Effect of phosphorus and potassium on gas exchanges of *Tachigali vulgaris*

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Abstract

*Tachigali vulgaris* L. G. Silva & H. C. Lima is a pioneer species with great potential for reforestation. The inadequate supply of phosphorus and potassium results in nutritional disorders, requiring nutritional complementation. This study aimed to evaluate the effect of phosphorus (P) and potassium (K) doses on *Tachigali vulgaris* gas exchange. Three doses of P (0, 26.7 and 53.5 kg·ha⁻¹) and three doses of K (0, 50 and 100 kg·ha⁻¹) were applied in a 3x3 factorial scheme as randomized block design. The data were submitted to analysis of variance using the Tukey 1% test and Pearson’s linear correlation test. Potassium fertilization provided increases of approximately 30% in the rate of liquid photosynthesis (Pₜ), stomata conductance (Gₛ), internal CO₂ concentration (Ci), perspiration (E), instantaneous caboxilation efficiency (ΦC), water use efficiency (EWU) and intrinsic water use efficiency (iEWU) were also favored at dose of 78.2 g kg⁻¹ K, suggesting their role in regulating essential physiological processes for plant growth. The highest Pₜ values were observed with application of 33.1 g kg⁻¹ P and 78.2 g kg⁻¹ K, with rates of 4.28 and 4.86 μmol CO₂ m⁻² s⁻¹ respectively, which also occurred with E, ΦC, EWU and iEWU. It was observed that P exerted antagonistic effects on K absorption, which may also have impaired Mg²⁺ absorption due to the fact that Ca²⁺ is an accompanying ion of potassium fertilizer.

Keywords: Efficiency of water use, Forest sustainability, Mineral fertilization, Photosynthesis rate, Stomatal conductance.

Abbreviations: Ci_Internal CO₂ concentration, E_Transpiratory rate, EWU_Water use efficiency, Gₛ_Stomatal conductance, iEWU_Intrinsic efficiency of water use, IRGA_Infrared gas analyzer, Lₛ_Leaf temperature, PAR_Photosynthetically active radiation, Pₚₜ_Net photosynthetic rate, ΦC_Instant carboxylation efficiency.

Introduction

Increasing the availability of water and nutrients accelerates forest stand growth by increasing leaf area, photosynthetic capacity (Munger et al., 2003) and plant tolerance to different conditions, including stresses (Shahabifar et al., 2019, Wu et al., 2019), which favors storage of primary metabolism and production of secondary metabolism substances (Gonçalves et al., 2012). Inadequate supply of an essential element results in nutritional disorders (Taiz and Zeiger, 2013). Therefore, nutritional complementation is one of the determining factors for success in reforestation projects.

To understand the factors that control the growth of forests and the use of natural resources, several studies have already been conducted (Hubbard et al., 2004, Yin et al., 2004, Teixeira et al., 2008, Machado et al., 2010, Ferreira et al., 2012). The efficiency of resource use, constitutes an important index for the definition of management practices that increase productivity and sustainability, since the final production of wood is the result of the interaction of genotype and environment. However, there are few works dealing specifically with fertilization management, with the perspective of increasing the efficiency of use by planted forests.

The species *Tachigali vulgaris* L. G. Silva & H. C. Lima, Fabaceae, occurs throughout the Amazon region, up to the western states of Bahia, Minas Gerais, Goiás and Mato Grosso (Silva et al., 2002, Saporetti Junior et al., 2003). It is a pioneer species that frequently initiates secondary succession in open areas (Carvalho, 1994), being considered ideal for reforestation due to its high biomass production capacity (Felfili et al., 1999), rapid growth in adverse conditions and high resistance to environmental disturbances. According to Freitas et al. (2012), *T. vulgaris* plants can be indicated for use in degraded area recovery projects, both for full sun conditions and for 50% seedling shading. Farias et al. (2016), found that *T. vulgaris* performed better than the eucalyptus in a reforestation experiment in a degraded area, with a three times higher survival and growth rate, in addition to additional benefits, such as double the production of burlap and lower growth of invasive grasses.

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Among essential macronutrients, phosphorus is one of the most striking due to its low availability in the soil, a condition resulting from the presence of kaolinite, Fe and Al oxides, and acidity conditions, which is normally observed in the field. The adequate availability of phosphorus is fundamental from the initial stages of plant development, where the subsequent compensation is not effective (Zucarello et al., 2006). Leguminous forest species are highly responsive to phosphate fertilization, where phosphorus deficiency results in decreased amounts of leaves and nodules and lower photosynthetic efficiency and biological fixation of atmospheric N (Chaudhary et al., 2008).

