Dry Matter and Phosphorus Partitioning, Phosphorus Uptake and Use Efficiency in Zoysiagrass and St. Augustinegrass Grown in Hydroponic Culture

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ABSTRACT

Improved understanding of the relationships among leaf tissue phosphorus concentration with dry matter (DM) partitioning, phosphorus (P) uptake rate and P-use efficiency (PUE) of home lawn warm season turfgrasses could help maintain adequate turf quality while minimizing P losses to the environment. This study was conducted to evaluate the effect of leaf tissue P concentration on DM and P partitioning, P uptake rate and PUE in *Stenotaphrum secundatum* (Walt.) [Kuntze] 'Floratam' St. Augustinegrass (SA) and *Zoysia japonica* 'Empire' zoysiagrass (EZ). Six levels of P were supplied (0, 90, 135, 203, 304, 456 mg P m^{-3}) as $KHPO_4$ in a continuous flow hydroponic system under glasshouse conditions. Dry matter contents as well as P concentrations in root, thatch and leaf tissues were determined. The major fraction of total DM and P per unit turf area was accumulated in thatch tissues. Increasing P supply resulted in greater leaf:root ratio. Leaf P concentration and P content were positively related to the P stored in the thatch layer. Phosphorus depletion rate (PDR) from the nutrient solution was inversely related to the P concentration in leaf tissues in the case of EZ, but no relationship between PDR and leaf tissue P was observed for SA. Phosphorus use efficiencies in EZ and SA were inversely related to P supply and P concentration in leaf tissue. Phosphorus depletion rate and relative-PUE (RPUE) were greater in SA than EZ. Excessive P fertilization can lead to high leaf tissue P, lower PUE and PDR.

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Adequate fertilization is required to maintain high quality home lawn turfgrasses (Trenholm and Unruh, 2005). Excessive P fertilization in turfgrass systems can lead to increased P losses to the environment through runoff and leaching (Shuman, 2002; Guertal, 2007; Soldat and Petrovic, 2008). Eutrophication of P-limited surface water bodies has been linked to enrichment with P from anthropogenic sources (Correll, 1998; Carpenter et al., 1998; Foy, 2005). In the state of Florida over 40,000 ha are dedicated to sod production of different turfgrass species (Satterthwaite et al., 2009). ‘Floratam’ SA is the most widely cultivated turfgrass species in Florida. Zoysiagrass occupies the fourth largest area of sod production in Florida and Empire is the predominant cultivar of this species in the state (Satterthwaite et al., 2007).

Plant P acquisition potential is relevant from the agronomic and environmental point of view. Maximum P influx increases under P deprivation (Clarkson, 1984). Leaf expansion, leaf surface area and number of leaves decreases in P deficient plants. Correspondingly, P deficient plants allocate greater amount of assimilates to roots (Marschner, 1995). Furthermore, in P starved plants, P is translocated from older tissues to young actively growing tissues (Schachtman et al., 1998). Geron et al. (1993) reported greater nitrate (NO_3-N) leaching from sodded ‘Baron’ Kentucky bluegrass (*Poa pratensis* L.) in comparison to seeded turf grown under field conditions. They attributed greater leaching to the significantly smaller root system observed in the sodded turf. Bowman et al. (2002) measured greater NO_3-N leaching from ‘Meyer’ zoysiagrass (*Zoysia japonica* Steud.) than from ‘Raleigh’ St. Augustinegrass [*Stenotaphrum secundatum* (Walter) Kuntze]. Nitrogen recovery of ‘Raleigh’ St. Augustinegrass was greater and it was associated to greater root density at depths > 30 cm (Bowman et al., 2002).

High P-use efficiency (PUE) is another desirable attribute in plants. Fagueria and Barbosa (2007) described different definitions and methods to calculate PUE. Physiological PUE has been defined as the biological yield obtained per unit nutrient uptake (Fagueria and Barbosa, 2007). Research conducted in many crops has shown that PUE is inversely related to P supply and leaf tissue P concentration (Hylton et al., 1965; Israel and Rufty, 1988; Fagueria and Baligar, 1997; Sharma and Parmar, 1998; Nanamori et al., 2004; Fagueria and Barbosa, 2007; Gonzalez, 2010; Sistani et al., 2010).

The objectives of this study were (i) to study the effect of P supply rate and leaf tissue P concentration on dry matter and P partitioning in SA and EZ and (ii) to evaluate the influence of leaf tissue P concentration on PDR and PUE in these turfgrass species.

MATERIALS AND METHODS

Hydroponic System Description and Experimental Design

The study was conducted in the Turfgrass Envirotron facility at the University of Florida campus (29° 38’ N, 82° 21’ W) under glasshouse conditions. Average relative humidity and temperature in the glasshouse were 70% and 28.4 °C, respectively. The relative humidity and the temperature oscillated between 20% and 89% and 21°C and 39°C, respectively. In addition, the average photosynthetic photon flux density (measured outside the glasshouse) between 0700 and 1800 h was 898 µmol m^{-2} s^{-1} and ranged from 1.63 to a 2,459 µmol m^{-2} s^{-1}. *Zoysia japonica* ‘Empire’ and *Stenotaphrum secundatum* [Walt] Kuntze ‘Floratam’ certified sod from the G.C. Horn Turfgrass Field Laboratory near Citra, Florida were selected as the test cultivars. The sod was washed thoroughly to remove soil from the root system, cut into 20 cm x 33 cm rectangles and transferred to a hydroponics system. Polyvinyl chloride (PVC, 22 mm outer diameter) pipe was used to construct a 22 cm by 33 cm frame and covered with poly hardware cloth (13-mm square openings). The sod was placed on the plastic screen which was used as a grass bedding surface. Turf roots were carefully passed through the openings of the plastic screen to promote contact with the nutrient solution. Each experimental unit was placed in a 25 cm x 36 cm x 23 cm plastic tub (~20 L) used as the hydroponic container. The tubs corresponding to a given treatment were connected to a larger nutrient reservoir (120 L). A submersible pump delivered nutrient solution to the corresponding tubs at a rate of 12 L per minute and the solution returned to the nutrient solution reservoir by gravity; hence, the nutrient solution was constantly circulating between the tubs and the nutrient solution reservoir.

