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Impacts of passion fruit woodiness disease (Cowpea Aphid-Borne Mosaic Virus) on single-leaf gas exchange of *Passiflora edulis.*

Marco Antônio da Silva Vasconcellos[1], Wallace de Paula Bernado[2], Ellen Moura do Vale[2], Anne Reis Santos[2], Guilherme Augusto Rodrigues de Souza[2], Weverton Pereira Rodrigues[3], Eliemar Campostrini*[2]

[1]Department of Plant Science, Institute of Agronomy, Federal Rural University Federal of Rio de Janeiro, BR 465, km 7, Seropédica, RJ 23890-000, Brazil
[2]Plant Physiology Laboratory, LMGV, Agricultural Science and Technology Center, State University of North Fluminense, Av. Alberto Lamego, 2000, Campos dos Goytacazes, RJ 28013-602, Brazil
[3]Universidade Estadual da Região Tocantina do Maranhão, CCANL Estreito – Maranhão

***Corresponding author: Eliemar Campostrini** ✉

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Abstract: Passion fruit woodiness disease (PWD) PWD is primarily caused by potyviruses (Cowpea Aphid-Borne Mosaic Virus) and is considered the most economically important and a limiting factor for passion fruit production in Brazil. Understanding the effects of the infectious process on the host is one of the goals of parasitism physiology. The experiment was conducted at the commercial panting in Rio de Janeiro state, Brazil, with 10 healthy plants of yellow passion fruit (*Passiflora edulis*) [control (CTL) leaf], cv. FB200 with 7 months of age (beginning of fruit production), and 10 plants with passion fruit woodiness virus (PWD) (PWD leaf) were selected. Leaves of field-grown passion fruit (*Passiflora edulis*) plants infected with PWD were selected to determine its influence on single-leaf gas exchange. Stomatal conductance, transpiration and net CO_2 assimilation rate in leaves of field-grown were reduced by PWD infection. Negative effects on single-leaf gas exchange in the yellow passion fruit supported our initial hypothesis that PWD cause impacts on stomatal conductance, transpiration, and net CO_2 assimilation rate. These results suggest that reduced growth, yield, and fruit quality common in PWD-infected passion fruit plants is caused, at least partially, by reduced single-leaf gas exchange.

Keywords: Photosynthesis, stomatal conductance, transpiration, Passiflora edulis

Abbreviations: A_{net} - net CO2 assimilation rate; CTL – Control; E – Transpiration rate; g_s – Stomatal conductance; LT – Leaf temperature; PPFD – Photosynthetic photon flux density; PWD - Passion fruit woodiness disease; PWD – Passion fruit woodiness disease.

Introduction

The yellow passion fruit (*Passiflora edulis*) is widely distributed in tropical and subtropical areas of the world and becomes popular because of balanced nutrition and health benefits (He et al., 2020). Currently, Brazil is the largest producer of this fruit. According to the Agricultural Census from 2021, 683,993 tons of passion fruit were harvested in Brazil on 44,827 hectares, thus estimating an average yield per hectare of 15.25 tons. The value of production reached 1,533,905 million reais (IBGE, 2024).

However, the cultivation and production of passion fruit are severely affected by various pathogens, such as viruses, bacteria, and fungi. Among them, viral disease is an extremely serious disease of passion fruit and a yield-limiting factor for the crop (Chen et al., 2021). Passion fruit woodiness disease (PWD) is considered the most economically important and a limiting factor for passion fruit production in Brazil (Cerqueira-Silva et al., 2014). The main characteristic symptoms of PWD are reduced size and deformation of the plants because of shortening of the internodes; different levels of wrinkling and mosaic formation, with the possible occurrence of bubbles or blisters on the leaf surface; formation of mosaics on leaves; and woodiness and deformation of the fruits (Oliveira et al., 2013; Cerqueira-Silva et al., 2014).

