

Tolerance to waterlogging in *Parkia gigantocarpa* Ducke saplings

Waldemar VIANA DE ANDRADE JÚNIOR¹
Benedito GOMES DOS SANTOS FILHO²
Cândido FERREIRA DE OLIVEIRA NETO¹
Eniel David CRUZ³
Ricardo SHIGUERU OKUMURA^{2,4}
Vitor RESENDE DO NASCIMENTO¹
Jéssica TAYNARA DA SILVA MARTINS^{2,5}
Liliane CORRÊA MACHADO^{2,5}
Diana Jhulia PALHETA DE SOUSA²
Jéssica Suellen SILVA TEIXEIRA²

¹ Federal Rural University of the Amazon
Forest Sciences Department
Laboratory of Biodiversity Studies of
Upper Plants
66.077-830 Campus Belém, Pará
Brazil

² Federal Rural University of the Amazon
Institute of Agronomists Sciences
66.077-830 Campus Belém, Pará
Brazil

³ Brazilian Agricultural Research
Corporation (Embrapa)
66017-970 Belém, Pará
Brazil

⁴ University of the Amazon (UFRA)
Agronomy student at Federal Rural
Belém, Pará
Brazil

⁵ Federal University of Santa Maria
Fitotecnia Department
97105-900 Campus Sede
Santa Maria, Rio Grande do Sul
Brazil

**Auteur correspondant /
Corresponding author:**

Waldemar Viana de Andrade Júnior –
waldemarandrade97@gmail.com



Photo 1.
Parkia gigantocarpa.
Photo E. D. Cruz.

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RÉSUMÉ

Tolérance à l'engorgement d'eau chez les arbrisseaux de *Parkia gigantocarpa* Ducke

Cette étude se propose d'évaluer les réponses biochimiques des arbrisseaux de *Parkia gigantocarpa* devant l'engorgement d'eau. L'engorgement est appliqué en inondant les arbrisseaux dans des pots de 14 kg jusqu'à approximativement 5 cm au-dessus de la surface du sol. Le plan expérimental a été façonné aléatoirement et comprenait deux types d'application de l'eau (contrôle et engorgement) sur cinq périodes d'évaluation (après 0, 4, 8, 12 et 16 jours d'engorgement), avec cinq répliques par traitement. Amidon, saccharose, hydrates de carbone solubles totaux et protéines solubles totales ont été mesurés. Les arbrisseaux soumis à engorgement ont montré des réductions significatives des concentrations d'amidon (62,50 %) et de protéines solubles totales (40,98 %), en particulier dans les feuilles. L'engorgement a réduit la concentration de saccharose dans les feuilles (44,38 %), tandis que cette concentration a augmenté dans les racines (76,78 %). La concentration d'hydrates de carbone solubles a augmenté de 106,9 % dans les racines des plantes exposées à l'engorgement. Cette étude a démontré la sensibilité des arbrisseaux de *Parkia gigantocarpa* à l'engorgement.

Mots-clés : amidon, saccharose, hydrates de carbone solubles totaux, protéines solubles totales, Brésil.

ABSTRACT

Tolerance to waterlogging in *Parkia gigantocarpa* Ducke saplings

This study aimed to assess the biochemical responses of *Parkia gigantocarpa* saplings to waterlogging. Waterlogging was imposed by flooding the saplings in 14 kg pots to approximately 5 cm above the soil surface. The experimental design was completely randomized and involved two water conditions (control and waterlogging) over five assessment periods (after 0, 4, 8, 12 and 16 days of waterlogging), with five replications per treatment. Starch, sucrose, total soluble carbohydrates and total soluble proteins were measured. The saplings exposed to waterlogging showed significant reductions in starch concentrations (62.50%) and total soluble proteins (40.98%), especially in the leaves. Waterlogging reduced the concentration of sucrose in leaves (44.38%) and increased it in the roots (76.78%). The total soluble carbohydrate concentration increased by 106.9% in the roots of plants exposed to waterlogging. This study showed the susceptibility of *Parkia gigantocarpa* saplings to waterlogging.

Keywords: starch, sucrose, total soluble carbohydrates, total soluble proteins, Brazil.