Light penetration through the outer surfaces of the tubs was restricted by black latex paint. During the first two weeks of the experiment, the nutrient solution level was maintained in contact with the plastic hardware net to stimulate root growth. Thereafter, the solution level was lowered to about 2.5 cm from the plastic screen to favor incorporation of oxygen as the continually circulating solution entered in contact with the solution present in the tub. The turfgrass was maintained from December 19th 2008 until May 24th 2009 on a modified half strength Hoagland solution (Hoagland and Arnon, 1950) without P to reduce tissue P levels. Phosphorus treatments were imposed on May 24th, 2009 and the study was continued for 140 days thereafter. Six levels of P (0, 90, 135, 203, 304 and 456 mg P m^{-3}) were supplied with reagent grade mono potassium phosphate (22.6 % P) in a modified full strength Hoagland (Hoagland and Arnon, 1950) nutrient solution. The P treatments were replicated five times and arranged in a split-plot randomized complete block design with turfgrass species as the main effect and P application rate as secondary effect. The initial concentrations of NH_4-N, NO_3-N, K, Ca, Mg, and S in the nutrient solution were 7.5, 7.5, 6, 2, 2, and 2 m*M*, respectively. The initial solution concentrations of Mn, Zn, Cu, B, and Mo were 9, 1.5, 1.5, 45 and 0.1 µ*M*, respectively.

Chelated iron (Sequestrene 330) was supplied biweekly through foliar application at a rate of 0.5 g Fe m^{-2} (Carrow, 2007). The nutrient solution was replaced twice per week. Initial solution pH oscillated between 5.5 and 6 and the initial nutrient solution temperature ranged between 25°C and 30 °C.

Tissue Sampling and Analysis

Top growth was harvested every two weeks to a height of about 10 cm. Roots were clipped to about 10 cm when their length was roughly 15 cm. All tissue samples were oven-dried at 70°C to constant weight, weighed, and then ground to pass a #40 (425 µm opening size) sieve. Dry tissue was ashed and digested according to Andersen (1976). Phosphorus concentration in the digestate was determined by colorimetry following the procedure described by O'Dell (1993). Leaf and root tissue growth rate (g m^2 d^{-1}) was monitored during the entire evaluation period. Phosphorus uptake rate into leaf tissue was calculated as the product of leaf tissue growth rate (i.e., g DM m^{-2} day^{-1}) and phosphorus concentration in leaf tissue (g P kg^{-1} DM).

Rate of Phosphorus Depletion from Nutrient Solution

The experimental units corresponding to treatments supplied with 203 mg P m^{-3}, 304 mg P m^{-3} and 456 mg P m^{-3}, were utilized in this part of the study. The turf was exposed to an initial solution P concentration of 409 mg P m^{-3}. The initial nutrient solution weight and its corresponding initial P concentration were determined prior to placing the turf in the solution. In addition, initial solution pH, electrical conductivity (EC) and temperature were also recorded. On average, the initial solution volume per experimental unit (assuming a solution density of 1 g cm^{-3}), initial soluble reactive P concentration, initial pH, initial EC and initial temperature were 13.7 L, 409 mg P m^{-3}, 5.8, 26 mS m^{-1} and 25.9 °C, respectively. The change in these variables was determined approximately every 90 minutes for a period of ten hours starting between the 800 and 1800 h during 5 consecutive days. However, only the data collected during the first 4 hours is presented herein. At the end of the evaluation period, all the roots from each experimental unit were harvested and scanned with an Epson Perfection V700 Photo dual lens scanner (Epson Corporation, Japan). The digital images obtained were then analyzed with WinRhizo Software Pro v. 2007d (Reagent Instruments Canada Inc., Ottawa, ON, Canada) to determine the total root length in each experimental unit. The rate of P depletion was calculated as the change in the solution P content over time per meter of root.

Statistical Analysis

Non linear regression analysis (Proc Reg) in SAS Statistical Software v. 9.2 (SAS Institute, 2009) was conducted to relate response variables such as rate of P accumulation in leaf tissue, rate of P depletion from nutrient solution and P use efficiency to explanatory variables like leaf tissue P concentration, initial solution P concentration and thatch tissue P content. Furthermore, treatment means separation was carried out using single degree of freedom contrast analysis (Proc GLM) in SAS Statistical Software.

RESULTS

Dry Matter and Phosphorus Partitioning

There was no treatment effect on thatch or root dry matter partitioning in EZ (Fig. 1). Total EZ dry matter accumulation in leaves increased with increasing P supply (Table 1); however, no treatment effect on the fraction of total DM accumulated in leaf tissue was observed above an initial P concentration in solution of 135 mg P m^{-3} (Fig. 1). St Augustinegrass DM partitioning to leaf tissue increased with increasing P supply. In contrast, as the P supply increased a lower fraction of the total DM accumulated per unit area of SA turf was partitioned to thatch tissue (Fig. 1). Phosphorus supply rate did not have a clear effect on the percent of total dry matter allocated to roots of SA (Fig. 1). Dry matter accumulation in leaves of SA exposed to an initial P solution concentration of 456 mg P m^{-3} was 3.3 times greater than in the control treatment (Table

1). Thatch dry matter accumulation was 13% greater in the P starved SA turf in comparison to the turf growing in the highest P supply treatment (Table 1).

On average across treatments 65.7% of the total P content (PC) per unit area of EZ turf was allocated to thatch, 19.7% to leaves and 14.6% to root tissue (Fig. 1). In the case of SA the fraction of total P accumulated per unit area that was allocated to thatch was 57%, 27% to leaves and 16% to root tissue (Fig. 1). The percentage of total PC in leaf tissue per unit area of EZ and SA turf increased with increasing P supply (Fig. 1). An initial P concentration in solution of 135 mg P m^{-3} was required to increase the PC in EZ leaves with respect to the control treatment (Fig. 1). The PC per unit area allocated to EZ leaves did not increase above an initial solution P concentration of 203 mg P m^{-3} (Fig. 1). The fraction of P stored in the thatch layer of EZ decreased with increasing P supply, while no treatment effect on EZ root P storage was established (Fig. 1). The total amount of P stored per unit area in the thatch layer of SA increased with increasing supply. Phosphorus concentration of SA thatch tissue supplied with high P levels was greater (Table 1) and it may account for the positive effect of increasing P supply on thatch P content. However, the fraction of the total P accumulated per unit area of SA that was partitioned to thatch decreased with increasing P rate, possibly due to the parallel increase in P partitioning to leaf tissue (Fig. 1). Phosphorus partitioning to SA root tissue did not show a clear trend in response to P supply; however, the lowest fraction of P partitioned to roots was observed in the control and 456 mg P m^{-3} treatments (Fig 1). The concentration of P in SA and EZ leaf, thatch and root tissues increased with increasing P supply (Table 1). St. Augustinegrass and EZ leaf growth rate increased in a quadratic manner with increasing leaf tissue P concentration (Table 1). No increase in root P concentration was observed above 90 mg P m^{-3} in EZ (Table 1). Zoysiagrass leaf:root ratio increased with increasing P supply reaching a plateau at about 203 mg

P m^{-3} and an average leaf tissue P concentration of 0.97 g P kg^{-1} (Table 1). Leaf:root ratio of SA increased with increasing P supply up to the highest application rate (456 mg P m^{-3}) and it increased at a faster rate above a leaf tissue P concentration of 1 g P kg^{-1} (Table 1). Phosphorus concentration and total P storage in leaf tissue were positively related to the size of the P pool in the thatch layer (Fig. 2).