When plants are attacked by pathogens, physiological and photosynthetic properties are often impaired. Infection by pathogens may lead to a decrease in photosynthesis rates and changes in the photosynthetic apparatus (Alves et al., 2011). To triggering defenses to deter the pathogen by allocating resources from growth to defense, a reduction in photosynthetic capacity in the remaining leaf tissues can represent a "hidden cost" of defense (Bilgin et al., 2010).

Understanding the effects of the infectious process on the host is one of the goals of parasitism physiology. Knowledge of the way in which a pathogen mobilizes and alters the physiology and growth of the host plant can help to establish the basis for disease control or management and allow for the suppression or reduction of damage to crops.

This study aimed to quantify the loss of photosynthetic capacity in virus-infected leaves, as viruses damage chloroplasts, to provide a disease restriction, supporting the decision-making process for uprooting (eradication) of plants exhibiting symptoms, since virus-infected plants exhibit reduced photosynthetic activity. Thus, we hypothesized that PWD cause negative impacts on single-leaf gas exchange.

Results

Micro-environmental data

The maximum Photosynthetic photons flux density (PPFD) values were 1340.3 ± 66.38 and 1271 ± 72.72 μmol m^{-2} s^{-1}, CTL and PWD treatments at 9:00h, respectively, during the measures (Fig. 1a). In both treatments, high PPFD was at 11:00h, showing 1792.7 ± 80.73 and 1847.9 ± 24.91 μmol m^{-2} s^{-1} for CTL and PWD treatments, respectively. However, maximum PPFD measured in both treatments was at 14:00h, reaching approximately 1933.1 ± 14.97 and 1814.3 ± 68.94 μmol m^{-2} s^{-1}, for CTL and PWD, respectively. At 16:00h, a considerable PPFD reduction was observed, showing 1589.5 ± 67.03 and 1390.7 ± 57.47 μmol m^{-2} s^{-1}.

In both treatments, leaf temperature (LT) values increased similarly as PPFD (Figure 1b), and the maximum LT value was obtained 14:00h reaching 37.79 ± 0.15 and 37.94 ± 0.2° C in CTL and PWD treatments, respectively. In addition, highest relative humidity was observed in both treatments at 9:00h with 51.03 ± 0.6 and 47.45 ±1.18 % in CTL and PWD, respectively (Figure 1c).

Leaf gas-exchange measurements

The PWD showed significant reduction on A_{net} during the day (Figure 2a). The PWD showed significantly decreased of 41.5 % in A_{net} values than CTL at 9:00h (ca. 9.74 ± 0.49 vs ca. 16.65 ± 0.68 μmol CO_2 m^{-2} s^{-1}, respectively). At 11:00h, PWD treatment maintained with significantly decreased (41%) in A_{net} values than CTL treatment (ca. 9.82 ± 0.54 vs ca. 16.39 ± 0.34 μmol CO_2 m^{-2} s^{-1}, respectively). At 14:00h, a decrease in C-assimilation in CTL occurred. However, PWD remained with significantly decreased (41%) in Anet values when compared to CTL treatment (ca. 9.53 ± 0.54 vs ca. 13.97 ± 0.60 μmol CO_2 m^{-2} s^{-1}, respectively). On the end of day (16:00h), a light increased in C-assimilation occurred in CTL and decreased in PWD treatment in C-assimilation when compared to 14:00h (ca. 9.03 ± 0.40 vs ca. 14.74 ± 0.72 μmol CO_2 m^{-2} s^{-1}, respectively).

The g_s values was always lower in PWD than CTL leaf in all diurnal period (Figure 2b). At 9:00h period, PWD treatment showed significantly lower g_s than CTL (± 36%) (ca. 0.16 ± 1.01 vs ca. 0.25 ± 0.01 mol H_2O m^{-2} s^{-1}). In the 11:00h and 14:00h, g_s in PWD was 0.16 ± 0.01 and 0.17 ± 0.01, while in CTL treatment was 0.21 ± 0.01 and 0.21 ± 0.01 mol H_2O m^{-2} s^{-1}. PWD treatment maintained somewhat lower values of g_s at 16:00h (ca. 0.18 ± 0.01 mol H_2O m^{-2} s^{-1}), while CTL maintained somewhat higher in g_s (± 22%) (ca 0.23 ± 0.01 mol H_2O m^{-2} s^{-1}) when compared to PWD treatment.