RESUMEN

Tolerancia al encharcamiento en los arbolitos de *Parkia gigantocarpa* Ducke

Este estudio tiene como objetivo evaluar las respuestas bioquímicas de los arbolitos de *Parkia gigantocarpa* al encharcamiento. El encharcamiento se consiguió inundando los arbolitos en recipientes de 14 kg hasta aproximadamente 5 cm por encima de la superficie del suelo. El diseño experimental fue completamente aleatorizado y tuvo en cuenta dos condiciones para el agua (control y encharcamiento) durante cinco períodos de evaluación (después de 0, 4, 8, 12 y 16 días de encharcamiento), con cinco réplicas por tratamiento. Se midieron: almidón, sacarosa, hidratos de carbono solubles totales y proteínas solubles totales. Los arbolitos sometidos a encharcamiento mostraron reducciones significativas de las concentraciones de almidón (62,50 %) y de proteínas solubles totales (40,98 %), especialmente en las hojas. El encharcamiento redujo la concentración de sacarosa en las hojas (44,38 %) y la incrementó en las raíces (76,78 %). La concentración total de hidratos de carbono solubles aumentó en un 106,9 % en las raíces de las plantas sometidas a encharcamiento. Este estudio ha mostrado la sensibilidad de los arbolitos de *Parkia gigantocarpa* ante el encharcamiento.

Palabras clave: almidón, sacarosa, hidratos de carbono solubles totales, proteínas solubles totales, Brasil.

Introduction¹

Waterlogging is an abiotic factor, common in many regions of the world, promoted by natural or anthropogenic causes, such as increase in the water level of rivers, poor irrigation management, unfavorable topography, poor soil drainage (Patel *et al.*, 2014), removal of vegetation and construction of dams and roads. In addition, as a result of global climate change, there are forecasts of extreme weather events such as heavy rains, which may affect the frequency, duration and intensity of waterlogging in certain regions (IPCC, 2012), thus representing a problem to forestry, agriculture, and permanent preservation areas.

Waterlogging fills the soil porous spaces, causing hypoxia or anoxia, changing the aerobic metabolic pathway into the anaerobic one, thus reducing energy (adenosine triphosphate, ATP) to the root system. Decreases root development, resulting in less absorption and transport of water and nutrients to the shoot, thereby negatively influencing the stomatal conductance, transpiration and photosynthesis of many plants (Mollard *et al.*, 2010). Due to the low efficiency of these processes, the energy and carbon metabolism of trees are usually strongly affected in the roots and shoots (Kreuzwieser *et al.*, 2009).

The increase of carbohydrate in the leaves, for example, is due to starch accumulation (Liu *et al.*, 2011) or decreased translocation, which is severely reduced by numerous species of plants that are non-tolerant to waterlogging environments (Bertolde *et al.*, 2012).

Accumulation of sucrose (Merchant *et al.*, 2010) and soluble carbohydrates (Bertolde *et al.*, 2012) fosters osmotic adjustment, i.e., accumulation of these compounds, especially in the cytoplasm, thus reducing the osmotic potential of leaf tissue cells, and, consequently their water potential (Jaleel *et al.*, 2007). As a result, a water potential gradient is found between air-root-shoot, allowing absorption and transport of soil water to the shoot, thereby contributing to the maintenance of cell turgor.

Parkia gigantocarpa known in Brazil as fava-atanã is a neotropical tree that occurs naturally in upland and lowland floodplains. In recent years, it has aroused the interest of researchers, especially related to seedling production (Oliveira *et al.*, 2012) and commercial timber activities in the Amazon region (Reis *et al.*, 2014). Because of its rapid growth, uniformity, low mortality rate and economic and ecological potential, it is seen as promising species for recovery of altered or degraded areas, especially those aimed at permanent preservation (Carvalho, 2010). Moreover, they can also be used in forestry systems (Andrade Júnior *et al.*, 2016).

Despite the economic, ecological and environmental importance of *P. gigantocarpa*, few studies (Andrade Júnior *et al.*, 2016) have been conducted to clarify its biochemical behavior in waterlogging conditions, especially in

the initial phase of development. The understanding of the behavior of tree species with economic and environmental potential in the early stages of vegetative development under flood conditions may support the reforestation of degraded areas. Thus, the aim of the study was to evaluate the biochemical responses of young *P. gigantocarpa* plants exposed to waterlogging conditions.