Potassium is the second most extracted nutrient by plants and seeds, having important functions, including increasing the tolerance of plants to different stresses (Zamani et al., 2020), despite remaining in ionic form within the plant. It acts in the regulation of physiological processes, such as enzymatic activation, cation/anion balance, sodium transporters and hydrogen pump (hydrogen-ATPases), opening and closing of stomata, sugar transport, protein synthesis and ATP production (Almeida et al., 2007; Zamani et al., 2020).

Therefore, the study of the ecophysiological strategies related to the use of physical resources, which is adopted by trees, is necessary to improve the management techniques of planted forests and to subsidize the assessment of the most efficient species and genotypes. In addition, definition of management practices may increase the productivity and sustainability of forest plantations. This work aimed to evaluate the effect of phosphorus and potassium fertilization on gas exchange in T. vulgaris plantations, considering the determining role of gas exchange for the understanding of carbon dynamics in the forest ecosystem.

Results

**Net photosynthesis rate**

For the rates of net photosynthesis per unit leaf area (Pa), there was a significant effect (p<0.01) for the factors doses of P and doses of K, as well as their interaction (PxK). The highest averages for Pa were found in treatments P,K (33.1 g kg⁻¹ P and 13 g kg⁻¹ Ca) and P,K (78.2 g kg⁻¹ K and 78 g kg⁻¹ Cl), with values 4.28 and 4.86 mmol CO₂ m⁻² s⁻¹, respectively, which differed statistically from the other treatments (Table 3 and Fig. 3A). It was observed that the highest mean values of Pa was occurred in the treatments with the highest doses of superphosphate and potassium chloride (Fig. 3A). The Pa was correlated positively and significantly (p<0.01), with Ci (0.593), E (0.507), Cl (0.771), EWU (0.852), iEWU (0.712), φC (0.997) and Lt (-0.375) using the T test (Table 4).

**Stomatal conductance**

There was a significant effect on Gs, with regard to the influence of P and K doses, in addition to the interaction of factors (PxK) (p <0.01). The highest averages of Gs were found in treatments P,K (without fertilizer application), P,K (39.1 g kg⁻¹ K and 39 g kg⁻¹ Cl) and P,K (33.1 g kg⁻¹ P, 78.2 g kg⁻¹ K, 13 g kg⁻¹ Ca and 78 g kg⁻¹ Cl), with the values of 0.36, 2.26 and 0.37 mol H₂O m⁻² s⁻¹, respectively (Fig. 3B). According to the values of Pearson's correlation coefficients, the Gs presented positive and significant correlations at the level of 1% probability of error with Pa (0.593), E (0.977), φC (0.65) and Lt (-0.648), by the T test (Table 4).

**Transpiratory rate**

There was a significant effect on Ev, regarding the influence of P and K doses, in addition to the interaction of factors (PxK) (p<0.01). The highest mean for E was found with the P2K2 treatment P2K2 (33.1 g kg⁻¹ P, 78.2 g kg⁻¹ K, 13 g kg⁻¹ Ca and 78 g kg⁻¹ Cl), with the value of 5.22 mmol H₂O m⁻² s⁻¹ (Fig. 3C). Analysis of Pearson's correlation coefficients appeared that E was positively and significantly correlated to the 1% probability of error with Pa (0.507), Gs (0.977), φC (0.57) and Lt (-0.618) by the T test.

**Internal CO₂ concentration**

There was a significant effect on the Ci of the factors P and K, in addition to the interaction between them (PxK) (p<0.01). The highest averages of Ci were found in treatments P,K (33.1 g kg⁻¹ P and 13 g kg⁻¹ Ca) and P,K (16.6 g kg⁻¹ P, 78.2 g kg⁻¹ K, 6.5 g kg⁻¹ Ca and 78 g kg⁻¹ Cl), resulting in 136.96 and 139.64 µmol CO₂ m⁻² s⁻¹, respectively (Fig. 3D). The Ci showed positive and significant correlations with Pa (0.77), φC (0.57) and Lt (-0.618) at 1% probability.

