The effect of xylem vessel diameter on potential hydraulic conductivity in different rice stem longitudinal positions

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ABSTRACT

The morphological characteristics of the xylem elements influence water ascent in the plants. Few models determine the physical process of water movement in the vascular system of plants based on the hydraulic architecture. This study aims to determine the anatomical characteristics of the xylem and potential hydraulic conductivity at different positions along the stem of rice (*Oryza sativa* L.). The xylem vessels characteristics were examined in four internodes using three segments in each internode. The analogy between Ohm's law and Hagen-Poiseuille was used to determine the hydraulic conductivities at three temperatures (18, 25, and 33 °C). A successive decrease in the mean vessel diameters from bottom to top stem was observed, with a significant difference between internodes. Between the Internode I and II, there was a 12% reduction in the mean diameter; between the II and III, and III and IV, the decrease was 10 and 28%, respectively. When separated into groups (left and right metaxylem), there was variation in the hydraulically weighted vessels. There was variation in the estimated value of hydraulic conductivity as a function of temperature and along the stem from the base (Internode I) to the plant's top (Internode IV). The decrease in hydraulic conductivity was 41.1 (I–II), 24 (II–III), and 73.4% (III–IV). The estimated value of hydraulic conductivity was increasing with increase in temperature. The variation of the hydraulic conductivity along the useful length of rice allowed a better application of the Hagen-Poiseuille equation.

1. Introduction

The water potential is a fundamental measurement of plant water status, which can be decomposed from the effects of gravitational, chemical, and pressure potential on the cells and their surroundings (Hsiao, 1973; Kramer and Boyer, 1995). The morphological characteristics of the xylem elements influence this status and the water ascent in the plants. The hydraulic conductivity (K_h) is a physical phenomenon, a resistive variable that has an effective action on the flow, being the focus of the main approaches in the research of water ascent in the plant (Fan and Xie, 2004). K_h is a function of physical-chemical factors inherent to mechanism of xylem sap ascent, Cruiziat et al. (2002) defines it as the inverse of the flow resistance in the vessels. Scientific evidence suggests that the variability of K_h occurs as a function of the longitudinal position of the vessel on the stem and its size (height and diameter) (Choat et al., 2005; Petit et al., 2008; Zach et al., 2010; Anfodillo et al., 2012; Tyree and Zimmermann, 2013; Olson and Rosell, 2013; Skelton et al., 2018; Soriano et al., 2020). K_h changes in function of resistive forces associated with xylem geometry, affected by the anatomical characteristics and vessel structures (Koch et al., 2004; Tyree and Zimmermann, 2013; Jensen et al., 2016).

Although the anatomy of the tracheal elements influences the movement of water, what commonly defines its movement are the pressures imposed on the system, either by the forces involved in capillarity or by the positive or negative pressures that are formed from environmental conditions. When considering only the diameter of the vessel elements, the smaller it is, the greater is the pressure that drives the rise of water due to the increase in the specific surface, which,

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consequently, increases the adhesion force between water and the cell wall, and therefore, the force necessary to overcome gravity (Kathpalia and Bhatla, 2018). When considering the water ascension only by capillarity, it is not expected that the water column will ascend to a height greater than 60 cm in the thinnest tracheal element, the tracheids. In the case of vessel elements, which are typical of angiosperms, like rice, an ascension greater than 8 cm is not expected (Fukuda et al., 2007). However, either the positive root pressure or the tension formed in the leaves act concomitantly with capillarity forces and unconditionally influence the movement of water in the xylem, whose flow can vary from 1 to 60 m h^{-1}, depending on the species and the environmental conditions.

The consistent and predictable tapering of the xylem conduit diameter from base to top of the plant is enough to maintain a constant hydraulic resistance along the main stem (West et al., 1999; Becker et al., 2000; Anfodillo et al., 2006). Tapering can potentially maintain constant conductance in plants as a function of resistive variability caused by changing vessel diameters (Savage et al., 2010). Soriano et al. (2020) have defined that the xylem changes anatomical features predictably along the stem in consistent ways with the universal tip-to-base vessel widening pattern. Furthermore, climatic factors influence the average diameter of the new vessels formed from the activity of the vascular cambium meristematic cells in perennial plants, promoting the formation of narrower vessels in plants submitted to dry or cold stresses. Because of that there is a reduction of embolism formation, which is prone to happen in wide vessels and situations that impose greater xylematic tension (Baas and Carlquist, 1985; Carlquist, 2012, 1989; Olson et al., 2014).