Materials and methods

Study location

The experiment was conducted in a greenhouse at the Instituto de Ciências Agrárias (Institute of Agricultural Sciences, ICA) of the Universidade Federal Rural da Amazônia (Federal Rural University of the Amazon, UFRA) in the city of Belém, State of Pará, Brazil (0°28'03"S, 48°29'18"W) during 120 days.

Plant materials

P. gigantocarpa Ducke seeds were collected from Rio Capim farm (03°41'07"S and 48°38'04"W). Seeds were scarified in the lateral region and adjacent to the hilum, and were immediately sown in 5 L plastic trays containing sterile sand. After emergence, the seedlings were transplanted to black opaque polythene bags measuring 25 cm x 15 cm in height and diameter, respectively, with perforations in all sides, containing the substrate Plantmax® (composed of composted pine bark, peat, vegetal charcoal, and vermiculite). The seedlings were grown for 60 days. After this period, plants were evaluated for height, stem diameter, number of leaves and number of leaflets, and transferred to 14 kg plastic pots, containing the same substrate used in transplanting. The pots with the young plants were placed in a greenhouse for acclimation, during 45 days.

Experimental design

The experimental design used was factorial randomized with two water conditions (control and waterlogging) combined with five evaluation periods (0, 4, 8, 12 and 16 days of waterlogging conditions). The experiment was assembled with five replications in a total of 50 experimental units, with one plant per unit.

Waterlogging treatments

After the acclimation period, at approximately 4 months of vegetative growth, all young *P. gigantocarpa* plants were subjected to water treatments. Control plants were irrigated daily with 2.5 L of water to replace water lost by evaporation; this was done individually for each pot, while considering the daily weighting set (pot + plant + soil). In the treatment exposed to waterlogging conditions, the plants were placed in pots without drains to avoid water drainage, with water level maintained at 5 cm above the soil surface. Control and waterlogging plants remained for 16 days under these conditions.

¹ **Abbreviations:** Ψ_x: foliar xylem water potential; TSC: total soluble carbohydrates; TSP: total soluble proteins; Stleaf: Starch in leaf; Stroot: Starch in root; Sacleaf: Sucrose concentration in leaf; Sacroot: Sucrose concentration in root; ATP: Adenosine triphosphate; GLU⁻: Glutamic acid; DM: Dry matter.

Starch content

For determination of starch content, 50 mg of milled material (leaf and root) were incubated with 5 mL ethanol at 80 °C for 30 min, centrifuged at 2,000 rpm for 10 mn at 25 °C, and the supernatant was removed. In addition, a second extraction was carried out with the same milled material incubated with 5 mL of 30% HClO₄ at 25 °C for 30 min and centrifuged in the conditions described previously. The supernatants of the two extractions were mixed. The quantifications of the total soluble carbohydrates and starch were carried out at 490 nm using the method of Dubois *et al.* (1956), using glucose (Sigma Chemicals) as a standard.

Sucrose content

Determination of sucrose was carried out with 50 mg of powder (leaf dry matter), which was incubated with 1.5 mL of MCW solution (methanol, chloroform and water), in a 12:5:3 ratio (v:v-1) at 20 °C by 30 mn and under agitation. Subsequently, the homogenate was centrifuged at 10,000 rpm by 10 mn at 20 °C and the supernatant was removed. Sucrose quantification was carried out at 620 nm according to Van Handel (1968), and sucrose (Sigma chemicals) was used as a standard.

Determination of total soluble carbohydrates (TSC)

Total soluble carbohydrates were determined with 50 mg of leaf dry matter, which was incubated with 5 mL of ultra pure water at 100 °C by 30 mn; subsequently, the homogenate was centrifuged at 2,000 rpm for 5 mn at 20 °C and the supernatant was removed. Quantification of total soluble carbohydrates was carried out at 490 nm according to the method of Dubois *et al.* (1956), and glucose (Sigma Chemicals) was used as a standard.

