphological and physiological traits. *Annals of Botany* 98:693–713.

Landell, M. G. A., Prado, H., Vasconcelos, A. C. M., Perecin, D., Rosseto, R., Bidoia, M. A. P., Silva, M. A. and Xavier, M. A. (2003). Oxisol subsurface chemical attributes related to sugarcane productivity. *Scientia Agricola* 60:741–745.

Raij, B. van, Cantarella, H., Quaggio, J. A. and Furlani, A. M. C. (1997). *Recomendações de Adubação e Calagem Para o Estado de São Paulo*, 2nd edn. Campinas: Instituto Agronômico.

Roháček, K. (2002). Chlorophyll fluorescence parameters: the definitions, photosynthetic meaning, and mutual relationships. *Photosynthetica* 40:13–29.

Singh, P., Rai, R. K., Suman, A., Srivastava, T. K., Singh, K. P. and Yadav, R. L. (2013). Ratooning induced rhizospheric changes impede nutrient acquisition and growth in sugarcane ratoon crop during grand growth stage in sub-tropics. *Sugar Tech* 15:52–64.

Smith, D. M., Inman-Bamber, N. G. and Thorburn, P. J. (2005). Growth and function of the sugarcane root system. *Field Crops Research* 92:169–183.

Thorton, B., Millard, P., Duff, E. I. and Buckland, S. T. (1993). The relative contribution of remobilization and root uptake in supplying nitrogen after defoliation for regrowth of laminae in four grass species. *New Phytologist* 124:689–694.

Wissuwa, M., Gamat, G. and Ismail, A. M. (2005). Is root growth under phosphorus deficiency affected by source or sink limitations? *Journal of Experimental Botany* 56:1943–1950.

Yadav, R. L., Shukla, S. K. and Singh, P. N. (2002). Trichoderma inoculation and trash management effects on soil microbial biomass, soil respiration, nutrient uptake and yield of ratoon sugarcane under subtropical conditions. *Biology Fertility of Soils* 45:461–468.

Zambrosi, F. C. B. (2012). Adubação com fósforo em cana-soca e sua interação com magnésio. *Bragantia* 71:400–405.

Zambrosi, F. C. B., Mattos, Jr. D., Boaretto, R. M., Quaggio, J. A., Muraoka, T. and Syvertsen, J. P. (2012). Contribution of phosphorus (^{32}P) absorption and remobilization for Citrus growth. *Plant and Soil* 355:353–362.

Zambrosi, F. C. B., Ribeiro, R. V., Marchiori, P. R., Cantarella, H. and Landell, M. G. (2015). Sugarcane performance under phosphorus deficiency: physiological and genotypic variation. *Plant and Soil* 386:273–283.