Phosphorus Uptake Rate

Leaf phosphorus accumulation rate increased linearly with increasing initial solution P concentration (Fig. 3). This response is the result of the cumulative effect over time of an increased biomass accumulation rate and increased tissue P concentration in response to greater P supply. During the period of highest growth rate about 23 mg P m^{-2} day^{-1} were taken up and allocated to leaves by turf supplied with an initial P concentration of 456 mg P m^{-3} (Fig. 3).

The PDR from the nutrient solution by EZ was inversely related to leaf tissue P concentration (Fig. 3). Zoysiagrass minimum P depletion rate from solution of 0.99 µg hr^{-1} m^{-1} of root was estimated to occur at a leaf tissue P concentration of 1.65 g P kg^{-1} (Fig. 3). Phosphorus depletion rate from solution and P concentration in SA leaf tissues were not related (Fig. 3). St. Augustinegrass PDR was greater than in EZ across a wide range of P concentrations in leaf tissue (Fig. 3).

Phosphorus Use Efficiency

Phosphorus use efficiency for leaf growth (PUE_L) was defined as the mass of leaf dry matter accumulated per unit mass of P allocated to leaf tissue (i.e., kg leaf DM g^{-1} of P). Zoysiagrass and SA PUE_L decreased with increasing initial P concentration in the nutrient solution (Fig. 4). A minimum PUE_L of 0.50 kg leaf DM g^{-1} P was estimated for EZ exposed to an initial P concentration in solution of 357 mg P m^{-3}. St. Augustinegrass PUE_L reached a minimum of 0.54 kg leaf DM g^{-1} P at an initial P concentration in solution of 377 mg P m^{-3} (Fig. 4).

Moreover, PUE_L was inversely related to P concentration in leaf tissue (Fig. 4). A minimum PUE_L of 0.56 kg leaf DM g^{-1} P in EZ corresponded to a leaf tissue P concentration of 1.58 g P kg^{-1}. St. Augustinegrass minimum PUE_L (0.60 kg leaf DM g^{-1} P) was attained at a P concentration in leaf tissue of 1.65 g P kg^{-1} (Fig. 4).

Relative P use efficiency is equivalent to PUE but expressed in a scale between 0 and 1. Since PUE is influenced by the leaf tissue P concentration, comparisons of PUE between plants with different tissue P concentrations could be misleading. By expressing PUE in a relative scale, the confounding effect of differences in leaf tissue P concentration is removed. Zoysiagrass RPUE for leaf production ($RPUE_L$) decreased by 81% when the P solution concentration was increased from 0 mg P m^{-3} (i.e., control treatment) to 357 mg P m^{-3} (i.e., P concentration at which $RPUE_L$ reached a minimum). St. Augustinegrass exposed to a P concentration in solution of 377 mg P m^{-3} had a $RPUE_L$ 76% lower than when grown in nutrient solution without P (Fig. 4). Phosphorus use efficiency for root accumulation (PUE_R) was defined as the mass of root dry matter produced per unit mass of P allocated to leaf tissue (i.e., g root DM g^{-1} P accumulated in leaves). St. Augustinegrass relative PUE_R ($RPUE_R$) decreased more gradually and to a lesser extent than in EZ with increasing P supply or leaf tissue P concentration (Fig. 4). On average across replicates within a given treatment, increasing leaf tissue P concentration from severe P deficiency to adequate P concentration resulted in a reduction of the $RPUE_R$ of 86% in EZ and 41% in SA (Fig. 4).

DISCUSSION

Dry Matter and Phosphorus Partitioning

Zoysiagrass leaf:root ratio increased with increasing P supply to a maximum value and reached a plateau between 203 mg P m^{-3} and 456 mg P m^{-3}. On the contrary, SA leaf:root ratio continued to increase with increasing P supply up to 456 mg P m^{-3}. Even though the sum of leaf and root dry matter accumulation increased with increasing P supply in both turfgrass species, the partitioning of DM to leaf tissue as the leaf tissue P concentration increased was much greater in SA than EZ. The leaf:root ratio of SA supplied with 456 mg P m^{-3} was about 81% greater than in EZ. Nanamori et al. (2004) reported an 80% increase in shoot:root ratio of 'Mulato' *Brachiaria* hybrid forage grown in solution culture under a gradient of P supply ranging from 0 to 32 µM P. Shoot:root ratio of Italian ryegrass (*Lolium multiflorum* Lam.) grown in nutrient solution increased four-fold with increasing P supply from 0.16 mg P $plant^{-1}$ to 165 g P $plant^{-1}$ (Hylton et al., 1965). Fageria and Baligar (1997) observed an average four-fold increase in shoot:root ratio across nine genotypes of corn (*Zea mays* L.) grown in an oxisol (clayey, kaolinite, isothermic Typic Haplustox) under greenhouse conditions.

The combined effect of greater dry matter allocation to leaves and greater leaf tissue P concentration with increasing P supply explains the greater PC in leaves as a result of increasing initial solution P concentration. Liu et al. (2006) evaluated the response of 'Floratam' St. Augustinegrass to increasing P supply from 0 mg P m^{-3} to 775 mg P m^{-3} in hydroponic culture. They reported an increase in leaf tissue P concentration and leaf growth rate in response to increasing P supply. Leaf tissue P concentration and leaf growth rate of 'Floratam' St. Augustinegrass grown in sandy soils (Alaquods and Quartzipsamments) under glasshouse conditions, increased with increasing P supply from 0 to 1.09 g P m^{-2} applied every 4 weeks (Liu et al., 2008). Leaf tissue P concentration of creeping bentgrass (*Agriostis stolonifera* Huds.) grown in a calcareous sand green increased quadratically with increasing P supply from 5.5 to 110 kg P ha^{-1} $year^{-1}$ (Johnson et al., 2003).