Concentrations of total soluble proteins (TSP)

Determination of total soluble proteins was carried out with 100 mg of powder, incubated with 5 mL of extraction buffer. This was homogenized and kept in agitation for 2 h, and centrifuged at 2,000 rpm for 10 mn at 20 °C. Quantification of total soluble proteins was carried out at 595 nm in accordance with Bradford (1976) with albumin bovine (Sigma Chemicals) as a standard.

Data analysis

The data were subjected to variance analysis and significant differences between means were determined using the F-test at the 5% error probability level (Steel *et al.*, 2006). Standard deviations were calculated for each treatment at all evaluation points. A correlation analysis was performed using Pearson's parametric method, and the statistical analyses were performed using the SAS software (SAS, 2007).

Results

Waterlogging effects on starch concentration

Starch concentrations in the leaf tissue were significantly lower in plants exposed to waterlogging (figure 1a). There was interaction between the factors ($P < 0.001$), statistical differences between treatments ($P < 0.001$) and evaluation periods ($P < 0.001$) (figure 1). At 16 days of the experiment, starch concentrations were 0.24 mmol/g GLU residue in control plants and 0.09 mmol/g GLU residue in waterlogged plants, with a reduction of 62.5% in plants exposed to waterlogging (figure 1a). Starch concentrations in root also showed significant interaction between the factors ($P < 0.001$), statistical differences between treatments ($P < 0.001$) and evaluation periods ($P < 0.001$) (figure 1).

At 16 days of the experiment, concentrations of starch reduced from 0.09 mmol/g GLU (control) to 0.04 mmol/g GLU (waterlogged) residue, a decrease of 55.55% in plants exposed to waterlogging (figure 1b).

Sucrose concentration in *P. gigantocarpa*

In relation to sucrose concentration, there was interaction between the factors ($P < 0.001$), statistical differences between treatments ($P < 0.001$) and periods of evaluation ($P < 0.001$) (figure 2ab). The concentrations of sucrose in leaves at 16 days were, 27.66 and 15.38 mg in the control and waterlogged plants, respectively, a decrease of

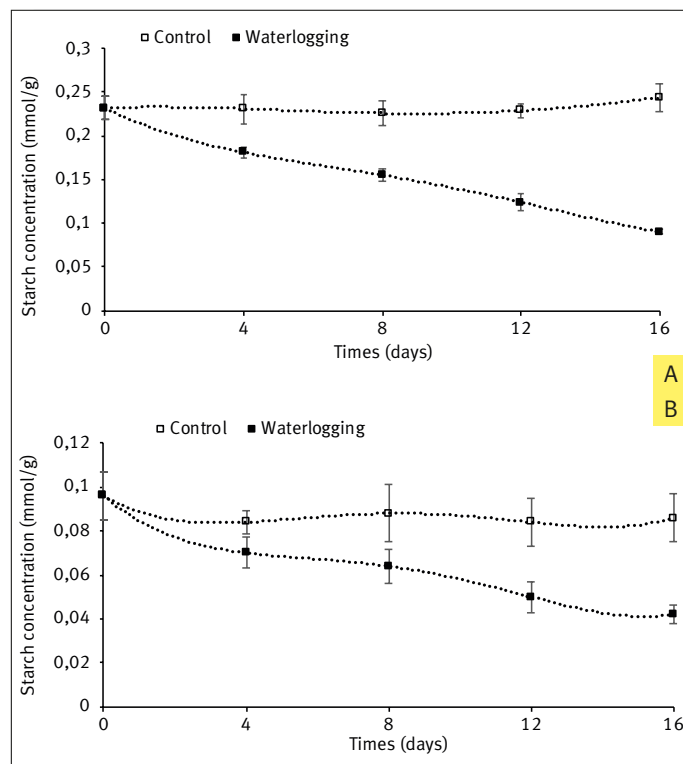


Figure 1.

Starch concentration in the root (A) and the leaf (B) in young *Parkia gigantocarpa* plants exposed to waterlogging conditions. Squares represent the mean values of five replicates, and error bars represent the mean standard errors.

44.38% in plants exposed to waterlogging (figure 2a). In root of plants exposed to waterlogging conditions, the concentration of sucrose increased substantially, especially on 4th day of experiment (76.78%), followed by decrease, with a 24.75% lower sucrose concentration in waterlogged plants (16th day) compared to control (figure 2b).