**Water use efficiency**

There was a significant effect on the EWU, concerning the influence of P and K doses, in addition to the interaction of factors (PxK) (p<0.01). The treatments P,K (78.2 g kg⁻¹ K and 78 g kg⁻¹ Cl) and P,K (16.6 g kg⁻¹ P, 78.2 g kg⁻¹ K, 6.5 g kg⁻¹ Ca and 78 g kg⁻¹ Cl), presented the highest averages of EWU, with the values of 0.9531 and 0.9709 µmol CO₂ mmol⁻¹ H₂O, respectively (Fig. 3F). In relation to Pearson's correlation coefficients (Table 4), it appeared that the EWU correlated positively and significantly with Pa (0.852), Ci (0.977), φC (0.812) and iEWU (0.965).

**Intrinsic efficiency of water use**

A significant effect on iEWU was observed, reagarding the influence of P and K doses, in addition to the interaction of factors (PxK) (p<0.01). The highest averages were found in the P,K treatment (16.6 g kg⁻¹ P, 78.2 g kg⁻¹ K, 6.5 g kg⁻¹ Ca and 78 g kg⁻¹ Cl), with the values of 15.19 mmol m⁻² s⁻¹ H₂O (Fig. 3G). The iEWU correlated positively and significantly with Pa (0.712), Ci (0.977), φC (0.661) and EWU (0.965) (Table 4).

**Instant carboxylation efficiency**

There was a significant effect on φC regarding the influence of P and K doses, in addition to the interaction of factors (PxK) (p <0.01). The highest mean for the variable was found with the P2K2 treatment (78.2 g kg⁻¹ K and 78 g kg⁻¹ Cl), resulting in 0.0353 (µmol m⁻² s⁻¹ Pa⁻¹) (Fig. 3E). We found that the φC correlated positively and significantly with Pa (0.997), Gs (0.65), Ci (0.722), E (0.57), EWU (0.812), iEWU (0.965) and Lt (-0.417).

**Leaf temperature**

There was a significant effect on the Lt of the doses of P, K and the interaction of factors (PxK) (p <0.01). The Lt means...
were statistically equal to each other, with no difference between treatments, ranging from 25.1 to 26.8 °C (Fig. 3H).

The $L_t$ showed positive and significant values correlations with $P_{hi}$ ($-0.375$), $G_2$ ($-0.648$) and $\Phi C$ ($-0.417$) at the level of 1% probability of error, by the T test.

**Discussion**

The high $P_{hi}$ rates of *T. vulgaris* plants corroborate the values of $G_2$ (Fig. 3B), which also reflected on higher rates of $E$ on the plants under higher doses of $K$ (Fig. 3C). In a study by Gazola et al. (2019), the dose of 180 kg ha$^{-1}$ of $K_2O$ provided the highest total biomass values, with an increase of 18.2% compared to the control, which translated into high photosynthetic rates. Silva et al. (2012) evaluated the impacts of fertilization on eucalyptus plantations in the initial growth stage in Quartzarenic Neosol for 24 months, and found that the group that received the highest dose of fertilizer had 50% more biomass, compared to the other groups. Studies show that fast-growing forest species respond to $K$ fertilization in the leaf area index (Christina et al., 2015, Epron et al., 2011, Inocêncio et al., 2014), increasing the efficiency of the use of light in forest plantations.

Thus, fertilization with $K$ can favor a greater intensity of interception of sunlight and photosynthetic processes, which in turn, result in greater growth. This effect is also due to the functions performed by $K$ in the plant, including the regulation of the osmotic potential of plant cells, controlling the opening and closing of stomata, resulting in greater efficiency in the use of water (Siddiqui et al., 2008, Taiz and Zeiger, 2013).

Photosynthetic activity can be affected by non-stomatal factors that have a biochemical origin (Farquhar and Sharkey, 1982). This aspect can be studied when considering $\Phi C$, which is given by the relationship between photosynthesis and intracellular $CO_2$ concentration (Zhang et al., 2001). Photosynthesis is usually reduced by $P$ deficiency (Turnbull et al., 2007) because there is a requirement for a balanced concentration of orthophosphate (Pi) in the cytosol (Walker and Robinson, 1978). The clear limitation of photosynthesis by cytosolic Pi was demonstrated in *Eucalyptus globulus* sequestering cytosolic Pi with mannose, when Pi was kidnapped with mannose, the maximum rate of photosynthesis was reduced by 83% (Turnbull et al., 2007).