The PWD showed significant lower E than CTL treatment in all diurnal period (Figure 2b). PWD showed significantly decreased of 30.5 % in E values than CTL at 9:00h (ca. 4.2 ± 0.00023 vs. ca.6.0 ± 0.23 mmol H_2O m^{-2} s^{-1}, respectively). At 11:00h, E in PWD treatment was 6.2 ± 0.25 while CTL was ca. 6.9 ± 0.23 mmol H_2O m^{-2} s^{-1}. During 14:00h, PWD maintained with reduced values in E than CTL treatment (ca 7.5. ± 0.53 vs. ca. 8.9 ± 0.39 mmol H_2O m^{-2} s^{-1}, respectively). At 16:00h), PWD showed significantly decreased of 17 % in E values than CTL treatment, which values of 6.9 ± 0.30 and 8.3 ± 0.28 mmol H_2O m^{-2} s^{-1}, respectively.

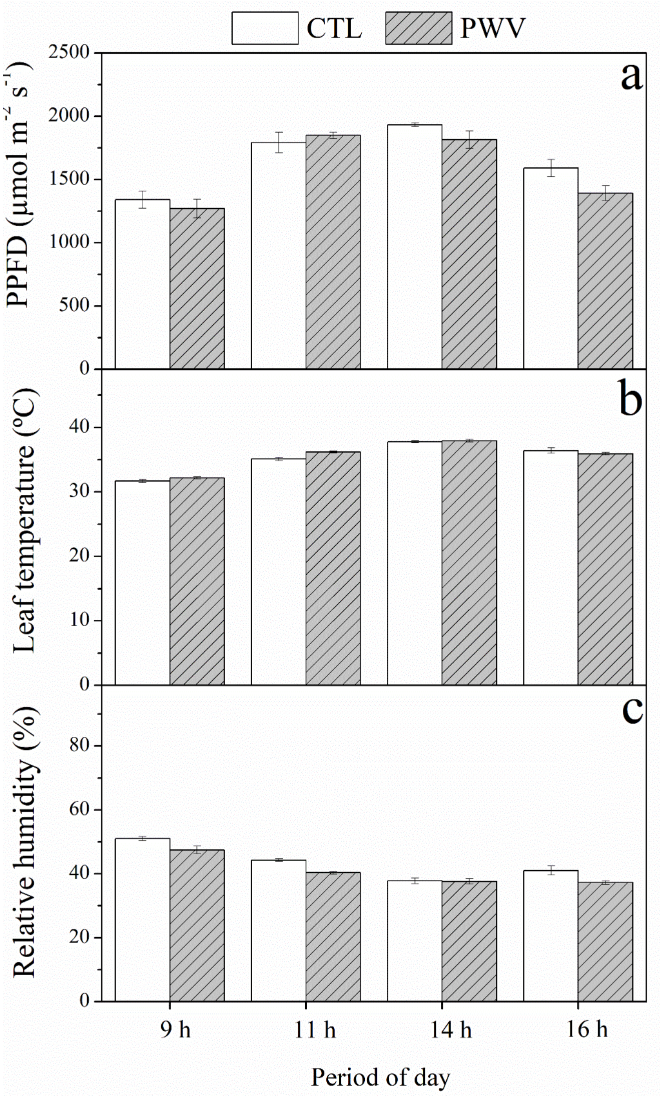

Fig 1. Add a general legend. a) PPFD (μmol m^{-2} s^{-1}) on the leaf. b) Leaf temperate (°C). c) Relative humidity (%) inside of LI-6200 chamber. Results during the measures. CTL (healthy leaf) and PWD (leaf-associated vírus).