Phosphorus is a phloem mobile nutrient element and thus it can be remobilized from older plant tissues to actively growing points (Marschner, 1995). Once older leaves and stems die, they may become part of the thatch layer. Broschat and Elliot (2005) observed a decrease in 'Floratam' St. Augustinegrass leaf tissue P concentrations with increasing leaf age. As the thatch layer decomposes it could release P to the solution from where it could be absorbed and translocated back to actively growing tissues, such as leaf and root tips. The leaf tissue P concentration required for maximum leaf growth rate of EZ was determined to be 1.67 g P kg^{-1} (Gonzalez, 2010). Average P accumulation rate in leaf tissue over the entire growth season (May through September) in turf with a leaf P concentration near the critical level was 18.5 mg P m^{-2} day^{-1} for EZ and 17.5 mg P m^{-2} day^{-1} for SA. According to non-linear regression analysis, P content in the thatch layer of turfgrass with a leaf tissue P concentration near the critical for maximum leaf growth would be 2 g P m^{-2} for EZ and 2.03 g P m^{-2} for SA. Under the conditions of this experiment and assuming full depletion of thatch layer P pool, turfgrass growing in a medium with very low P concentration or very low P bioavailability could use the P storage pool in the thatch layer to meet the P demand required for maximum leaf growth during a period of approximately 108 days (2000 mg P m^{-2}/ 18.5 mg P m^{-2} day^{-1}) in the case of EZ and 116 days (2030 mg P m^{-2}/ 17.5 mg P m^{-2} day^{-1}) for SA. If the clippings are returned to the turf and eventually become part of the thatch layer, only about 40% and 36% of the P stored in leaf clippings of EZ and SA, respectively, would have to be mineralized and absorbed by the plant to meet the P demand for maximum leaf growth during a period of 180 days.

Under the climatic conditions where this experiment was conducted (North Central Florida) the length of the period that promotes high leaf growth rate is shorter than 180 days. Since the rate of P accumulation in leaf is a function of leaf growth rate, lower P demand would result from a decrease in leaf growth. Accordingly, the amount of P required to be absorbed from the thatch layer to support leaf growth would be lower and the thatch P reserve would last longer.

Gonzalez (2010) reported that after 243 days of P starvation, the fraction of the turf surface covered by green leaves was on average 67% in EZ and 43% in SA. The later corresponded to 74% of the maximum green leaf cover attained in EZ and 53% in SA turf growing with adequate P supply. In addition, significant ($p<0.0001$) positive relationships among leaf P concentration and leaf PC with the size of the P pool in thatch tissue were found. These results emphasize the importance of the thatch P storage pool and P remobilization from older tissues to meet the P demand of actively growing parts of the plant. Inspection of the equations obtained for the relationships between leaf PC and thatch PC indicate that for a given thatch PC, the amount of P stored in leaf tissue of SA would be greater than in EZ. The later suggests greater remobilization of P from thatch tissues to leaf tissues in SA than in EZ. Clipping removal would result in an even faster depletion of the thatch P storage in SA than in EZ, and greater P fertilizer input could be required over time to maintain adequate leaf tissue P levels and sustain new leaf growth in SA.   About 33% of the whole plant N content in a mixture of Kentucky bluegrass (*Poa pratensis* L.) and red fescue (*Festuca rubra* L.) grown under field conditions was allocated to thatch tissue (Starr and DeRoo, 1981). In addition, a substantial amount of the N absorbed by the grass was supplied by mineralization of previously returned clippings (Starr and DeRoo, 1981). The greater apparent remobilization of P from thatch to leaf tissues observed in this study may be related to differences in decomposition rates of thatch tissue between EZ and SA. Remobilization of P from older tissues to actively growing tissues may require depletion of P storage pools and the breakdown of organic P forms present in older tissues (Schachtman et al., 1998). Berndt (2008) observed greater decomposition rates of thatch tissue of ‘Tifdwarf’ bermudagrass [*Cynodon dactylon* (L.) Pers. x *Cynodon transvaalensis* Burtt-Davy] than in ‘Tifeagle’ bermudagrass [*Cynodon dactylon* (L.) Pers. x *Cynodon transvaalensis* Burtt-Davy]. ‘Tifeagle’ bermudagrass had higher stolon mass, greater lignin content and a higher C:N ratio (Berndt, 2008). Diagnosis of the P nutritional status of these turfgrass species should not be based solely on soil tests but it should also include leaf tissue analysis to account for the size of the P storage pool in the thatch layer.

Phosphorus Uptake Rate

Greater P supply increased the leaf growth rate and the P concentration in leaf tissue. As a result, the rate of P accumulation in leaf tissue increased linearly with increasing P supply. Leaf tissue P concentration, clipping yield and P uptake rate of creeping bentgrass (*Agriostis palustris* Huds.) and annual bluegrass (*Poa annua* L.) grown in a pot study, increased with increasing P application raging from 0 to 80 mg P kg^{-1} (Kuo, 1993). Bemudagrass (*Cynodonon dactylon* L. Pers.) forage yield and P uptake increased with increasing rates of P (0 to 263 kg P ha^{-1}) applied as broiler-litter (Sistani et al., 2010).

The PDR from the nutrient solution equates to the whole plant P uptake rate. On the contrary to the rate of P accumulation in leaf tissue over time, PDR from solution is not affected by differences in biomass accumulation rate resulting from a gradient of tissue P concentration. Instead, P concentration in tissue is the main controlling factor of P depletion rate. The later premise is justifiable in this study because the duration of the P depletion rate evaluation period was not long enough (i.e., less than 240 minutes) to yield different plant biomass accumulation among experimental units with different tissue P concentrations. The PDR indicates the instantaneous P uptake rate as a function of tissue P concentration and the leaf P uptake rate represents the long term cumulative P accumulation rate as a function of growth rate and leaf tissue P.