Waterlogging conditions effects on total soluble carbohydrate concentration

Concentrations of total soluble carbohydrate in leaves were significantly higher in plants exposed to waterlogging (figure 3a). There was interaction between the factors ($P < 0.001$) and statistical differences among treatments ($P < 0.001$). However, showed no difference between evaluation periods ($P < 0.05$) (figure 3). In control and waterlogged plants, concentrations at 16 days were 1.21 and 2.36 mmol/g GLU residue, respectively, showing an increase of 96.7% in plants exposed to waterlogging (figure 3a). In relation to total soluble carbohydrate concentrations at root, there was interaction between the factors ($P < 0.001$), statistical differences between treatments ($P < 0.001$) and periods of evaluation ($P < 0.001$) (figure 3b). In control and waterlogged plants, at 16 days, the values were 0.87 and 1.80 mmol/g GLU residue, showing an increase of 106.9% in plants exposed to waterlogging (figure 3b).

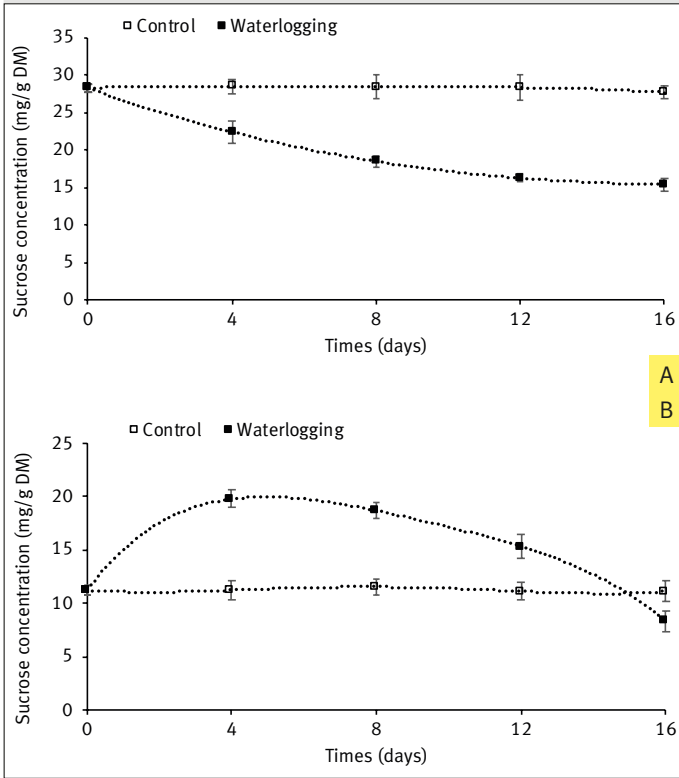


Figure 2. Sucrose concentration in the root (A) and the leaf (B) in young *Parkia gigantocarpa* plants exposed to waterlogging conditions. Squares represent the mean values of five replicates, and error bars represent the mean standard errors.