Plant hydraulic traits are subject to wide, unexplained variability that might be due to sampling at different heights or lengths of the hydraulic pathway. Under this assumption, quantifying the variation in hydraulic conductivity (K$_h$) in different longitudinal positions can help clarify plant water ascent dynamics associated with xylem anatomy variation (Lacointe and Minchin, 2008; Soriano et al., 2020). The relation between anatomical features and K$_h$ increases the understanding of water rise in the plant, associated with the pressure gradient in transpiration. Well-developed vessels that are not collapsed by embolism or cavitation tend to have a higher K$_h$, positively influencing water and nutrient rise. Thus, knowledge of hydraulic vessel characteristics coupled with mathematical modeling can improve our understanding about water relation in plants (Gea-Izquierdo et al., 2012; Bryukhanova and Fonti, 2013; Chen et al., 2015).

There are not many empirical models for determining water flow in plants. Many authors use "*in loco*" measurements to determine K$_h$ due to their higher accuracy. However, there is evidence that sampling in different longitudinal positions along the stem length of plants improves the estimates of the Hagen-Poiseuille equation (Longui et al., 2017; Crang et al., 2018). The Hagen-Poiseuille equation is defined as a physical law that denotes the head loss in the flow of an incompressible Newtonian fluid through a cylindrical tube, in botany this equation to determine a series of resistances where the head loss is defined as one of a series of resistances inserted into a system analogous to the electrical system defined by Ohm's law (Cruiziat et al., 2002). In this way, the evaluation of K$_h$ variation in different stem longitudinal positions based on hydraulic architecture can help to improve approaches to evaluate dynamics of water ascent in the plant (Lacointe and Minchin, 2008).

Based on that, this study aimed to determine the xylem diameter variation pattern and the hydraulic conductivity in the stem of rice plants. It was based on the hypothesis that the anatomy along the stem differs. A higher number of sampling points across stem longitudinal positions leads to a better hydraulic conductivity value based on the analogy of Ohm's law, using the Hagen-Poiseuille equation.

2. Material and methods

The study was conducted using the rice crop. Rice has a well-defined vessel anatomical organization, including vascular tissues in the stem, arranged in concentric circles, parallelized, and easily identifiable for analysis (Scarpella and Meijer, 2004). The rice [*Oryza sativa* L. (cv. 'Usen')] was grown in a greenhouse in pots containing soil with a clay texture (53% sand, 22% silt, and 25% clay). The polythene pots had 18 cm diameter and a depth of 15 cm. The pots were placed into trays, keeping a continuous water layer of 2 cm. The water potential was kept near −10 kPa in the substrate, replenishing overnight the daily water loss measured by weighing lysimeter. Air temperature and relative humidity were recorded in the greenhouse using an automatic weather station (Bristom EMS-210 PRO; Bristom Inc., Brazil).

Four plants were collected and placed in a 70% ethyl alcohol solution. The plants had four internodes in stem, where three samples were sectioned in each one, being located after the node, in the middle, and at the end of the internode. The plants had a total height of 54.2 cm ± 4.8 cm. The three-cut sections occurred in Internode I, II, III, and IV, respectively, at the portion 26%, 32%, 37%; 38%, 42%, 49%; 50%, 61%, 73%; and 74%, 85% and 95% of maximum plant height, totalizing twelve samples from longitudinal positions (L$_P$) along the stem (Fig. 1).

The samples were dehydrated in ethyl alcohol following a sequence of concentration increase (70% → 80% → 90% → 95% → 100%) with three replicates for 30 min and dried with a critical point dryer (Tousimis AutoSamdri 815; Tousimis, USA). The samples were placed on aluminum plates using carbon-coated double-sided tape and then covered by gold. The samples were analyzed using a scanning electron microscope (SEM), with X-ray analysis of dispersive energy (Jeol JSM-IT300LV, JEOL USA Inc, USA) (Shi and Butenko, 2018). The anatomical xylem structures were analyzed near the interface of the vessel elements. Micrographs were analyzed using 100 × magnification and overlaid to create a complete orthogonal mosaic of the cross-section from the observed sample (Fig. 2).

The area of the xylem vessels was measured from the orthogonal mosaics created by the collected sample images, using the image analysis plugin integrated with computer-aided design software (AutoCAD Raster Design, 2018). The vessels' area was converted into diameter, assuming circularity of the vessels (Ewers and Fisher, 1989). The continuity of the sample segments was defined by overlapping the images of three L$_P$ in each of the internodes. The vessels were classified into two groups of metaxylem (left and right) (Fig. 3). This classification is a parameter of statistical control, a palliative measure to decrease the standard error and the variance of the vessels measured in the same Internode variables. The protoxylem structures were removed from the analysis when their fragments were observed in the sample, since after degradation they become an intercellular space, where the flow is not significant, being this structure a protoxylem gap (Zeng et al., 2016).