Furthermore, the inverse relationship between PDR and leaf tissue P in EZ suggests that there is a feedback mechanism in this turf species that limits P uptake as the P concentration in tissue approaches the critical for maximum leaf growth rate. Phosphorus may be retranslocated from shoots to roots to send a feedback signal that regulates the uptake of P by roots based on shoot phosphorus demand (Marschner, 1995). The PDR from solution by SA did not change over a wide range of leaf tissue P concentration. Phosphorus deficient SA absorbed P from solution at the same rate of turf with a P concentration in leaf tissue above the critical for maximum leaf growth, indicating that SA has a tendency for luxury P consumption. The continued increase in SA leaf biomass accumulation and associated maintenance of high shoot P demand in response to increasing leaf tissue P, may explain the relative constant PDR observed for this turf species. The later indicates that SA has great potential to uptake excess P from the soil solution which otherwise could be lost to the surrounding environment (i.e., P leaching).

Despite the fact that P uptake dynamics from soil solution under field conditions may be entirely different from those in hydroponic culture (i.e., P in the nutrient solution is in a soluble form, fully available and in direct contact with the root surface), it is necessary to emphasize the importance of the genetic control on P uptake rate depending upon the P nutritional status of the plant. Greater P uptake efficiency will depend on the relative amount of P that the turf can absorb and how fast it can uptake the P from the soil solution while it remains available.

Phosphorus Use Efficiency

Minimum PUE_L and PDR of EZ were reached at leaf tissue P concentrations between 1.58 g P kg^{-1} DM and 1.65 g P kg^{-1} DM which is fairly close to previously reported (Gonzalez, 2010) critical leaf tissue P concentration (1.67 g P kg^{-1}) for this species. In addition, PUE_L of SA reached a minimum at a leaf tissue P concentration of 1.65 g P kg^{-1} and this value is in close agreement with critical leaf tissue P concentration obtained for SA (1.6 g P kg^{-1} and 1.8 g P kg^{-1}) in previous research (Liu et al., 2006; Liu et al., 2008; Gonzalez, 2010). The leaf tissue P at which maximum leaf growth rate is achieved should be fairly close to the leaf tissue P at which the ratio of leaf DM accumulation to P allocated in leaf tissue (PUE_L) reaches a minimum. Our results are in agreement with this argument. Greater $RPUE_L$ of SA over EZ may be due to the greater fraction of total dry matter and P content per unit area that was partitioned to leaf tissue in SA as the P supply increased. St. Augustinegrass showed great ability to maintain high P uptake rates even at high P concentrations in leaf tissue. Consequently, the factor that appears to limit leaf growth rate of SA as the leaf tissue P concentration increases is the associated decrease in the PUE_L.

Sistani et al. (2010) reported a decrease in PUE of bermudagrass (*Cynodon dactylon*) forage in response to increasing rates of P supplied in the form of broiler-litter. Phosphorus use efficiency of 'S-308' wheat (*Triticum* sp.) grown under field conditions decreased 37% by increasing P application rate from 26 kg ha^{-1} to 78 kg ha^{-1} (Sharma and Parmar, 1998). The PUE for top dry matter accumulation of Merion and common Kentucky bluegrass (*Poa pratensis* L.) decreased from 1.74 to 0.61 kg tops DM g^{-1} P uptake in tops tissue with increasing P application rate from 0 to 230 kg P ha^{-1} (Juska et al., 1965). Hylton et al. (1965) observed an inverse relationship between increasing P supply in hydroponic culture and the rate of Italian ryegrass (*Lolium multiflorum* Lam.) DM accumulation per unit of P supplied (mg DM mg^{-1} P). They observed that the change in DM accumulation per unit P supplied reached a minimum at the P supply that corresponded to maximum top growth, hence; minimum PUE was attained at the critical nutrient solution P concentration for maximum top growth.

Tissue P concentration is equivalent to the ratio of P uptake rate to growth rate. The critical leaf tissue P concentration for maximum leaf growth of these turfgrass species would be a function of the plant's ability to withstand greater leaf tissue P concentrations without minimizing the rate of P assimilation it into leaf biomass. Fletcher et al. (2008) observed a quadratic increase in photosynthetic rate (µmol m^{-2} s^{-1}) of 'Challenger' sweet corn (*Zea mays* L.) with increasing specific leaf P concentration (g P m^{-2} leaf).

As previously indicated PUE_L and leaf tissue P were inversely related in both EZ and SA, but PDR only decreased with increasing leaf tissue P in the case of EZ. Greater partitioning of DM to leaf tissue and greater shoot P demand in SA may partially account for the different response of PDR to leaf tissue P concentration between species. On average across treatments SA accumulated 15% more leaf biomass than EZ. The fraction of total PC allocated to leaf tissue was 34% greater in SA than in EZ. At low P concentration in leaf tissue the ability of EZ and SA to growth roots per unit P accumulated in leaf tissue was similar in EZ and SA. At high P supply and leaf tissue P concentration, SA was more efficient than EZ in assimilating P into root tissue. The abrupt decrease in $RPUE_R$ of EZ with increasing leaf tissue P concentration, suggests that this turf species down-regulates root growth under high P supply.

Reduced EZ efficiency to grow roots with increasing leaf tissue P concentration could result in limited ability of this turfgrass species to explore greater soil volumes and scavenge for soil P. This situation would be particularly problematic if P application rate exceeds plant requirements and soil P retention capacity under high precipitation conditions. A more extensive and deeper root system could result in lower P losses to the environment. Bowman et al. (1998) evaluated the influence of root architecture of two genotypes of creeping bentgrass (*Agriostis palustris* Huds.) on NO_3-N leaching. They observed lower concentration and reduce NO_3-N leaching in deep rooted genotypes. Gonzalez (2010) studied the relationship between P application rates to EZ and SA established on an uncoated-sand under field conditions. Significantly greater leaching was measured in EZ than in SA. The difference was attributed to the greater P uptake by SA, which also had a greater and deeper root system.

CONCLUSIONS

Dry matter and P partitioning to leaf tissue increased with increasing P supply in both turf species with the concomitant decrease in the fraction of PC accumulated in thatch tissues. On average across treatments 65.7% of the total P content per unit area of EZ turf was allocated to thatch, 19.7% to leaves and 14.6% to root tissue. In the case of SA, the fraction of total P accumulated per unit area that was allocated to thatch was 57%, 27% to leaves and 16% to root tissue. Leaf tissue P concentration and content were positively related to the P storage in the thatch layer, suggesting that it functions as a P reservoir for actively growing plant tissues. 'Empire' Zoysiagrass reduced ability to synthesize root tissue with increasing leaf tissue P concentration indicates that P fertilization to EZ with adequate P status may increase the risk of P losses.