Person's correlations show that the greater $P_{hi}$ leads to the greater values of $G_2$, $E$, $Ci$, $EWU$, $JEWU$ and $\Phi C$. In the case of $L_t$, the results indicate that the lower the $P_{hi}$ value causes a higher leaf temperature. The regulation of stomatal opening through the absorption and release of $K^+$ is among the main mechanisms for controlling water loss by plants (Maathuis, 2009). Similar behavior can be observed with the management of fertilization, corroborating the high correlation found between the variables $P_{hi}$ and $\Phi C$, in which the highest photosynthetic rates were accompanied by the highest values of instantaneous carboxylation efficiency (Fig. 3A and 3E).

The highest $G_2$ value was found in the treatment with the maximum doses of $P$ and $K$, which presented an average of 0.37 mol H$_2$O m$^{-2}$ s$^{-1}$ (Fig. 3B). In an ecophysiological context, the way in which $P_{hi}$ and gas are related is extremely important. Since these two physiological variables vary proportionally, they allow $Ci$ and $EWU$ to remain at adequate levels, enabling the optimization of gas exchange and controlling absorption of carbon dioxide, which are essential in the formation of compounds from photosynthesis. In fact, there was a positive and significant correlation between $G_2$ and $P_{hi}$, $E$ and $\Phi C$, indicating the existence of interdependence between the variables in question. The growth performance of plants can be improved by the supply of $K$ through an improvement in stomatal movements (Lebady et al., 2008), mesophyll conductance (Longstreth and Nobel, 1980), chlorophyll synthesis (Onanuga et al., 2012) and assimilation and export to leaves (Zhao et al., 2001, Jin et al., 2011). The observed reduction in $G_2$, besides implying a drop in $CO_2$ assimilation, also affects $E$ (Fig. 3C), since both are diffusive processes and lead to a reduction in the production of photoassimilates. During gas exchange, the absorption of carbon dioxide from the external environment promotes water loss and the reduction of this loss also restricts the entry of $CO_2$ (Shimazaki et al., 2007). This interdependence expressed by the relationship between photosynthesis and transpiration indicates the $EWU$, in which the observed values relate to the amount of carbon that the plant fixes for each unit of evapotranspired water (Jaimez et al., 2005, Taiz and Zeiger, 2013). This process is influenced by climatic conditions. However, the adequate nutritional supply tends to promote higher photosynthetic rates, implying higher yields (Melo et al., 2009).

Therefore, plants that are well supplied with $K$ have higher $EWU$, which would result in an increase in the useful life of the leaves (Silva et al., 2002, Laclau et al., 2009), and consequently can increase the production of biomass. $P$ supplementation may be related to an accumulation of proline, which is an osmotic adjuster. This could influence the osmotic regulation of stomatal guard cells, favoring the maintenance of cell turgor (Zamani et al., 2020).

It was observed that $Ci$ showed a high correlation with $P_{hi}$ and $EWU$, with similar behavior in treatments with the application of intermediate doses of $P$, while the highest overall average found by interaction with treatments with the application of the highest doses of $K$, resulting in a value of 136.87 μmol $CO_2$ m$^{-2}$ s$^{-1}$. Mori et al. (2018), evaluated the fertilization with potassium and magnesium in Acacia mangium planting and found that the quantity of soil nutrients were not affected by the triple superphosphate fertilization. However, the fertilizer application increased the Mg content in the leaves. Mg is necessary in other physiological processes, in addition to its function in the photosynthetic process as a structural component of chlorophyll. In most cases, the involvement of Mg in metabolic processes depends on the activation of numerous enzymes, such as ribulose-1,5-bisphosphate (RuBP) carboxylase, a key enzyme in the process of photosynthesis and the most abundant on the planet. Several scientific studies report that a small reduction in leaf magnesium content has a significant impact on the photosynthetic rate (Farhat et al., 2016, Marschner, 2012). According to Mulder’s chart, $P$ has antagonistic effects on $K$ uptake and synergistic on Mg uptake, and Ca has antagonistic effects on K and Mg uptake (Crous et al., 2015). Following this theory, fertilization with $P$ (and Ca as an accompanying ion) in plantations with fast-growing forest species can influence the harvest, reducing K uptake and increasing or reducing Mg uptake.
Table 1. Chemical and physical attributes of the soil in the experimental area up to 1.2 meters deep, determined before the experiment was implemented.

