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Application of *Rhodopseudomonas palustris* Moderates Some of the Crop Physiological Parameters in Mango Cultivar 'Keitt'

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Abstract

The bacterium *Rhodopseudomonas palustris* is a microorganism able to fix CO_2 and absorb sunlight and, therefore, can increase plant photosynthetic activity and mitigate the effects caused by abiotic stresses. Therefore, this work aimed to evaluate the effect of *R. palustris* on gas exchange and nitrate reductase activity of mango cv. 'Keitt' grown under tropical semiarid environmental conditions. The experiment was carried out simultaneously in two orchards with the same mango cultivar and crop management practices in Petrolina, Pernambuco, Brazil. The study followed a randomized block design with treatments distributed in a factorial arrangement (7 × 8), referring to different application methods of *R. palustris*: T1) control treatment; T2) 1.43×10^7 CFU/plant via fertigation; T3) 2.85×10^7 CFU/plant via fertigation; T4) 4.27×10^7 CFU/plant via fertigation; T5) 5.70×10^7 CFU/plant via fertigation; T6) 1.43×10^7 CFU/plant via fertigation $+1.43 \times 10^7$ CFU/plant via leaf spray; T7) 2.85×10^7 CFU/plant via fertigation $+1.43 \times 10^7$ CFU/plant via leaf spray; and evaluation at 0, 30, 60, 90, 120, 150, 180, and 210 days after application of *R. palustris*. The variables analyzed included: net photosynthesis, internal CO_2 concentration, stomatal conductance, transpiration rate, water-use efficiency, and nitrate reductase activity in leaves and roots. *R. palustris* affects gas exchange and nitrate reductase activity in mango cv. 'Keitt' grown in Brazilian semiarid, but the effects depend on the phenological phase evaluated. The application of *R. palustris* following 1.43×10^7 CFU/plant via fertigation $+1.43 \times 10^7$ CFU/plant via leaf spray were found to increase the photosynthetic activity of mango.

Keywords Mangifera indica · Abiotic stresses · Bacterioclorophylls · CO_2-fixing bacteria · Photosynthesis

Abbreviations

A	Net photosynthesis
aRN	Nitrate reductase activity
CFU	Colony forming units
Ci	Internal CO_2 concentration
CO_2	Carbon dioxide
E	Transpiration rate
FF	Full flowering
FI	Flowering induction

Data availability statement Raw data were generated at the Federal University of São Francisco Valley. Derived data supporting the findings of this study are available from the corresponding author ÍHLC on request.

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FP	Fruiting
gs	Stomatal conductance
PBZ	PBZ application
PC	Plant characterization
R	Use of different application methods of *R. palustris*
SM	Shoot maturation
VP	Vegetative phase
WUE	Efficiency of water use

Introduction

The São Francisco Valley, which has a tropical semiarid climate, is an important mango growing region, where 64% of the total Brazilian mango is harvested and 85% of the Brazilian exported mangoes comes from (Kist et al. 2021). This region is characterized by high solar radiation, high temperatures (~27 °C), low precipitation (420 mm), and low air humidity (~49%) (Alvares et al. 2013).

Under such conditions, the mango floral management includes water blade reduction during the branch maturation phase (Davenport 2007; Cavalcante et al. 2018; da Cunha et al. 2022b), to stimulate mango plant to accumulate carbohydrates (da Cunha et al. 2022a). The water blade reduction under high temperature cause stomata closure, and consequently, reduce CO_2 absorption that limits the photosynthetic activity (Santos et al. 2014; Chen et al. 2016; Abdellal et al. 2020, 2021).

Plant biostimulants have been used to mitigate the deleterious effects caused by the adverse conditions in São Francisco Valley, which leads to increased water and nutrients efficiency (Maçik et al. 2020; Mudo et al. 2020; Carreiro et al. 2022). Among the microorganisms used as biostimulants, the growth-promoting bacteria *Rhodopseudomonas palustris* has great potential in agriculture, mainly for promoting the increase of plant photosynthetic activity.