Phosphorus depletion from the nutrient solution by EZ was inversely related to the P concentration in leaf tissues, but it did not influence PDR in SA. Phosphorus use efficiencies of EZ and SA were inversely related to P supply and P concentration in leaf tissue. Minimum PUE_L was observed at approximately the critical leaf tissue P concentration for maximum leaf growth. Consequently, the reduction in leaf growth rate as the leaf tissue P concentration approached the critical for maximum growth rate appears to be associated with the concomitant decrease PUE_L. Over a wide range of leaf tissue P concentrations PDR from solution $RPUE_L$ and $RPUE_R$ were greater in SA than in EZ.

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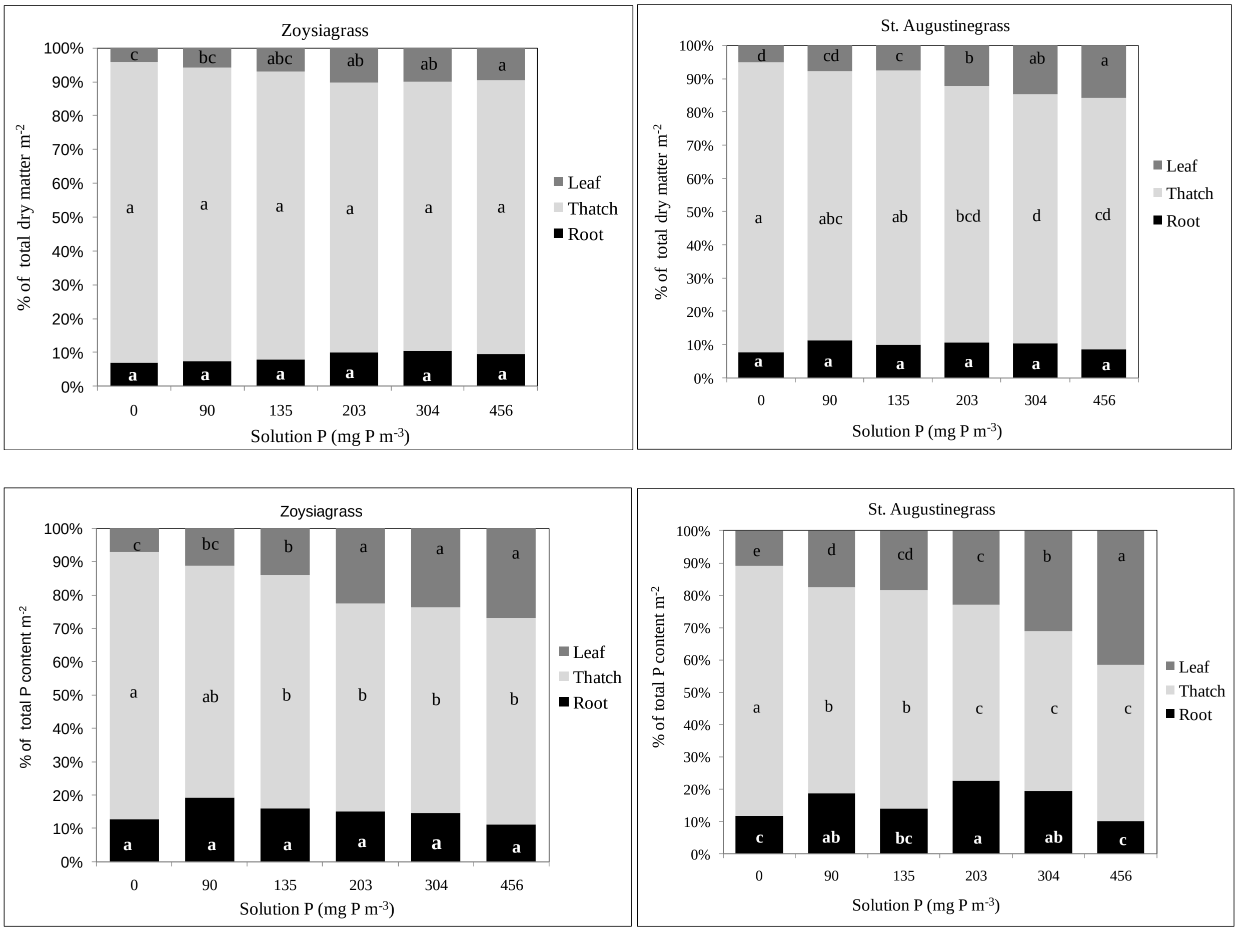

Fig. 1. Partitioning of dry matter and total P content into leaves, thatch and roots relative to solution P concentration. Columns labeled with the same letter within a tissue type (i.e., leaf, thatch or roots) across treatments are not significantly different at $p = 0.05$ by single degree of freedom contrasts analysis.

Table 1. Tissue P concentration and growth parameters relative to P supply.

Turf species	P Rate	Leaf	Thatch	Root	Leaf	Thatch	Root	Leaf growth rate‡	Leaf : Root Ratio
	mg P m^{-3}	------- g P kg^{-1} ------			-----kg DM m^{-2}† -----			g m^{-2} d^{-1}	
EZ§	0	0.23^{e}	0.13^{c}	0.25^{b}	0.26^{c}	5.60	0.44	2.14^{e}	0.62^{b}
	90	0.43^{e}	0.25^{bc}	0.64^{a}	0.45^{b}	6.70	0.57	6.91^{d}	0.83^{a}
	135	0.68^{d}	0.29^{bc}	0.67^{a}	0.46^{b}	5.67	0.52	9.33^{c}	0.89^{a}
	203	0.97^{c}	0.37^{ab}	0.66^{a}	0.53^{a}	4.22	0.52	11.61^{b}	1.03^{a}
	304	1.18^{b}	0.45^{ab}	0.71^{a}	0.53^{ab}	4.18	0.55	12.23^{ab}	0.96^{a}
	456	1.85^{a}	0.60^{a}	0.72^{a}	0.49^{b}	4.20	0.49	13.16^{a}	1.03^{a}
SA¶	0	0.50^{d}	0.21^{c}	0.35^{d}	0.26^{e}	4.61	0.40	2.37^{d}	0.77^{c}
	90	0.86^{c}	0.30^{bc}	0.63^{c}	0.36^{d}	3.75	0.52	6.57^{c}	0.69^{c}
	135	1.00^{c}	0.35^{ab}	0.56^{c}	0.43^{d}	4.77	0.57	9.39^{b}	0.77^{c}
	203	0.91^{c}	0.34^{ab}	1.02^{b}	0.57^{c}	3.62	0.49	10.67^{b}	1.16^{b}
	304	1.32^{b}	0.41^{a}	1.17^{a}	0.69^{b}	3.53	0.48	12.99^{a}	1.44^{b}
	456	1.79^{a}	0.44^{a}	0.83^{a}	0.85^{a}	4.08	0.46	13.00^{a}	1.86^{a}

Data values within a given column and turfgrass species followed by the same letter are not significantly different at p=0.05 by single degree of freedom contrast analysis.