Discussion

Passion fruit woodiness virus (PWD) is one of the most important phytosanitary problems which affects the passion fruit crop, causing large production losses worldwide (Santos-Jiménez et al., 2022). When infected, plants have a decreased in leaf area and fruit weight, with a decreased in the number of fruits, quality, and your commercial values (Nascimento et al., 2006). In the leaves, the major symptoms of disease include severe foliar mosaic, chlorotic spots, roughness, leaf blister, distortion, deformation, and irregular thickness (Peruch et al., 2009;

Colariccio et al., 2018)In addition, plants infected with PWD can cause sever yield losses and reduction on plant life by 50% (Fischer and Rezende, 2008).

In this study, physiological responses in the yellow passion fruit (*Passiflora edulis*) supported our initial hypothesis that PWD cause impacts on single-leaf gas exchange. The PWD negatively effects on ± 41% on A_{net} during the all-day periods (Figure 2a). Leaf infected with PWD showing anatomical changes in the cell wall structure and/or the conformation and distribution of organelles, altering the biochemical processes and synthesis and productivity (Grove and Marsh, 2011; El-Banna et al., 2014; Xiao et al., 2016). Consequently, reduction on CO_2 assimilation, which dependent of stomatal conductance, and green leaf area, since photosynthesis use the sunlight energy intercepted for leaves for convert CO_2 in carbohydrates, being responsible for 90% of the biomass and yield of crops (Zelitch, 1982; Simkin et al., 2019). In fact, PWD shows a bubbles or blisters occurrence on the leaf surface, which can affetct on net CO_2 assimilation rate (Rezende, 2006).

Stomatal conductance (g_s) is quantified as the capacity for exchanging CO_2 and water vapor, typically normalized by leaf area (Xiong and Flexas, 2020). Our study showed that CTL plants had higher g_s than PWD infected plants (Figure 2b), which supports their higher A_{net} values in CTL plants (Figure 2a). The stomata can differ in density and size, in addition, their distribution can generate high g_s impact (de Boer et al., 2016; Muir, 2018; Drake et al., 2019). We suggest that PWD leaves showed the greatest morphological and anatomical changes, with an important impact on leaf expansion, stomatal distribution, consequently metabolism and production of photoassimilates (Fernández-Calvino e al., 2014; Murray et al., 2016). Thus, gs is the main key physiological parameter can affect the productivity under both optimum growth and abiotic conditions (Roche et al., 2015; Rahnama et al., 2010). In addition, any change in leaf morphological traits, mainly stomatal density and distribution, and epidermal parameters can significantly affect single-leaf gas exchange and their relationships with an environmental factor (Woodward, 1987; Nilson and Assmann, 2007).

The morphological and anatomical leaves changes of PWD cause a stronger reduction on g_s, consequently a significantly reduction in net CO_2 assimilation rate and transpiration per unit leaf area (*E*) (Figure 2c). Once, the balancing carbon assimilation and transpiration depends on the fine-tuning of the stomatal aperture (Hasanuzzaman et al., 2023). Our results suggest that , which can reduce mineral nutrient absorption, biomass production, as well as yield of passionfruit.