R. palustris can convert sunlight and atmospheric carbon dioxide into biomass and increases the plant chlorophyll contents (Hu et al. 2011; Nunkaew et al. 2014; Ge et al. 2017) by producing aminolevulinic acid, which is the first endogenous compound and the first compound in the porphyrin's synthesis (Streit et al. 2005; Taiz et al. 2017). The beneficial effects of *R. palustris* have already been verified for several crops such as Chinese cabbage—*Napa cabbage* (Xu et al. 2016), rice—*Oryza sativa* (Nunkaew et al. 2014), and cucumber seedlings—*Cucumis sativus* (Ge et al. 2017). However, there are no studies on application in fruit crops grown in tropical regions, including mango.

Thus, the objective of this study was to evaluate the effect of *R. palustris* of the crop physiological parameters of mango cv. 'Keitt' grown under tropical semiarid environmental conditions.

Materials and Methods

Plant Material and Growth Conditions

Mango plants (*Mangifera indica* L.) with 7 years of graft, cv. 'Keitt,' with uniform size and vigor in the fifth year of production were used in this study. The experiments were conducted from 2019 to 2020 simultaneously in two experimental orchards located in the municipality of Petrolina (09° 18′ S and 40° 25′ W; at an altitude of 349 m above mean sea level), State Pernambuco, Brazil. The climate of this region is classified as BSh (Köppen), which corresponds to a semiarid region. During the experiment, mean air temperature and relative humidity ranged from 24.1 °C to 34.6 °C and from 54.4% and 79.1%, respectively, with accumulated precipitation of 424 mm year^{-1}.

Treatments and Experimental Design

The treatments consisted of different application methods of *R. palustris*: T1) control treatment; T2) 1.43×10^7 CFU/plant via fertigation; T3) 2.85×10^7 CFU/plant via fertigation; T4) 4.27×10^7 CFU/plant via fertigation; T5) 5.70×10^7 CFU/plant via fertigation; T6) 1.43×10^7 CFU/plant via fertigation $+1.43 \times 10^7$ CFU/plant via leaf spray; T7) 2.85×10^7 CFU/plant via fertigation $+1.43 \times 10^7$ CFU/plant via leaf spray, with four blocks and three plants per plot. For the leaf spray treatments, it was used a mechanized sprayer (Arbus 2000 model) with a regulated volume of 1.2 L per plant.

The source of *R. palustris* used was Bioavance® (Vinhedo, Brazil), which contains 750.000 FCU/ml of *R. palustris*, with density of 1.0 g cm^{-3}, based on studies of Ge et al. (2017). Treatments were applied at every 30 days after the production pruning until the beginning of the fruit set, totaling seven applications.

The experiments were carried out in two orchards, simultaneously, with the same mango cultivar and management practices, in an experimental unit of 12.0 m^2. The plants, spaced with 6.0 m between the rows and 2.0 m between the plants, were daily drip-irrigated with twelve emitters per plant, for a flow of nearly 1.5 L h^{-1} each. All management practices such as pruning, control of weeds, pests, and diseases, plant growth regulators for gibberellin inhibition (Cultar®, Syngenta, Basel, Switzerland), and break dormancy (calcium nitrate and potassium nitrate) were performed following the instructions of Genú and Pinto (2002). Nutrient management was performed through a fertigation system, according to plant demand (Genú and Pinto 2002). Tip pruning was performed to synchronize vegetative flush events in the canopy.

Table 1 Analysis of net photosynthesis (*A*), internal CO_2 concentration (*Ci*), stomatal conductance (*gs*), transpiration (*E*), water use efficiency (WUE), and leaf chlorophyll indexes of mango 'Keitt' before treatments

Gas exchange				
A	*Ci*	*gs*	*E*	*WUE*
μmol CO_2 m^{-2} s^{-1}	mmol CO_2 m^{-2} s^{-1}	mmol of H_2O m^{-2} s^{-1}	mmol of H_2O m^{-2} s^{-1}	μmol of CO_2 m^{-2} s^{1} mmol H_2O m^{-2} s^{-1}
13.35	209.20	0.128	3.70	3.64

Data Gathered and Statistical Analysis

Gas Exchange

Before the treatments (Table 1) and after each treatment application, two evaluations of gas exchange were carried out, at 15 and 30 days after treatments (DAT), reaching 14 evaluations in each experiment. Readings were performed on the second plant of each plot, between 09:00 and 11:00 a.m.