†Dry matter (DM) accumulation per plant tissue type at the end of the growth season.

‡Leaf growth rate during the season's period of highest growth rate.

§EZ= Empire Zoysiagrass.

¶SA= Floratam St. Augustinegrass.

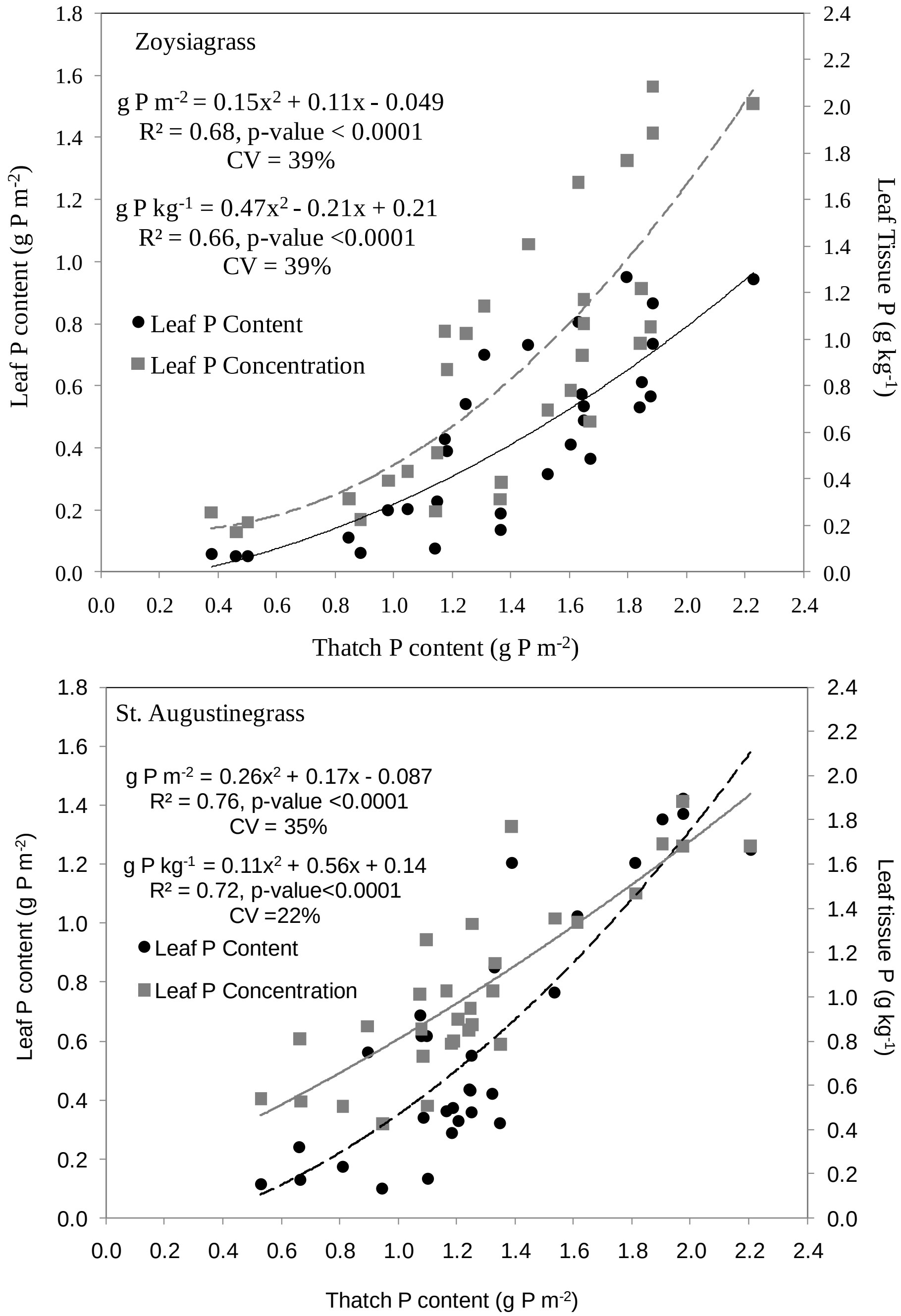

Fig. 2. Relationship between P content and P concentration in leaf tissue and phosphorus storage in the thatch layer of ‘Empire’ zoysiagrass (top) and ‘Floratam’ St. Augustinegrass (bottom).