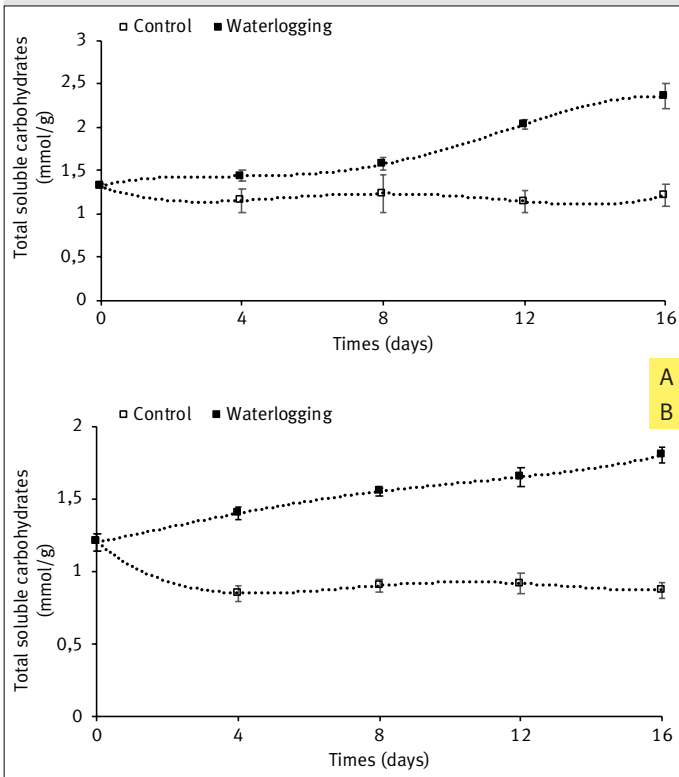


Figure 3. Total soluble carbohydrates concentration in the root (A) and the leaf (B) in young *Parkia gigantocarpa* plants exposed to waterlogging conditions. Squares represent the mean values of five replicates, and error bars represent the mean standard errors.

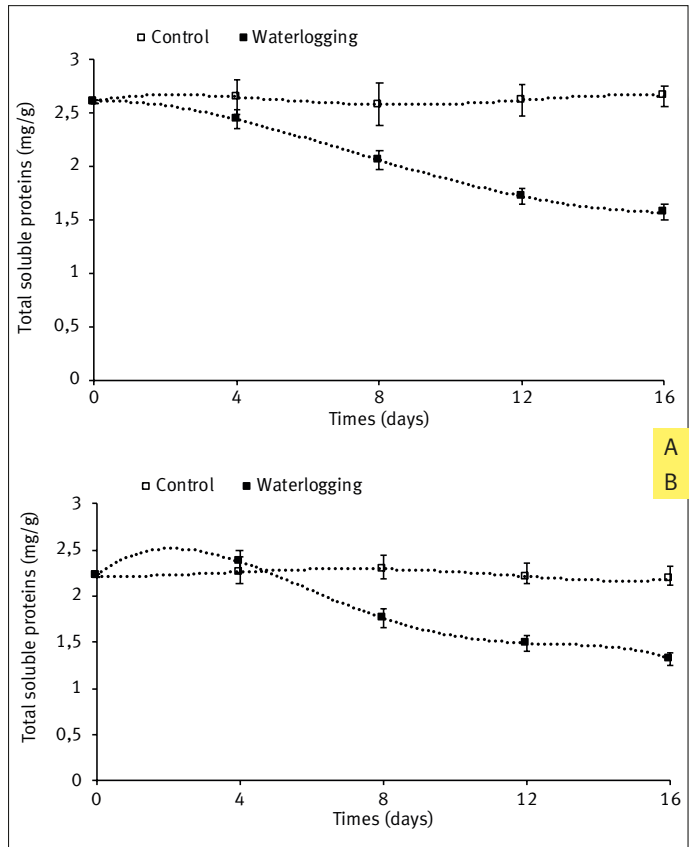


Figure 4. Total soluble proteins concentration in the root (A) and the leaf (B) in young *Parkia gigantocarpa* plants exposed to waterlogging conditions. Squares represent the mean values of five replicates, and error bars represent the mean standard errors.

Total soluble proteins concentration in leaves and roots

Total soluble protein concentrations in leaves and roots of waterlogged plants were significantly reduced (figure 4ab), showing a significant interaction between factors ($P < 0.001$), difference between treatments ($P < 0.001$) and evaluation times ($P < 0.001$) (figure 4). At 16 days, total soluble protein concentrations in leaves were 2.66 and 1.57 mg/g DM protein in the control and waterlogged plants, respectively, showing a reduction of 40.98% in plants exposed to waterlogging (figure 4a). Soluble protein concentrations in roots at 16 days were 2.18 mg/g protein DM (control plants) and 1.32 mg/g DM protein (waterlogged plants), showing a reduction of 39.45% in plants exposed to waterlogging (figure 4b).

Discussion

The reduction in starch concentration (figure 1) in *P. gigantocarpa* exposed to waterlogging conditions could be related to a decrease in stomatal conductance (gs), as shown by the significant positive correlation ($P < 0.001$) between the variables (table I). Thus, the reduction of gs must have increased resistance to internal flow of CO_2 in leaf tissues and influenced the lower acquisition of carbon through photosynthesis for construction of starch molecules. Another explanation is the activity of enzymes hydrolases α and β amylase, acting on starch degradation in order to form sugars, especially sucrose, which promoted osmotic

adjustment of tissues for the conservation of the internal flow of water plants by reducing water potential.