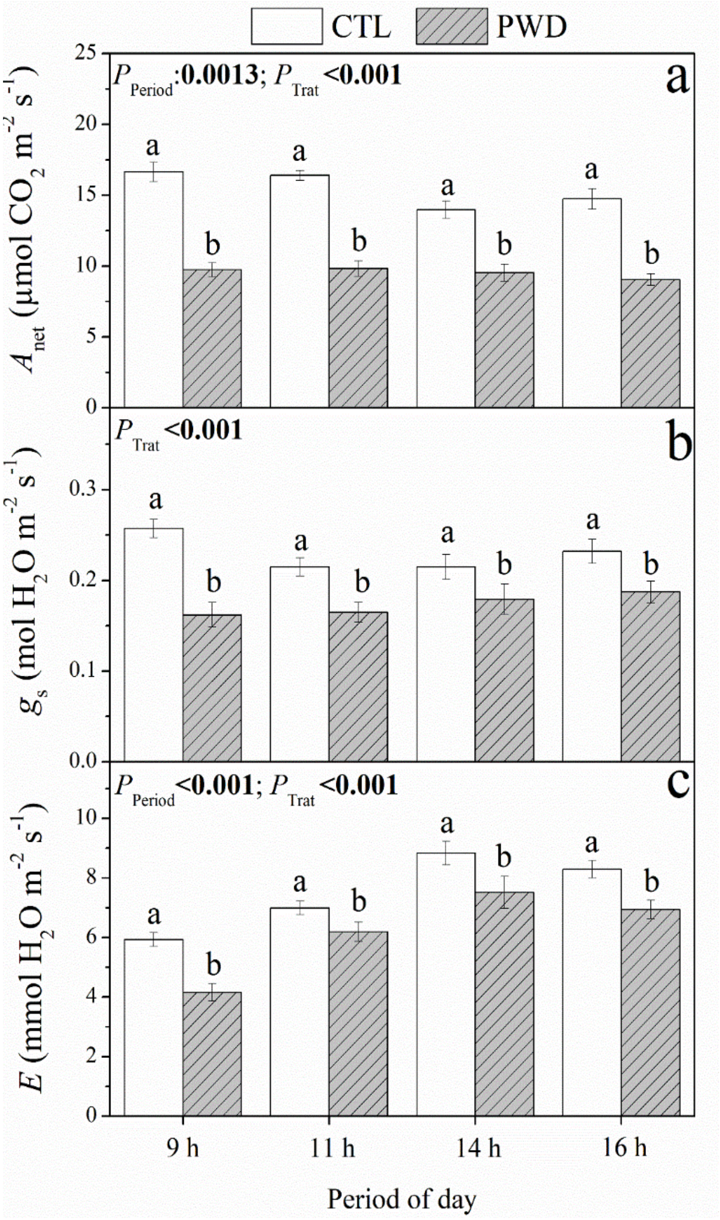

Fig 2. a) Net CO_2 assimilation rate (A_{net}). b) Stomatal conductance (g_s). c) Transpiration (*E*). (n=10). CTL (healthy leaf) and PWD (leaf-associated virus) treatments. The ANOVA P-vales are shown (n=10). P < 0,05 was considered significant. Vertical bars represent estimated S.E.

Materials and methods

Experimental site and species description

The experiment was conducted at the commercial panting of yellow passion fruit (*Passiflora edulis* FB200 with 7 months of age (beginning of fruit production), in Vera Cruz (22º13'11" S and 49º49'10" W, at 628 m de altitude), Rio de Janeiro state, Brazil. On April 1999, 10 healthy plants of yellow passion fruit (*Passiflora edulis*) [control (CTL) leaf], and 10 plants with passion fruit woodiness virus (PWD) were selected after showing the typical visual symptoms of of mosaic virus. Plants were set at a spacing of 3.5 m x 3.0 m in topography with mild slopes and sandy-textured soil classified as a Dark Red Latosol (Oxisol) prepared, fertilized and irrigated (≈ 6 and 10 L H_2O $plant^{-1}$ day^{-1}) in accordance with (Piza Júnior et al., 1997). The remaining cultural practices were carried out in accordance with (Rizzi et al., 1998).

Virus detection

The presence of virus in *Passiflora edulis* plants was confirmed according by Inoue et al. (1995). For this, four isolates of PWD were collected from *Passiflora edulis* and characterized. Filamentous virus particles, typical of potyviruses, were seen in leaf dip preparations from infected samples. In many leaf parenchyma cells of infected plants some chloroplasts appeared with different degrees of disorganization. Serological reactions using

Table 1. Average temperature (°C), Minimum temperature (°C), Maximum temperature (°C), Rain (mm), Humidity (%), Rainy days (d); Photoperiod (p). Date obtained in 1998 and 1999.