| Soil layer (cm) | pH  | K⁺ | Ca²⁺ | Mg²⁺ | Al³⁺ | H⁺Al³⁺ | SB | CEC | P   | V  | O.M. | Granulometry |
|-----------------|-----|----|------|------|------|--------|----|-----|------|----|------|-------------|
| (cm)            | (CaCl₂) | (cmol/dm³) | (mg/dm³) | % | % | (g/kg) |    |     |      |    |      | Sand  Silt Clay |
| 0-20            | 4.1 | 0.041 | 0.2 | 0.1 | 0.4 | 2 | 5.9 | 2.34 | 3 | 15 | 1.2 | 170  140 690 |
| 20-40           | 4   | 0.021 | 0.2 | 0.1 | 0.6 | 2.2 | 4.2 | 2.52 | 2 | 13 | 0.5 | 230  80 690 |
| 40-60           | 4   | 0.01  | 0.2 | 0.1 | 0.6 | 2.2 | 4.2 | 2.51 | 2 | 12 | 0.5 | 270  130 600 |
| 60-80           | 4.1 | 0.01  | 0.2 | 0.1 | 0.5 | 2 | 4.6 | 2.31 | 1 | 13 | 0.5 | 270  150 580 |
| 80-100          | 4.1 | 0.01  | 0.2 | 0.1 | 0.4 | 2 | 5.8 | 2.31 | 4 | 13 | 0.5 | 290  150 560 |
| 100-120         | 4.1 | 0.031 | 0.2 | 0.1 | 0.4 | 1.8 | 5.3 | 2.13 | 1 | 16 | 0.5 | 370  120 510 |

pH = hydrogenionic potential, K⁺ = potassium, Ca²⁺ = calcium, Mg²⁺ = magnesium, Al³⁺ = aluminium, H⁺Al³⁺ = hydrogen and aluminium, SB = sum of bases, CEC = cation exchange capacity, P = phosphorus, V = base saturation, O.M. = organic matter. The levels of K, Na, Ca and Mg, exchangeable in the soil were determined by atomic absorption spectrophotometry and flame spectrophotometry (Raij et al., 2000).

Fig 1. Monthly rainfall (mm), maximum, average and minimum monthly temperatures (°C), at the experiment site, during the period of evaluation of the planting of T. vulgaris in Igarapé-azu, PA.

Table 2. Amounts of fertilizers applied (commercial products) and amount of nutrients actually offered, per treatment, to establish the factorial test for the planting of T. vulgaris.

| Treatments | Fertilizers applied | Effectively provided nutrients |
|------------|---------------------|--------------------------------|
|            | TSP                | KCl                           | P2O5 | P | K2O | K | Ca | Cl |
| P₀K₀       | 0                   | 0                | 0    | 0 | 0   | 0 | 0  | 0  |
| P₀K₁       | 0                   | 0                | 0    | 0 | 50  | 39.1 | 0 | 39 |
| P₀K₂       | 0                   | 0                | 0    | 0 | 100 | 78.2 | 0 | 78 |
| P₁K₀       | 65.2                | 0                | 26.7 | 16.6 | 0  | 0   | 6.5 | 0  |
| P₁K₁       | 65.2                | 100              | 26.7 | 16.6 | 50 | 39.1 | 6.5 | 39 |
| P₁K₂       | 65.2                | 200              | 26.7 | 16.6 | 100| 78.2 | 6.5 | 78 |
| P₂K₀       | 130.4               | 0                | 53.5 | 33.1 | 0  | 0   | 13  | 0  |
| P₂K₁       | 130.4               | 100              | 53.5 | 33.1 | 50 | 39.1 | 13 | 39 |
| P₂K₂       | 130.4               | 200              | 53.5 | 33.1 | 100| 78.2 | 13 | 78 |

TSP: Triple superphosphate, KCl: Potassium chloride
Fig 2. Schematic representation of the plots (A), biomass sampling performed with bordering plants (B) soil collection sites for fertility assessment performed inside the sampling unit, at 12 (C-1) and 24 months (C-2), Igarapé-açu, PA.

Table 3. Average results of gas exchange variables in T. vulgaris planting, submitted to fertilization doses with phosphorus and potassium.