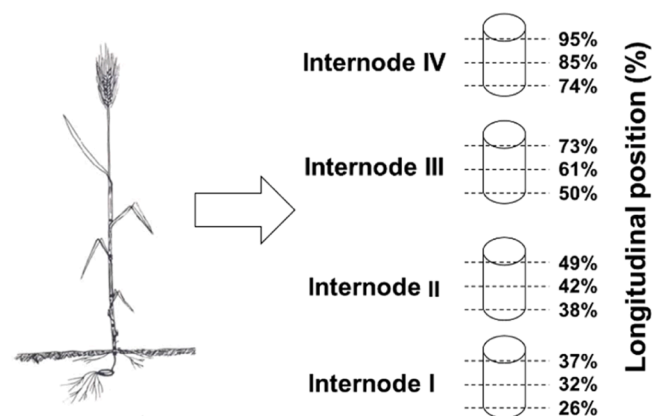The Hagen-Poiseuille equation (Eq. (1)) was used to be applicable

Fig. 1. Position of cut sections sampled along the Internode I, II, III and IV along the stem of a rice plant, where percentages represent the portion location in relation to the maximum plant height.
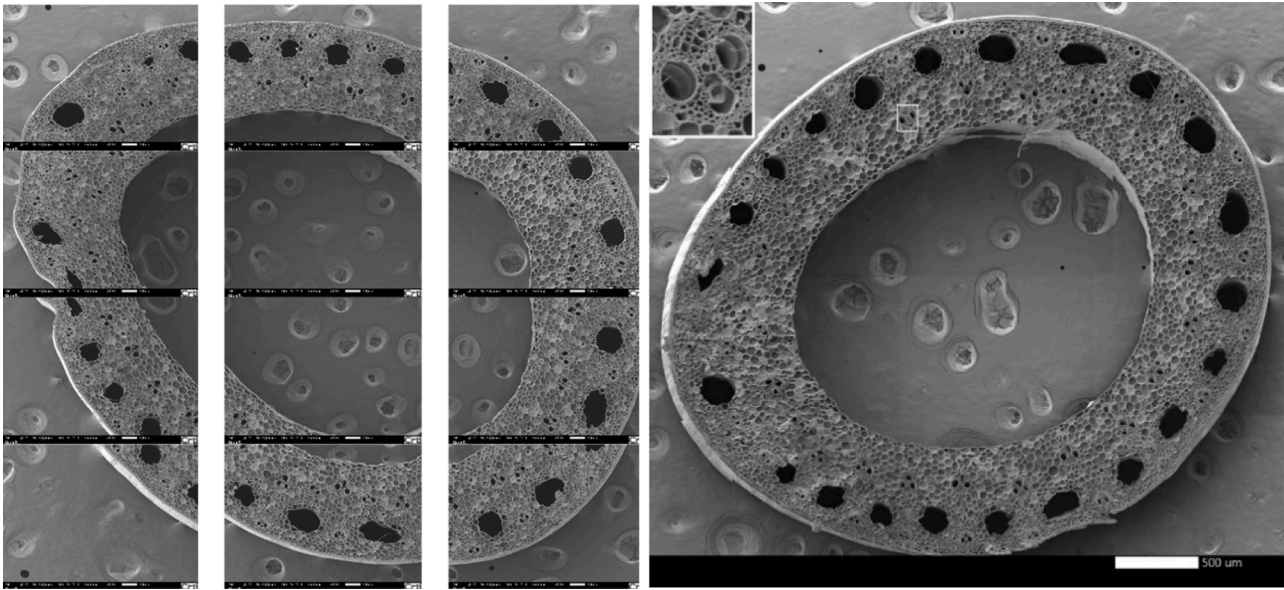
Fig. 2. Representation of the orthogonal mosaic organization of the sample cross-section in the 32% longitudinal position at the Internode I of the rice plant. A structure of xylem vessels stands out in the upper left corner.
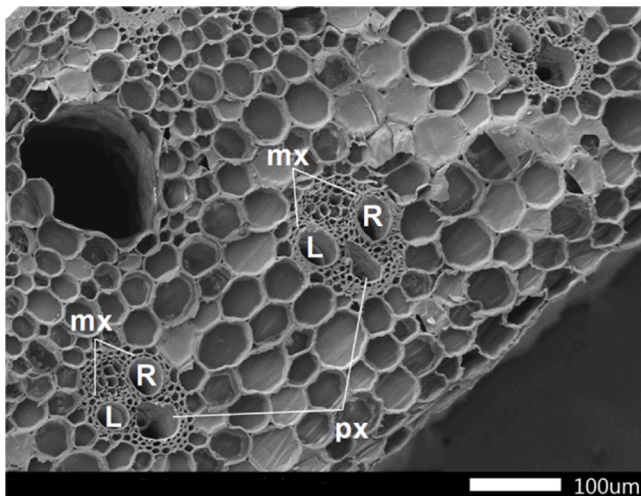