For the quantification of gas exchange, healthy and fully expanded leaves from the last vegetative shoot were selected. The leaves were positioned in the middle third of the plant canopy, on the east side, and completely exposed to solar radiation. The measures were carried out with the aid of an IRGA—Infrared Gas Analyzer, model LCi Portable Photosynthesis System® (ADC BioScientific Limited, Hoddesdon, UK), with irradiation of 1800 μmol photons m^{-2} s^{-1} and airflow 300 mL min^{-1}.

The variables evaluated were net photosynthesis (*A*—expressed in μmol CO_2 m^{-2} s^{-1}), internal CO_2 concentration (*Ci*—mmol CO_2 m^{-2} s^{-1}), stomatal conductance (*gs*—mol H_2O m^{-2} s^{-1}), transpiration rate (*E*—mmol of H_2O m^{-2} s^{-1}), and the efficiency of water use (WUE = A/E) expressed in (μmol of CO_2 m^{-2} s^{-1}/mmol H_2O m^{-2} s^{-1}).

Nitrate Reductase Activity (aRN)

At 15 and 30 DAT, the nitrate reductase activity (aRN) in vivo in leaves and roots was determined. Samples were collected between 09:00 and 11:00 a.m., with three fully expanded leaves from the second vegetative flush, exposed to solar radiation and located at the medium height of the plant canopy; and secondary roots at 0.0–0.10 m soil depth layer, close to the drippers. The leaves were placed in plastic bags and the roots were wrapped in aluminum foil, and both were immediately submerged in ice and transported to the Plant Physiology laboratory of Federal University of São Francisco Valley following the methodology proposed by Majerowicz et al. (2003) and Santos et al. (2021).

Statistical Analysis

The data obtained were subjected to the analysis of variance (ANOVA). Statistical analysis was performed with the software 'R' (R Core Team 2019), using combined data of both experimental orchards. The means were compared by Scott-Knott's test with $p < 0.05$ and $p < 0.01$.

Results and Discussion

As show in Table 2, there was a significant interaction between the different application methods of *R. palustris* (R) and the evaluation dates after the first treatment application (DAT) for net photosynthesis (*A*), internal CO_2 concentration (*Ci*), stomatal conductance (*gs*), transpiration rate (*E*), and water use efficiency (WUE) (Table 2).

Net Photosynthesis

Between the second and fourth treatment application, the control treatment (T1) showed lower values of photosynthetic activity compared to other treatments, maintaining this trend until the end of the cycle (Fig. 1). In the sci-

Table 2 Net photosynthesis (*A*), internal CO_2 concentration (*Ci*), stomatal conductance (*gs*), transpiration (*E*), and water use efficiency (WUE) of mango 'Keitt' as a function of different application methods of *Rhodopseudomonas palustris* (R) and days after the first treatment (DAT)

	A	*Ci*	*gs*	*E*	*WUE*
Application methods of *R. palustris* (R)					
Value 'F'	12.16^{**}	15.27^{**}	1.28^{ns}	31.76^{**}	18.98^{**}
Evaluation dates after the first treatment application (DAT)					
Value 'F'	174.71^{**}	24.11^{**}	48.50^{**}	10.15^{**}	59.95^{**}
R × DAT					
Value 'F'	2.885^{**}	1.65^{**}	1.85^{**}	1.92^{**}	1.94^{**}
CV (%)	11.32	12.80	16.68	15.88	12.60

ns Not significant by the Scott-Knott test, *CV (%)* Coefficient of variation, *DAT* days after treatments
Means with the same letters do not differ by Scott-Knott test at 1% (**) probability error