Moreover, the reduction of starch in plants exposed to waterlogging conditions would be an alternative to support fermentative metabolism, which requires higher sugar concentration (Miro and Ismail, 2013). Another possible explanation is that the synthesized carbohydrates were not stored as starch during the day, but directly transported to the phloem to supply the roots with additional carbohydrates (Peuke *et al.*, 2015). Therefore, suggests that *P. gigantocarpa* in a short period of hypoxia increased the concentration of sucrose in root for the energy synthesis through fermentation, later, the reduction of sucrose would be justified by root necrosis with time of exposure of plant to stress.

The reduction in sucrose concentration in the leaves of young *P. gigantocarpa* plants is related to reduction in starch concentration, evidenced by the significant positive correlation ($P < 0.001$) between the variables (table I) or due to increased rate of sucrose translocation from the leaves to the roots promoted by the activity of enzymes hydrolases α and β amylase, which act in the degradation of starch. Alternatively, such reduction could be related to possible changes in the enzyme invertase (Arora *et al.*, 2017).

The increase in sucrose concentration in the root (figure 2) possibly occurred to supplement or compensate the demand for carbohydrates needed to sustain the anaerobic metabolism of plants (Kreuzwieser *et al.*, 2009; Arora *et al.*, 2017) at least in the initial stages of waterlogging.

Table I.

Pearson correlation coefficient between starch in leaf (St_{leaf}), starch in root (St_{root}), Total soluble carbohydrates in leaf (TSC_{leaf}), Total soluble carbohydrates in root (TSC_{root}), sucrose concentration in leaf (Sac_{leaf}), Sucrose concentration in root (Sac_{root}), stomatal conductance (gs) and foliar xylem water potential (Ψ_x) in young *Parkia gigantocarpa* plants exposed to waterlogging conditions.

Conditions		Ψ_x	gs	St_{leaf}	St_{root}
Control	TSC_{leaf}	-0.1135 ^{ns}	-	-	-
	TSC_{root}	0.0353 ^{ns}	-	-	-
	Sac_{leaf}	-	-	0.1144 ^{ns}	-0.2938 ^{ns}
	Sac_{root}	-	-	0.0451 ^{ns}	-0.2538 ^{ns}
	St_{leaf}	-	-0.0244 ^{ns}	-	-
	St_{root}	-	0.0372 ^{ns}	-	-
	N_{leaf}	-	0.2238 ^{ns}	-	-
	TSC_{leaf}	-0.6893 ^{***}	-	-	-
	TSC_{root}	-0.8964 ^{***}	-	-	-
Waterlogging	Sac_{leaf}	-	-	0.9454 ^{***}	0.8335 ^{***}
	Sac_{root}	-	-	0.2401 ^{ns}	0.0306 ^{ns}
	St_{leaf}	-	0.8202 ^{***}	-	-
	St_{root}	-	0.7090 ^{***}	-	-
	N_{leaf}	-	0.4584 [*]	-	-

^{ns}: Not significant by F test; ^{*}: Significant by F test ($P < 0.05$); ^{***}: Significant by F test ($P < 0.001$).

In general, waterlogging conditions increases TSC concentration in plants (Rosa *et al.*, 2009). The accumulation of carbohydrates is considered to be important for protecting cellular structures such as biomembranes, which can be degraded by water stress in the hyaloplasm and by the increase in the concentration of ionic substances, inactivating several enzymes in the cytosol or for supply of the carbohydrate demand of shoots and root in anoxic conditions (Liu *et al.*, 2011).

The increase of TSC concentration in leaves and roots (figure 3) in young *P. gigantocarpa* plants exposed to waterlogging conditions is related to reduction of water potential (Ψ_x), as evidenced by the significant negative coefficient of correlation ($P < 0.001$) between the variables (table I). The accumulation of this compatible osmolyte, especially in the cytoplasm, reduces the osmotic potential of leaf tissue cells, and therefore its Ψ_x (Jaleel *et al.*, 2007) results in the Ψ_x gradient between shoot-root-soil, allowing the absorption and soil water transport to the shoot, contributing to the maintenance of turgor cell. Thus, it can be inferred that during waterlogging conditions, *P. gigantocarpa* accumulated TSC that were used in osmotic adjustment of plant tissues to maintain water absorption.