Fig. 3. Fragment of a scanning electron microscopy (SEM) image of anatomical structures of the metaxylem (mx) classified into left (L), right (R) and protoxylem structures, showing the protoxylem gap (px) of rice.

when many vessels of different diameters are present in parallel, efficiently describing the laminar flow in capillary vessels (Schultz and Matthews, 1993). The rice has xylem vessels arranged in concentric circles, parallel to each other (Scarpella and Meijer, 2004), complying with the Hagen-Poiseuille approach requirement, where the potential hydraulic conductivity is described by Eq. (1) (Cruiziat et al., 2002).

$$K_p = \frac{\pi \rho}{128\eta} \frac{\sum_{i=1}^{n} d^4}{N} \tag{1}$$

where K_p is potential hydraulic conductivity (kg m MPa^{-1} s^{-1}), ρ is the water density (kg m^{-3}), η is the water viscosity (MPa), d is the equivalent vessel diameter (m) and N the total number of vessels.

The water physical properties used in the model followed the maximum, mean and minimum temperatures during the cultivation period (18, 25, and 33 °C). The fluid density was 998.6, 997.1, and 994.7 kg m^{-3} and the fluid viscosity were 1.0×10^3, 0.9×10^3, and 0.7×10^3 Pa, respectively at 18, 25, and 33 °C.

The Chi-Square test was applied to assess the distribution of vessel diameters in the internodes and the Shapiro-Wilk normality test in the frequency of mean diameter values. In addition, the vessel diameters and anatomical variability were submitted to a repeated measures two-way analysis of variance (ANOVA) and the differences between means determined by the post-hoc analysis ($P < 0.05$).

3. Results

The vessel diameters frequency distribution is shown in Fig. 4 for internodes I, II, III, and IV, including the mean vessel diameters. The vessels showed normal distribution for the mean diameters according to the Shapiro-Wilk test ($P > 0.05$) for all internodes (Fig. 4). However, the frequency distribution pattern of diameters differed between internodes (Fig. 4). At Internode I, 47% of the vessel diameter varied between 36.0 to 42.0 μm, followed by Internode II, with 44% of the vessels between varying of 32.0 to 36.0 μm, internodes III and IV, with 52 and 54%, ranging from 28.00 to 32.0 μm, and from 22.0 to 24.0 μm, respectively.

The mean diameters of the left and right metaxylem vessels are shown in Fig. 5 for internodes I, II, III, and IV along the total length of the stem. Mean vessel diameters tended to decrease between the bottom and top internodes in the left and right groups (Fig. 5a and 5b). The mean diameter was 40.91 μm and 40.20 μm at the bottom (14.8 cm), respectively, for left and right metaxylem, which was reduced to 17.98 μm and 18.39 μm at the top (52.9 cm). This represents a decrease of 44 and 41% for vessel diameters, respectively, for the left and right groups. However, there was no difference between the Left and Right.

Table 1 shows the results from the post-hoc analysis ($P > 0.05$) for the mean of xylem vessels diameters in rice stems, including the twelve longitudinal positions (L_P's), classified into two groups (Left and Right) and the means from both groups. There was a significant difference between the values of the mean vessel diameters for rice based on the Chi-Square test in Internode I, II, III, and IV ($P < 0.05$). Between Internode I and II, there was a 12% reduction in the mean diameter; between Internodes II and III and III and IV, the decrease was 10 and 28%, respectively.