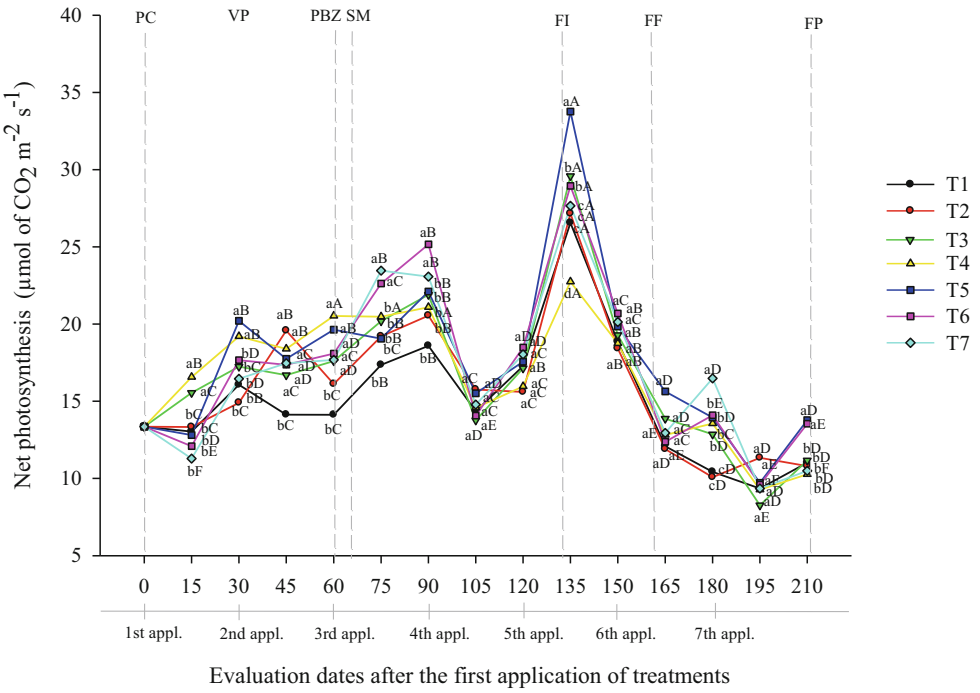

Fig. 1 Net photosynthesis of 'Keitt' mango as a function of different application methods of *Rhodopseudomonas palustris* application and days after the first application of treatments. *PC* plant characterization, *VP* vegetative phase, *PBZ* PBZ application, *SM* shoot maturation, *FI* flowering induction, *FF* full flowering, *FP* fruiting. Means followed by the same capital letters (different application methods of *R. palustris* application treatments) and common lowercase letters [evaluation dates] do not differ according to Scott-Knott's test (5%). *T1* control treatment, *T2* 1.43×107 CFU/plant via fertigation, *T3* 2.85×10^7 CFU/plant via fertigation, *T4* 4.27×10^7 CFU/plant via fertigation, *T5* 5.70×10^7 CFU/plant via fertigation, *T6* 1.43×10^7 CFU/plant via fertigation $+1.43 \times 10^7$ CFU/plant via leaf spray, *T7* 2.85×10^7 CFU/plant via fertigation $+1.43 \times 10^7$ CFU/plant via leaf spray

entific literature, there are reports that *R. palustris* has bacteriochlorophylls that, in addition to absorbing ultraviolet light, also absorb wavelengths between 800 and 870 nm, which comprise infrared waves (Hayashi et al. 1982; Gall and Robert 1999; Phongjarus et al. al. 2018). These broader wavelengths (ultraviolet and infrared) than chlorophylls are wavelength ranges in which plants cannot absorb (Soundararajan et al. 2019).

Photosynthetic activity increased for all treatments from 60 DAT, the time in which paclobutrazole (PBZ) was applied, up to 90 DAT, with emphasis on treatments applied via fertigation + leaf spray (T6, and T7), which increased by 30% and 35% at 75 DAT and 35% and 24% at 90 DAT, respectively, in relation to the control (T1), the treatment that presented the lowest *A* results (Fig. 1). This result suggests that after PBZ, the treatments performed in two application forms (fertigation and spray) were more efficient for *A* than the application of a higher dose only via fertigation (soil). Treatments via fertigation may be more affected by biotic and abiotic factors, which is a disadvantage compared to the foliar route (Pandey et al. 2013). *R. palustris* located on the surface of leaves and roots, grouping in colonies greater in the intercellular sulci, in a period between 0 h and 72 h when applied to tobacco plants (*Nicotiana benthamiana* cv. 'Changsha') via spraying and fertigation (Zhai et al. 2019).