| Doses of K | Doses of P | 0 | 100 | 200 | Average (1) |
|------------|------------|---------------|----------------|---------------|---------------|
| 0          | P<sub>K</sub> (1) | P<sub>K</sub> (2) | P<sub>K</sub> (3) | P<sub>K</sub> (4) |
| 0          | 2.96 aB     | 1.65 aA       | 4.86 bC         | 3.16 a     |
| 65,22      | 3.43 aB     | 2.26 ba       | 3.69 aB         | 3.13 a     |
| 130,43     | 4.28 bc     | 2.19 ba       | 3.81 aB         | 3.43 a     |
| Average (B)| 3.76 b      | 2.03 a        | 4.12 c          |             |
| 0          | g<sub>Q</sub> (1) | g<sub>Q</sub> (2) | g<sub>Q</sub> (3) | g<sub>Q</sub> (4) |
| 0          | 0.36 bB     | 0.26 ba       | 0.35 bB         | 0.32 b     |
| 65,22      | 0.27 aB     | 0.18 aA       | 0.24 aB         | 0.23 a     |
| 130,43     | 0.33 bb     | 0.25 bA       | 0.37 bB         | 0.32 b     |
| Average (C)| 0.32 b      | 0.23 a        | 0.32 b          |             |
| 0          | Ci (1)      | Ci (2)        | Ci (3)          | Ci (4)     |
| 0          | 126,32 aA   | 123,45 aA     | 137,53 aBb      | 129,11 a   |
| 65,22      | 135,12 bA   | 134,34 bA     | 139,64 bB       | 136,37 b   |
| 130,43     | 136,96 bB   | 129,05 abA    | 133,45 aA       | 133,15 ab  |
| Average (D)| 132,81 a    | 128,95 a      | 136,87 b        |             |
| 0          | E (1)       | E (2)         | E (3)           | E (4)      |
| 0          | 5,58 bB     | 4.19 ba       | 5.09 bBA        | 4.95 b     |
| 65,22      | 4.06 ac     | 3.23 aA       | 3.81 aB         | 3.69 a     |
| 130,43     | 5.01 bb     | 4.01 ba       | 5.22 bc         | 4.75 b     |
| Average (E)| 4.88 b      | 3.91 a        | 4.71 b          |             |
| 0          | φ<sub>C</sub> (1) | φ<sub>C</sub> (2) | φ<sub>C</sub> (3) | φ<sub>C</sub> (4) |
| 0          | 0.0234 aAB  | 0.0134 aA     | 0.0353 bB       | 0.0240 a   |
| 65,22      | 0.0254 aB   | 0.0168 bA     | 0.0264 aB       | 0.0228 a   |
| 130,43     | 0.0312 bB   | 0.0171 bA     | 0.0286 aB       | 0.0256 a   |
| Average (F)| 0.0267 b    | 0.0157 a      | 0.0301 c        |             |
| 0          | EWU (1)     | EWU (2)       | EWU (3)         | EWU (4)    |
| 0          | 0.5313 aB   | 0.3948 aA     | 0.9531 bC       | 0.6265 a   |
| 65,22      | 0.8445 bB   | 0.7019 cA     | 0.9709 bC       | 0.8391 b   |
| 130,43     | 0.8541 bB   | 0.5481 bA     | 0.7338 aB       | 0.7119 a   |
| Average (G)| 0.7434 b    | 0.5482 a      | 0.8859 b        |             |
| 0          | IEWU (1)    | IEWU (2)      | IEWU (3)        | IEWU (4)   |
| 0          | 8.22 aB     | 6.14 aA       | 13.71 bC        | 9.35 a     |
| 65,22      | 12.36 ba    | 12.42 ca      | 15.19 cB        | 13.33 b    |
| 130,43     | 12.61 bC    | 8.77 ba       | 10.12 aB        | 10.51 a    |
| Average (H)| 11.06 b     | 9.11 a        | 13.01 b         |             |
| 0          | L<sub>1</sub> (1) | L<sub>1</sub> (2) | L<sub>1</sub> (3) | L<sub>1</sub> (4) |
| 0          | 25.23 aA    | 25.49 aA      | 25.16 aA        | 25.29 a    |
| 65,22      | 25.11 aA    | 26.83 aA      | 26.11 aA        | 26.01 a    |
| 130,43     | 25.93 aA    | 26.57 aA      | 25.84 aA        | 26.11 a    |
| Average (I)| 25.42 a     | 26.29 a       | 25.71 a         |             |

(1) Average values in the absence of interaction between the treatments of P and K, and the means followed by the same letter did not differ by 1% by the Tukey test. (2) Mean values in the significant interaction between the treatments of P and K, and the means accompanied by lower case letters in the same column (P) and upper case letters in the same line (K) do not differ by 1% by the Tukey test.
However, the effects of P (and Ca) fertilization on Mg and K acquisitions have been tested mainly on agricultural crops and there are no reports on tree species plantations, despite the importance of assessing nutrient loss from plantation soils during the harvest.