There was a significant difference in vessel diameter between L_P. Between the L_P of 26 and 42%, there was a 12% reduction in the average diameter of the vessels. Between L_P of 42 and 49% vessel diameter is reduced by 15%. We observed a more significant decrease between L_P of 74 and 85%, namely 37%.
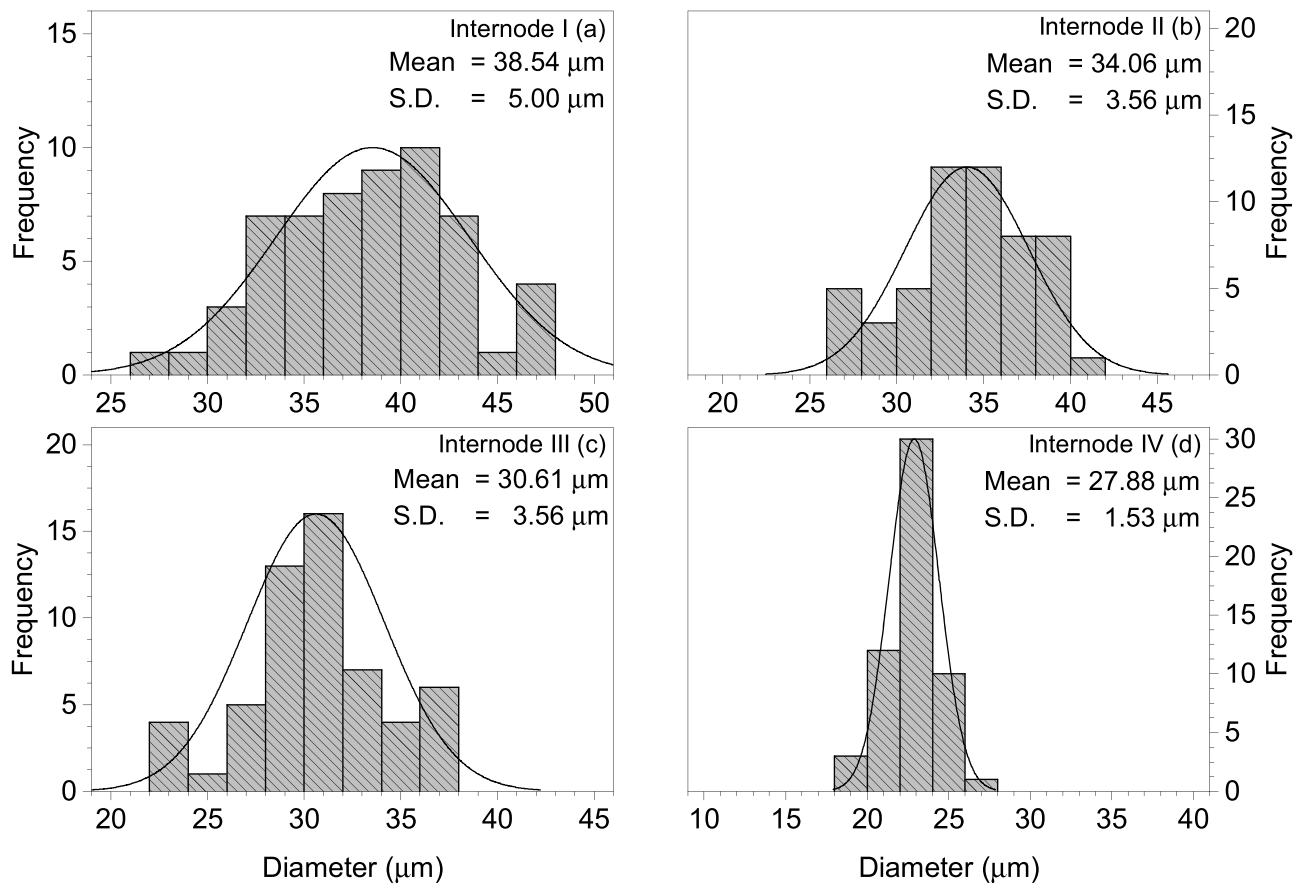
Fig. 4. Frequency distributions (n) of vessel diameters in rice observed along the stem in the four internodes.
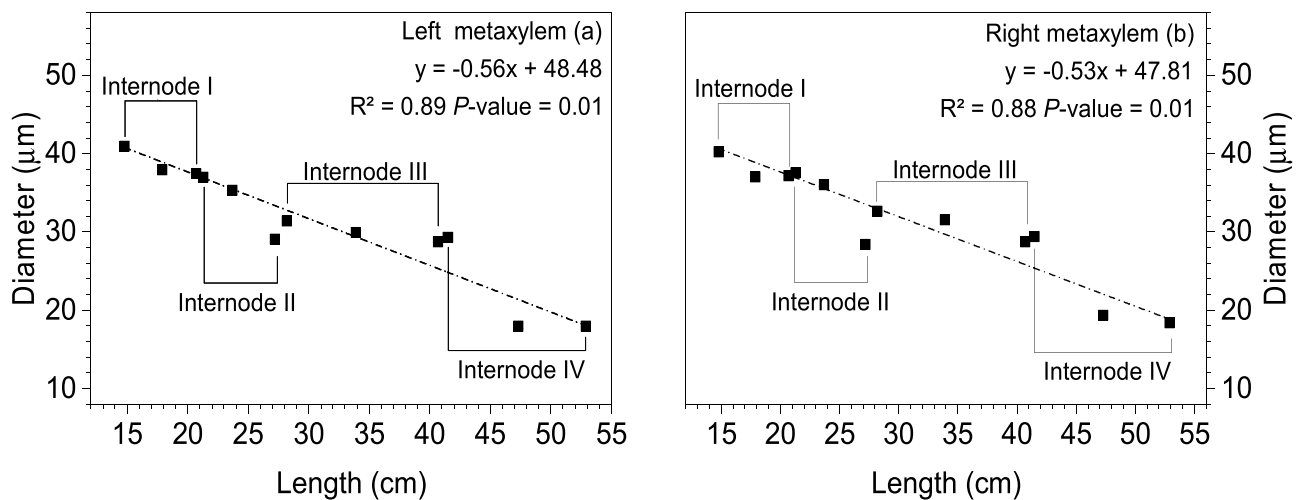