	January	February	March	April	May	June	July	August	September	October	November	December
Average temperature °C)	26.4	26.6	26.7	26	25.1	24.2	23.5	23.4	24.1	25	25.7	26.3
Minimum temperature (°C)	24.8	25	25.1	24.5	23.8	23	22.3	22.2	22.7	23.6	24.2	24.7
Maximum temperature (°C)	28.3	28.4	28.5	27.5	26.4	25.5	24.9	24.9	25.7	26.9	27.8	28.4
Rain (mm)	69	72	94	162	189	158	129	95	75	71	70	51
Umidity (%)	78%	78%	80%	82%	82%	81%	79%	78%	77%	78%	78%	78%
Rainy days (d)	12	13	15	17	17	17	17	16	13	11	10	9
Photoperiod (p)	9.6	9.3	8.8	8.1	7.6	7.6	7.7	7.9	8.1	8.5	9	9.5

antiserum against a Brazilian isolate of PWD gave positive results. Indirect ELISA demonstrated that all isolates were serologically related to each other and also to cowpea aphid-borne mosaic virus (CABMV). Leaf samples were collected and subjected of mechanical inoculation in other individuals of yellow passion fruit (*Passiflora edulis*) and cowpea (*Vigna unguiculata*), Virus infection was confirmed by serology and inoculation of indicator plants. The four viral isolates obtained from passionfruit were capable of infecting several plant species, although a difference in the intensity of symptoms induced by each isolate was observed in some hosts. Indirect ELISA method showed that the passion fruit isolates were serologically related to each other, and also to the potyvirus *Cowpea aphid-borne mosaic virus* (CABMV).

Leaf gas-exchange measurements

Leaf gas exchange was determined at 9 h, 11 h, 14 h, and 16 h, in a mature sunlight leaf (6th leaf from apex) from each plant, using an infrared gas analyzer (LI-6200, Li-Cor Inc., Lincoln, NE). The CO_2 concentration was ≈370 µmol mol^{-1} inside the leaf chamber. The leaf area was 0,00068 m^2 (volume chamber was 125 mL). Incident photosynthetic photons flux density (PPFD) on the chamber, leaf temperature and relative humidity inside the chamber were recorded. Net CO_2 assimilation rate (Anet, µmol CO_2 m^{-2} s^{-1}), stomatal conductance (g_s, mol H_2O m^{-2} s^{-1}), and transpiration rate (E, mmol H_2O m^{-2} s^{-1}) were measured.

Experimental design and statistical analysis

The experiment was carried out using a completely randomized design, in a 2 x 4 double factorial scheme for the evaluations carried with the leaf gas exchange measurements, considering 2 treatments (CTL, PWD), four periods (9 h, 11 h, 14 h and 16 h). Ten repetitions were performed for each treatment, totaling 20 plants, with measurements taken from one leaf per plant. The data were submitted to analysis of variance (ANOVA). Least-squares means and respective statistical errors (S.E.) were estimated from the fitted GLMs, the S.E. derived from GLM ANOVA being a residual mean square error for each response variables. Statistical analyses were performed using a R version 4.3.2, package 'ExpDes' (R Core Team, 2021). Graphs were generated using a OriginPro 2017 software.

Conclusion

Negative effects on single-leaf gas exchange in the yellow passion fruit (*Passiflora edulis*) supported our initial hypothesis that PWD cause impacts morphological and anatomical on the leaves. Consequently, reduction on stomatal conductance, transpiration, and net CO_2 assimilation rate. These results suggest that reduced growth, yield, and fruit quality common in PWD-infected passion fruit plants is caused, at least partially, by reduced single-leaf gas exchange.

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