Initially, it should be noted that the climatic conditions during the evaluation period (Figure 1) favored an increase in the content of water stored in the soil, with no water limitation for the growth of the trees. The results show that the intermediate dose of P together with 39.1 g kg$^{-1}$ and 78.2 g kg$^{-1}$ of K has the best results on EWU, as well as for $iEWU$. These treatments also showed reduced $E$ rates. During gas exchange, the absorption of carbon dioxide from the external environment promoted water loss and the reduction of this loss also restricts the entry of CO$_2$ (Shimazaki et al., 2007).

This interdependence expressed by the relationship between $P_N$ and $E$ indicates the efficiency in use of water, in which the observed values relate to the amount of carbon that plant fixes for each unit of evapotranspired water (Jaimez et al., 2005, Taiz and Zeiger, 2013).

Such interdependence was observed in high Pearson correlation coefficients between the variables $P_N$, $Ci$, $ΦC$ and $iEWU$. This process is influenced by climatic conditions. However, the adequate nutritional supply tends to promote higher photosynthetic rates, implying higher yields (Melo et al., 2009). Several studies show that potassium fertilization allows a considerable increase (up to 100%) in EWU, as reported by Stape et al. (2004), Binkley et al. (2004), Almeida et al. (2007) and Teixeira et al. (2008), working with Eucalyptus grandis. Ferreira et al. (2012), evaluating young plants of Bertholletia excelsa Humb. & Bonpl. subjected to green abdution and found EWU values close to 3.5 µmol CO$_2$ mmol$^{-1}$ H$_2$O. In order to restrict water loss through transpiration, the stomatal closure mechanism can be considered an adaptive strategy used by different species to limit water loss and to exceed water deficiency, as was verified for the woody species Tabebuia aurea Benth. & Hook. f ex S. Moore (Cabral et al., 2004) and Minquartia guianensis Aubl. (Liberato et al., 2006). The information in the literature suggests that the higher productivity in response to K is directly related to the fact that this element...
activates numerous enzymes and also participates as an intracellular solute in the stoma opening and closing process, regulating the process of carbon assimilation and water loss, increasing turgor and leaf expansion, providing greater use of solar radiation.

The instantaneous carboxylation efficiency showed a reduction of approximately 30% in the mean values in the control compared to the P0K0 treatment, which showed the best result. This reduction followed the behavior of the other physiological variables (Pn, Gs, Ci, E, EWU and iEWU). This was also observed by Nascimento et al. (2014) in the species Hymenaea courbaril L. in response to the omission of P. In an ecophysiological context, the way in which Pn and Gs are related is extremely important. As these two physiological variables vary proportionally, they allow Ci and the EWU remain at adequate levels, enabling the optimization of gas exchange and controlling the absorption of carbon dioxide, which is essential in the formation of compounds resulting from photosynthesis (Simões et al., 2018).

For Lc, there was a negative and significant correlation of this variable with some of the physiological variables studied (Pn, Gs, E and Qc). Nascimento et al. (2014) evaluated the species Hymenaea courbaril L. in response to suppression of N, P and K. They found that the absence of nitrogen resulted in a significant increase in leaf temperature compared to suppression of P and K. Aspects such as the reduction in transpiration, a consequence of the reduction in stomatal conductance (smaller stomatal opening), restricts heat dissipation together with the loss of water vapor (Taiz and Zeiger, 2013). Considering the microclimate conditions of planting, in which the canopy is formed, the results show mild temperatures in the middle third of the plants, as a result of the greater retention of solar radiation in the upper third of the planting.

**Materials and methods**

**Experimental site**

The experiment was installed in March 2016 at Fazenda Escola de Igarapé-Açu (FEIGA), an experimental station at the Federal Rural University of the Amazon (UFRA), which is located in the municipality of Igarapé-Açu, State of Pará, Brazil (01°07′33″ S, 47°37′27″ W). The region’s climate falls under the category of wet megathermic, type Am of the Köppen classification, with annual average temperature of 25°C, relative humidity of 85% and precipitation of 2350 mm, with a strong concentration between the months of January to June and rarer from July to December (Hohnwald et al., 2019, Ramos et al., 2009). At the site of the experiment, a meteorological station was installed that collected climatic data during the planting evaluation period (Fig 1).