Fig. 5. Mean diameters of the metaxylem vessels in the twelve longitudinal positions observed along the total length of the stem, in internodes I, II, III, and IV of the rice plants.

The potential hydraulic conductivity (K_p) in the rice stem is shown in Fig. 6. K_p was obtained for four internal episodes at the minimum, mean and maximum temperatures observed during the plant development in the greenhouse. K_p was higher at the stem base, decreasing 41.1% between Internode I and II. K_p had a decrease of 24.0% in Internode III when compared to Internode II. At the stem top (Internode IV), K_p showed a mean reduction of 73.4% compared to Internode III. The increase in temperature lead K_p to be 21.9% higher from 18 °C to 25 °C and 18.6% from 25 °C to 33 °C.

4. Discussion

We assumed that the xylem structure for water flux is variable along the rice stem. We observed a decreasing trend for the average diameters measured in the twelve L_P (Fig. 5). Considering only the forces involved in capillarity, the pressure of water gradient in xylem decreases from bottom to top due to vessel elements resistance to flow and gravity, which correspond to 0.01 MPa and 0.02 MPa per meter of the rising water column, respectively (Venturas et al., 2017). Likely, the reduction

Table 1

Mean and the standard error (± SE) of the vessel diameters of xylem in rice stems, divided into twelve longitudinal positions.

Longitudinal Position	Diameter (μm)
26%	40.56 ± 5.64 a
32%	37.49 ± 6.14 ab
37%	37.32 ± 4.37 ab
38%	37.25 ± 5.36 ab
42%	35.67 ± 4.25 b
49%	28.74 ± 4.34 c
50%	32.04 ± 4.03 c
61%	30.75 ± 3.56 c
73%	28.75 ± 4.23 c
74%	29.38 ± 2.62 c
85%	18.68 ± 2.51 d
95%	18.19 ± 1.86 d

*Values followed by the same letter do not differ significantly from each other by the post-hoc analysis ($P > 0.05$).
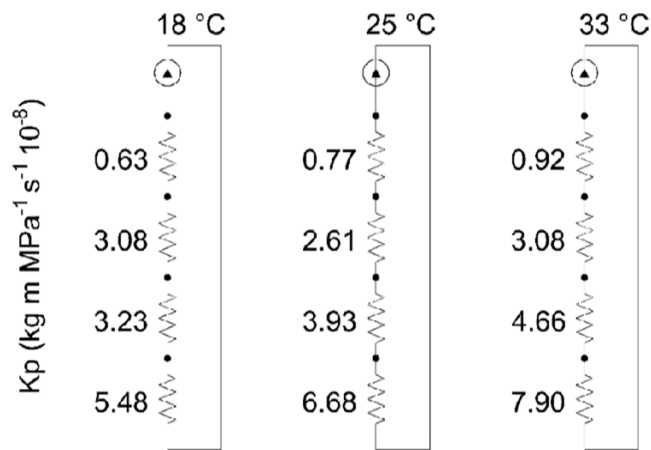

Fig. 6. Potential hydraulic conductivity (K_p) of the rice stem in the regions of the four internodes was empirically calculated applying Hagen-Poiseuille's law at three temperatures observed throughout the production cycle.

of the vessel's diameter from the bottom to the plant top occurs to compensate the pressure loss imposed by the resistance of the tracheal elements and gravity for water column rising; by reducing the diameter of the capillaries, the pressure necessary to transport the water to the top of the plant increases.