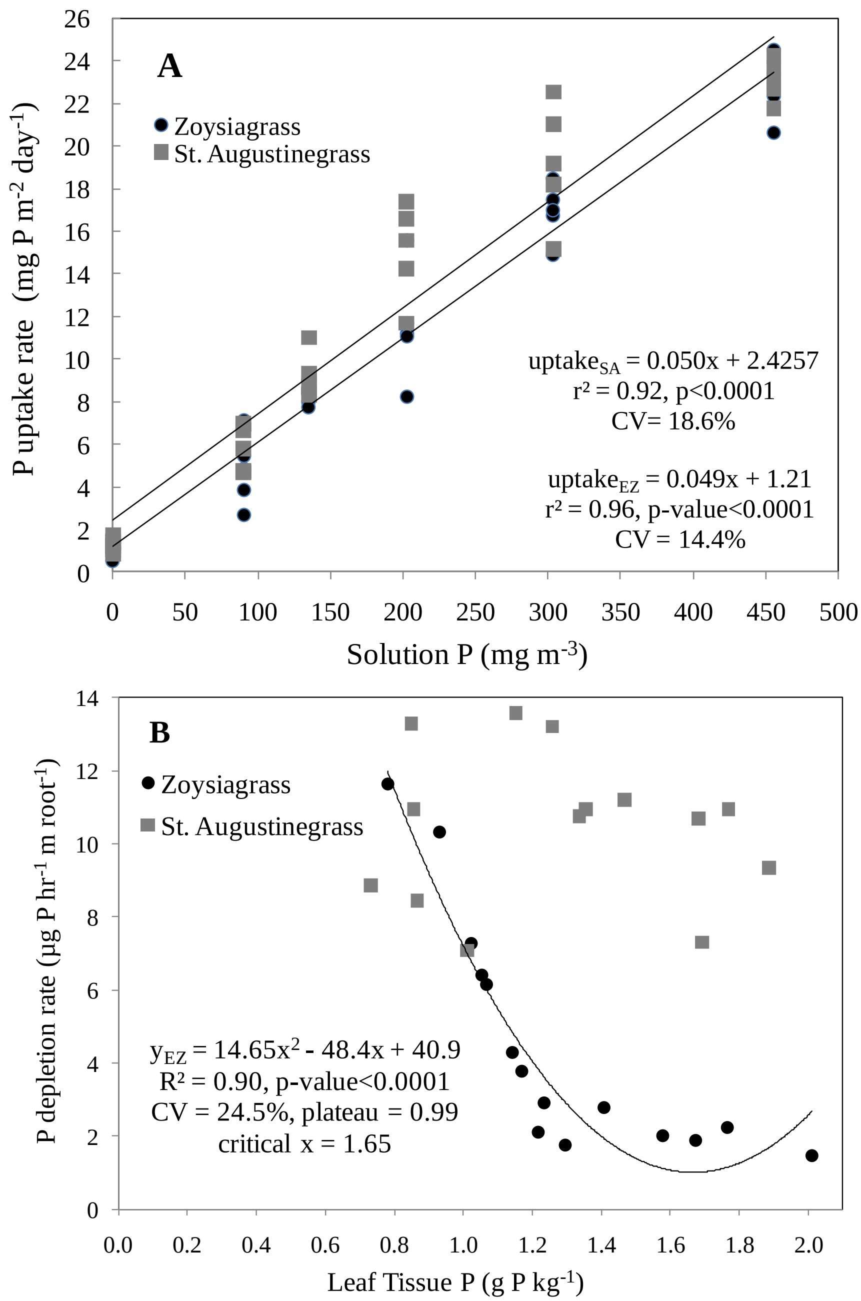

Fig. 3. Phosphorus uptake rate in leaf tissue as a function of nutrient solution P concentration (A) and P depletion rate from the nutrient solution as a function of leaf tissue P concentration (B) in ‘Empire’ zoysiagrass (EZ) and ‘Floratam’ St. Augustinegrass (SA).

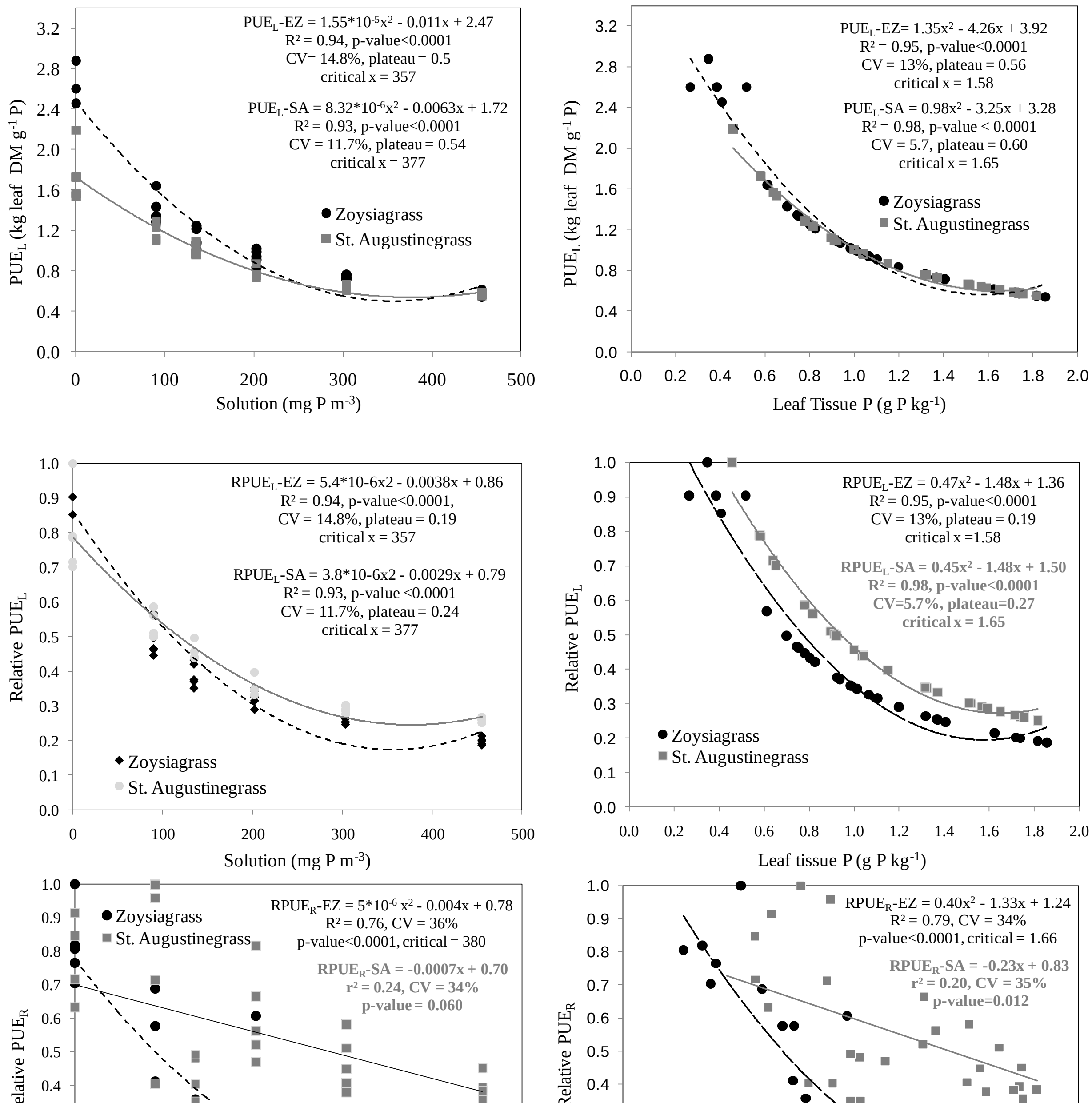

Fig. 4. Phosphorus use efficiency for leaf tissue growth (PUE_L) and relative PUE for leaf tissue ($RPUE_L$) and root tissue ($RPUE_R$) growth as influenced by phosphorus concentration in the nutrient solution and leaf tissue P concentration in 'Empire' zoysiagrass (EZ) and 'Floratam' St. Augustinegrass (SA).

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