Zhai et al. (2019) also verified the colonization efficiency of *R. palustris* and observed a different behavior found in tobacco. In rice (*Oryza sativa*), *R. palustris* showed a distribution linear along the leaf and root tissue, in the leaves, single cells occupied the longitudinal intercellular space of epidermal cells mesophiles; and in the root, the bacteria initiated colonization at the root apex, migrating longitudinally along the root. According to Su et al. (2019), strains such as *R. palustris* can colonize the phylosphere of plants and establish colonies of different adjustments to exert beneficial effects on the plant.

The increase in photosynthetic activity in 'Keitt' mango with *R. palustris* in the two forms of application is due to the greater production and excretion of 5-aminolevulinic acid (5-ALA) by plants (foliar route), which is one of the precursors of chlorophyll synthesis and a potential growth regulator and promotes greater metabolic activity of soil microorganisms, slightly altering specific bacterial groups that are beneficial to plants (via soil) (Xu et al. 2016; Ge and Zhang 2019).

The photosynthetic activity of 'Keiit' mango was reduced between the stages of shoot maturation and floral induction (105 DAT), but there was no statistical difference between treatments, although the application of 1.43×10^7 CFU/plant via fertigation (T2) was 14% higher

than the control (Fig. 1). This result was already expected, since the partial reduction of the irrigation amount associated with potassium or magnesium sulfate is a consolidated practice for mango in the São Francisco Valley to promote the maturation of branches before floral induction, which it can negatively affect gas exchange by exposing plants to water deficit (Santos et al. 2014). In comparison, the photosynthetic rate values obtained by Cunha et al. (2022a) in 'Tommy Atkins' mango with application of algae extract and proline as gas exchange stimulators, it appears that in the same phenological phase, our results (Fig. 1) were superior to those obtained by the authors (6.0 µmol of $CO_2\,m^{-2}\,s^{-1}$).

Mudo et al. (2020) reported a decline in photosynthetic metabolism during the branch maturation phase of mango cv. 'Tommy Atkins' in the Brazilian semiarid region, as also observed in present study (Fig. 1). Lu et al. (2012) also evaluated the *A* of five mango cultivars in northern Australia, and found reduced values during the dry season in comparison to the rainy season.

The highest peaks of net photosynthetic occurred after the 5th application of *R. palustris*, i.e., in the floral induction phase of 'Keiit' mango (135 DAT). In this phase, an application of 5.70×10^7 CFU/plant via fertigation (T5) showed the highest net photosynthetic between treatments (33.76 µmol of $CO_2\,m^{-2}\,s^{-1}$) and was 32.68% higher than the control treatment (T1) (Fig. 1). It is noteworthy that, for all evaluation periods, the application of the highest dose of *R. palustris* via fertigation promoted the highest net photosynthetic, which proves to be more advantageous for 'Keitt' mango than via foliar spraying, mainly during floral induction.

In the fruiting phase, at 210 DAT, treatments with 5.70×10^7 CFU/plant via fertigation (T5) and 1.43×10^7 CFU/plant via fertigation $+1.43 \times 10^7$ CFU/plant via foliar spray (T6) increased photosynthetic activity, with averages of 13.78 and 13.54 µmol of $CO_2\,m^{-2}\,s^{-1}$, corresponding to an increase of 25% (T5) and 22% (T6), respectively, in relation to the treatment control (T1). While the other treatments (T2, T3, T4, and T7) remain with lower photosynthetic rates and with values similar to the readings taken at 195 DAT (Fig. 1). The results quoted in Fig. 1 are similar to those of Lu et al. (2012) who also recorded *A* stabilization during the fruiting phase, even with adequate water supply, in five mango cultivars in Australia.

Internal CO_2 Concentration

For *Ci* (Fig. 2), control treatment (T1) presented practically constant data distribution, without statistical differences among all the evaluated dates and means varying