The increase of TSC concentration in the roots (figure 3) of *P. gigantocarpa* exposed to waterlogging conditions shows that translocation of these substances was not affected by stress, suggesting a continuous transport of these substances to the roots (Islam and Macdonald, 2004). Although increased TSC concentration in roots of waterlogged plants has been reported as a form of stress tolerance (Araki *et al.*, 2012), in this study the increase in TSC may have been a plant response as a result of lower demand of carbohydrates due to diminution of metabolism in roots and growth.

In hypoxic or anoxic conditions, protein synthesis is impaired, because it is a process for expenditure of energy demand (Nanjo *et al.*, 2010) and, in these conditions, there is a decrease in ATP production.

Thus, the reduction of TSP (figure 4) in *P. gigantocarpa* exposed to waterlogging conditions suggests that plants under low availability of oxygen inhibit certain enzymes related to aerobic metabolism or active proteolytic enzymes that degrade protein accumulated in plants. Possibly, it is a plant defense strategy, since the amino acids resulting from the breakdown of proteins would be subject to interconversion for biosynthesis of specific amino acids (Reggiani *et al.*, 2000), such as proline, which is directly related to osmotic adjustment of the leaf tissue. Alternatively, the amino acids would be used for synthesizing anaerobic polypeptides, such as alcohol dehydrogenase (ADH) and lactate dehydrogenase (LDH) as a way to compensate for the depletion of aerobic proteins (Zabalza *et al.*, 2009).

Another explanation for the reduction of TSP in *P. gigantocarpa* exposed to waterlogging conditions is that ATP reduction in roots causes reduction of nitrogen metabolism, adversely affecting the activity of nitrate reductase and glutamine synthetase (Andrade Júnior *et al.*, 2016). This can influence total nitrogen balance and amino acids, leading to a decrease of plant protein synthesis.

Conclusion

In plants exposed to waterlogging conditions, starch and soluble protein concentrations decreased in the leaves and roots, but total soluble carbohydrates increased in these organs.

Sucrose concentrations decreased in leaves and increased in the root of young *Parkia gigantocarpa* plants exposed to waterlogging conditions.

Thus, the data showed susceptibility of young *P. gigantocarpa* plants exposed to waterlogging conditions.

At 16 days of experiment, although in waterlogged plants the total soluble carbohydrates increased, the concentrations of starch, soluble protein and sucrose decreased, showing the sensitivity of young plants of *P. gigantocarpa* to waterlogging conditions.

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Viana de Andrade Júnior *et al.* – Author's contributions

Contributor role	Contributor names
Conceptualization	W. Viana de Andrade Júnior, B. Gomes dos Santos Filho, C. Ferreira de Oliveira Neto
Data Curation	W. Viana de Andrade Júnior, B. Gomes dos Santos Filho, C. Ferreira de Oliveira Neto
Formal Analysis	W. Viana de Andrade Júnior, B. Gomes dos Santos Filho, C. Ferreira de Oliveira Neto
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Investigation	W. Viana de Andrade Júnior
Methodology	W. Viana de Andrade Júnior, B. Gomes dos Santos Filho, C. Ferreira de Oliveira Neto
Project Administration	W. Viana de Andrade Júnior
Resources	C. Ferreira de Oliveira Neto, E. D. Cruz
Software	R. Shiguera Okumura
Supervision	B. Gomes dos Santos Filho, C. Ferreira de Oliveira Neto
Validation	W. Viana de Andrade Júnior, B. Gomes dos Santos Filho, C. Ferreira de Oliveira Neto
Visualization	W. Viana de Andrade Júnior
Writing – Original Draft Preparation	W. Viana de Andrade Júnior
Writing – Review & Editing	V. Resende do Nascimento, J. Taynara da Silva Martins, L. Corrêa Machado, D. J. Palheta de Sousa, J. S. Silva Teixeira

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