The experimental area has a flat relief and the soil was classified as dystrophic Red-Yellow Latosol, medium texture (266 g kg⁻¹ of clay) (Embrapa, 1999). Before installation of experiment, the chemical and physical attributes of the soil were characterized up to 1.2 meters depth in the Soil Analysis Laboratory of Embrapa Amazônia Oriental, in Belém, State of Pará (Table 1). Soil samples were collected randomly throughout the planting area to remove the composite samples. Although the acidity levels were high (Raij, 1991), we decided not to use limestone to correct the soil, considering the possibility of evaluating the growth potential of *T. vulgaris* with fertilizers under acidic conditions.

**Experiment installation and conduction**

After 30 days of implantation of the experiment, the planting of *T. vulgaris* was submitted to phosphate and potassium fertilization through the application of three doses of P (0, 26.7 and 53.5 kg ha⁻¹), in the form of superphosphate) triple) and three doses of K (0, 50 and 100 kg ha⁻¹, in the form of potassium chloride), as well as their combinations, in a 3x3 factorial scheme (Table 2). The fertilizer doses were defined according to recommendations for fast growing forest species in clayey soils of medium texture (Silveira et al., 2001, Andrade, 2004, Arco-verde et al., 2005), which were divided into two more applications, during the first year of cultivation, at 6 and 12 months.

The planting area was divided into four blocks, five meters apart, in order to maximize the effect of treatments on each plot. Each block was divided into nine plots (treatments), with an area of 80 m² (10 x 8 m), containing 16 plants in the 3 x 2 m spacing (Figure 2). The external line of each plot served as a border, so the useful area for evaluations was formed by the 4 central trees of each plot. The experimental design was in randomized blocks, with four replications, totaling 36 plots.

**Gas exchange analysis**

The gas exchange evaluations were carried out in April 2018, on fully expanded and mature leaves, in the middle third of the treetops, between 9:00 am and 11:00 am, representing the period when photosynthesis reaches its maximum values determined from the daytime leaf gas exchange curves. The net photosynthetic rate (Pn), stomatal conductance (Gs), transpiratory rate (E) and internal CO₂ concentration (Ci), were calculated using the values of the variations in CO₂ and H₂O vapor concentrations inside the chamber, using an infrared gas analyzer (Infrared gas analyzer - IRGA), model LI-6400 (Li-Cor, Biosciences Inc., Nebraska, USA). Leaf temperature (Ll) data were also obtained with IRGA. Photosynthetically active radiation (PAR), atmospheric CO₂ inside the leaf chamber and the chamber block temperature were kept constant during measurements, with values of 1000 μmol photons m⁻² s⁻¹, 400 μmol CO₂ m⁻² s⁻¹ and 26 to 27 °C, respectively (Silvestre et al., 2017). An artificial radiation source (ADC BioScientific Ltd., Hoddesdon, UK) was used, coupled to the IRGA, for constant maintenance of the photon quantity. Using the values of Pn, E, Gs and Ci, the following relationships were calculated: EWU = A/E, iEWU = Pn/Gs and Qc = Pn/Ci (Zhang et al. 2001), where EWU means efficiency in the use of water, iEWU means intrinsic efficiency of water use and Qc, which corresponds to instant carboxylation efficiency.

**Data analysis**

The experimental data were evaluated for normality and homogeneity of variances by the Shapiro-Wilk and Bartlett tests, respectively. Subsequently, for parametric variables, the means of treatments were subjected to analysis of variance and comparisons of means by the Tukey test and Pearson’s linear correlation test, using the statistical software SAS 9.1.3 (Sas, 2007). For non-parametric variables, the data were evaluated using the Kruskal-Wallis test with
Bonferroni and correction using RStudio software version 1.1.383 (R Core team, 2015). All analyzes were assessed at the level of 1% significance.

Conclusion

Potassic fertilization in T. vulgaris plantation provided increases of approximately 30% in the Pn. The variables Gr, Ci, E, iEC, EWU and iEWU, were also favored at the dose of 78.2 g kg$^{-1}$ of K, suggesting the action of K in the regulation of physiological processes such as control of plant water relations, sugar transport, protein synthesis and ATP production. Antagonistic effects were observed with the joint application of the highest doses of P and K, because the highest values of Pn were observed in treatments with 33.1 g kg$^{-1}$ of P and 78.2 g kg$^{-1}$ of K, with rates of 4.28 and 4.86 μmol CO$_2$ m$^{-2}$ s$^{-1}$, respectively, affecting the variables E, iEC, EWU and iEWU. This indicates that P exerted antagonist effects on the uptake of K, which may also have impaired the uptake of Mg due to Ca being an ion accompanying the potassium fertilizer.

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