Rosell et al. (2017) pointed out another importance for the last vessels being narrower in order to favor the flow of water out of the vessel's in leaves due to greater surface area. Thus, the decreasing variation in the mean vessel diameter occurring between the internodes is an expected anatomical pattern due to the physical phenomena in the water movement process. Another importance for reducing the diameter of the vessel elements is to reduce the chance of cavitation due to the greater specific surface at the water–cell wall interface, which contributes to a greater adhesion force, and, thus, disfavours cavitation. This is especially important when the movement of water in the xylem is determined by the tension formed in the leaves, a phenomenon that favours the establishment of a greater negative water potential at the top of the plant than at the base of the stem, and which, in turn, promotes a greater xylem tension, and then increasing the chance of cavitation (Venturas et al., 2017; Mrad et al., 2018; Pittermann et al., 2021) Although the rice growing conditions in the present study do not favor high tensions generated in the leaves, the anatomical behavior of tracheal elements tends to be constitutive in plants in response to evolutionary adaptations.

The mean xylem vessel diameters ranged between 40.56 and 18.19 μm. This range agrees with other study's measurements. Bauw et al.

(2019) found mean vessel diameters between 33.3 and 50.4 μm when evaluating anatomical responses of roots from two rice varieties to the combined stress of phosphorus and water deficit. Kim and Lee (2010) found a mean diameter of 15 μm for the initial leaves L1 – L4, and diameters of 29.0 μm in the old leaves. The authors proposed a non-destructive monitoring of the dynamics of sap flow through xylem vessel elements in rice leaves. Kim and Lee (2010) also described that the mean internal diameter of the xylem vessels in the stem decreased associated with higher leaves developed.

Plant height is the main factor responsible for the variation in the diameter of the vessels due to an evolutionary hydraulic adaptation that occurred in vascular plants and is inevitably involved with height (Christoffersen et al., 2016). As a result, plants have a diameter reduction of the vessel above the branches junctions called "hydraulic bottlenecks" (Tyree and Zimmermann, 2013). The hydraulic bottlenecks are the variation in the distribution pattern of the vessels in the junction constraints of the plant, as a node, branch, or lateral outlet to the leaf, where this can impact water conductivity under significant drop in diameters (Zimmermann, 2013).

The rice stem showed changes in the architecture between the internodes, leading to a decline in conductivities estimated from the base to the top (Fig. 6). This occurred due to the decrease in the vessel's diameters from internodes I, II, III, and IV and between L_P (Fig. 5a and 5b). The Hagen-Poiseuille law explains the variation pattern, showing that vessel resistance was linear with vessel length (Tyree and Ewers, 1991). However, the Hagen-Poiseuille law shows that minimal increases in tube diameter produced substantial increases in the flow (Vogel, 1993). Therefore, in agreement with the experimental data, it is expected that vessels must have larger diameters at the base and smaller at the top (West et al., 1999) to maintain resistance near to constant to ensure that the top vascular system receives the required water.

Nobel (2009) mentions that the flow density obtained by the Hagen-Poiseuille equation is different from the real values measured. This difference occurs due to the variability of the diameters found through segments of roots, stems, or leaves (Rosell et al., 2017). Based on this, a greater number of sample points in different L_Ps gives a better approximation of K_p values, as evidenced in Fig. 5, where a high degree of correlation was observed between vessel diameter and Lps following a linear tapering, corroborating the studies of Anfodillo et al. (2006) and Savage et al. (2010). This leads to more accurate predictability of the vessel's diameter in the rice. Furthermore, it denotes a better method of estimating the potential conductance proposed by Kolb and Sperry (1999), where it was possible to observe a conductance of 3.12 mmol s^{-1} MPa^{-1} at 18 °C, 3.81 mmol s^{-1} MPa^{-1} at 25 °C and 4.51 mmol s^{-1} MPa^{-1} in the rice stem.

It is important to point out that the water flow measured by specific devices in plants reveals a real movement, which is mainly due to the tension generated in the leaves, classically explained by Dixon's theory, or the propelling of the water movement originated in the positive pressure of the roots. In this sense, the real xylem water flux is a phenomenon that goes beyond the potential capacity of water conductivity by the vessel elements explained only by punctual and isolated forces.