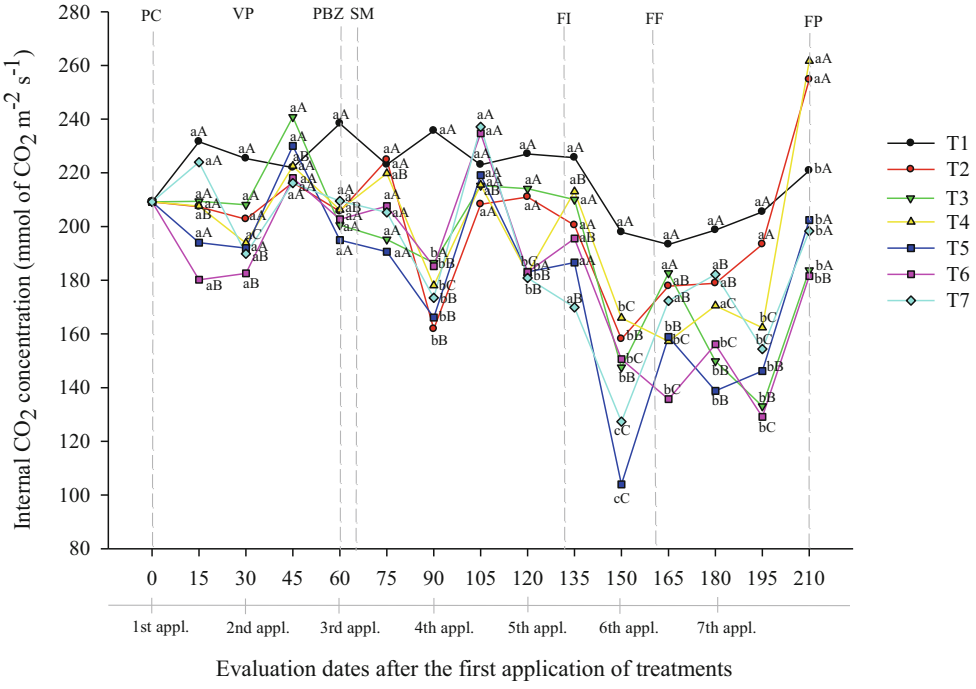

Fig. 2 Internal CO_2 concentration of 'Keitt' mango as a function of different application methods of *Rhodopseudomonas palustris* application and days after the first application of treatments. *PC* plant characterization, *VP* vegetative phase, *PBZ* PBZ application, *SM* shoot maturation, *FI* flowering induction, *FF* full flowering, *FP* fruiting. Means followed by the same capital letters (different application methods of *R. palustris* application treatments) and common lowercase letters (evaluation dates) do not differ according to Scott-Knott's test (5%). *T1* control treatment, *T2* 1.43×10^7 CFU/plant via fertigation, *T3* 2.85×10^7 CFU/plant via fertigation, *T4* 4.27×10^7 CFU/plant via fertigation, *T5* 5.70×10^7 CFU/plant via fertigation, *T6* 1.43×10^7 CFU/plant via fertigation $+1.43 \times 10^7$ CFU/plant via leaf spray, *T7* 2.85×10^7 CFU/plant via fertigation $+1.43 \times 10^7$ CFU/plant via leaf spray

between 193.34 and 238.35 mmol $m^{-2} s^{-1}$. Up to 75 DAT, there were no differences between the treatments, recording a difference at 90 DAT, when T1 was superior to the other treatments, with a mean of 235.68 mmol $m^{-2} s^{-1}$, which is 31.35% above T2, the lowest value found on this date.

CO_2 is a primary substrate for the photosynthesis process, thus, the CO_2 concentration available to plants has a direct effect on the photosynthetic rate, which tends to increase as the concentration of this gas is enhanced in the atmosphere (Taiz et al. 2017). However, in the present work, the higher *Ci* observed in control treatment is not associates with a higher photosynthetic activity in the plants of this treatment (Fig. 2).

The high *Ci* of control treatment in most evaluation dates may have been due to the plants in this treatment not using all the available substrate to carry out photosynthesis, suggesting that the photosynthetic activity may have been limited by biochemical factors involving the regeneration metabolism of enzymes that are consumed in the process and that are not supplied at the same speed (Lambers et al. 2008; Taiz et al. 2017).