In this study, with a larger number of samples and L_P, it was possible to observe the K_p variation of 41.1%, 24.0%, and 73.4%, occurring between the internodes I and II, II and III, III and IV, respectively. The higher portion sampling leads to estimate water flow in the plant with greater precision through the Hagen-Poiseuille Law. The K_p variability observed occurs due to the vessel diameters variation observed in the construction of the hydraulic architecture, which had a variability higher than 40% between the first and the last sample.

Miyamoto et al. (2001) determined the hydraulic conductivity under steady-state and transitory water flow conditions in rice roots, where the Azucena variety had a conductivity of 7.40×10^{-8} kg m MPa^{-1} s^{-1}. Kato and Okami (2011) determined the effect of hydraulic conductivity on plant–water relationships and stomatal conductance in rice. In the whole plant, hydraulic conductivity values were measured between 11.8

and 15.0×10^{-8} kg m MPa^{-1} s^{-1}. The values of hydraulic conductivity obtained in this work were near of 10^{-8} kg m MPa^{-1} s^{-1} in the four internodes (Fig. 6), which agrees with the results found in the literature.

The increase in K_p occurs proportionally to the increase in temperature due to the variability of the fundamental physical properties of water (Fig. 6). In the literature, changes in xylem hydraulic conductivity due to temperature variation are attributed to the water viscosity as a fundamental factor for mathematical models (Cochard et al., 2000). The xylem shows low variability of hydraulic properties against adverse climatic conditions due to its adaptive capacity (Bryukhanova and Fonti, 2013). One of the mechanisms is to decrease the internal diameter and increase the vessel density, where larger vessels can promote higher risk of cavitation due to changes in water viscosity (Gea-Izquierdo et al., 2012). Bryukhanova and Fonti (2013) highlighted that plant adjustment in the hydraulic architecture is significant over long periods, and the changes in the hydraulic architecture are visible in annual plants due to the variability of viscosity of the water at different temperatures.

Although temperatures of 18, 25 and 33 °C were used to estimate the potential water conductivity in tracheal elements as a function of the minimum, average and maximum temperatures of the atmosphere in the plant growing environment, it should be noted that the air temperature does not correspond to the temperature of the water that moves in the plant. However, the air temperature influences the water temperature in the plant, especially in plants with poor thermal isolation structures, such as rice. In this sense, the results obtained considering the supposed water temperature at 18, 25, and 33 °C revealed a greater potential of water conductivity in the xylem as its water temperature increases, which is extremely beneficial to plants, because the increase in water temperature in the plant comes from an increase in air temperature, even if it is not proportional. The higher atmospheric temperature leads to higher vapor pressure gradient between the leaf–air continuum in mesophyll and the atmosphere outside the leaves. This situation demands a greater loss of water vapor from the leaves through transpiration, which is necessary to cool the leaves, preventing damage to the leaf metabolism. The increase of xylem water conductivity at higher temperatures favours the flux of water that is needed to reach leaves for transpiration.

The water flow in the xylem helps to understand the physiological mechanisms of plants that regulate transpiration, which is related to the hydraulic efficiency of vessels and the strategies to avoid embolism. Furthermore, these estimates can generally solve environmental problems inherent to agricultural production, such as excessive irrigation water consumption, where a base knowledge is fundamental to develop tools for rational water use in agriculture.

5. Conclusions

The hydraulic architecture of rice changes along the stem consistently, i.e., mean diameters decreases from the bottom to the top. The anatomical characteristics in different longitudinal positions along the stem allowed a better approximation of the hydraulic conductivity values estimated using the Hagen-Poiseuille law and improvement of the comparability of the hydraulic characteristics. The influence of temperature on hydraulic conductivity was due to the variability of the fundamental physical properties of water, its viscosity.

CRediT authorship contribution statement

Diogo Henrique Morato de Moraes: Investigation, Data curation, Writing – original draft. **Marcio Mesquita:** Supervision, Project administration, Writing – review & editing. **Dalva Graciano-Ribeiro:** Resources, Writing – original draft. **Daniel Somma de Araújo:** Investigation, Data curation. **Rafael Battisti:** Formal analysis, Writing – original draft, Writing – review & editing. **Rilner Alves Flores:** Writing – review & editing. **Hyrandir Cabral de Melo:** Writing – review & editing. **Derblai Casaroli:** Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The authors do not have permission to share data.

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