During the floral induction and full bloom phases, control treatment was higher than other treatments (Fig. 2). At 150 DAT, the control treatment *Ci* was 197.88 mmol $m^{-2} s^{-1}$, which is 93.95 mmol $m^{-2} s^{-1}$ above the lowest mean (for 5.70×10^7 CFU/plant via fertigation) found on this date and during all the evaluations. Between 165 and 195 DAT control treatment (T1) and 1.43×10^7 CFU/plant via fertigation (T2) were similar, with an increase in T2 during the fruiting phase (210 DAT), concomitantly with a decrease in T1 on that date, with a difference of 15% between them. At 30 days after the 7th treatment application (210 DAT), 1.43×10^7 CFU/plant via fertigation and 4.27×10^7 CFU/plant via fertigation reached the highest *Ci* values among all evaluation dates, with averages of 254.73 and 261.63 mmol $m^{-2} s^{-1}$, respectively.

The low *Ci* values on most evaluation dates of treatments that received the *R. palustris* are due to the increase in photosynthesis (Fig. 1) promoted by the bacteria, causing greater demand and consumption of this substrate and, consequently, reducing the internal concentration of CO_2 in leaves (Lopes and Lima 2015).

Stomatal Conductance

For *gs* (Fig. 3), there was a similar trend for all treatments, which have higher values from vegetative growth to branch maturation, with a decline starting in the floral induction phase until full flowering, rising again in the fruiting phase.

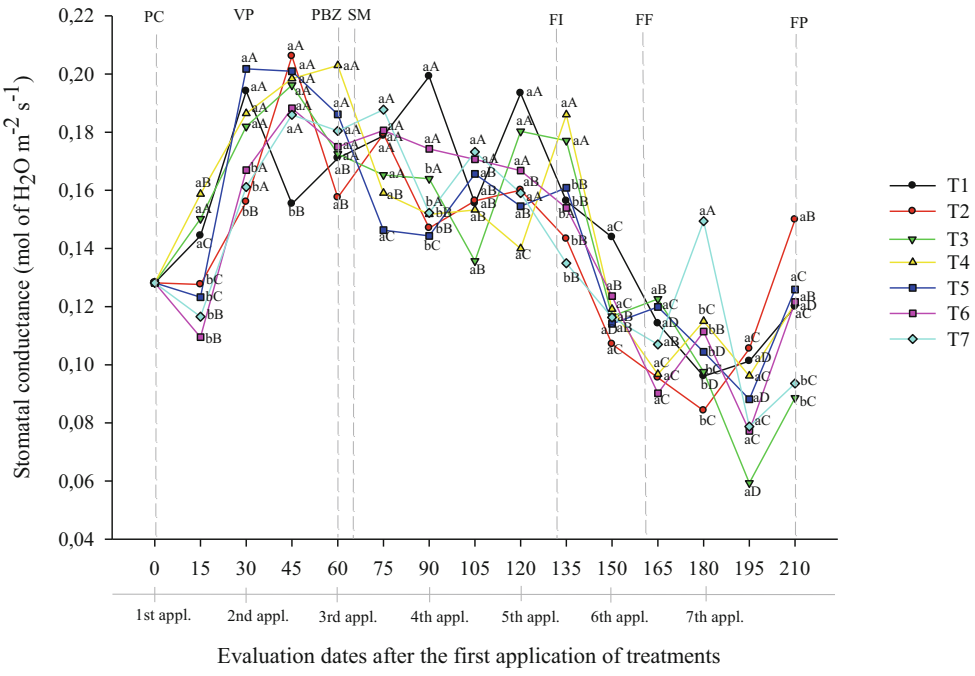

Fig. 3 Stomatal conductance of 'Keitt' mango as a function of different application methods of *Rhodopseudomonas palustris* application and days after the first application of treatments. *PC* plant characterization, *VP* vegetative phase, *PBZ* PBZ application, *SM* shoot maturation, *FI* flowering induction, *FF* full flowering, *FP* fruiting. Means followed by the same capital letters (different application methods of *R. palustris* application treatments) and common lowercase letters (evaluation dates) do not differ according to Scott-Knott's test (5%). *T1* control treatment, *T2* 1.43×10^7 CFU/plant via fertigation, *T3* 2.85×10^7 CFU/plant via fertigation, *T4* 4.27×10^7 CFU/plant via fertigation, *T5* 5.70×10^7 CFU/plant via fertigation, *T6* 1.43×10^7 CFU/plant via fertigation +1.43×10^7 CFU/plant via leaf spray, *T7* 2.85×10^7 CFU/plant via fertigation +1.43×10^7 CFU/plant via leaf spray

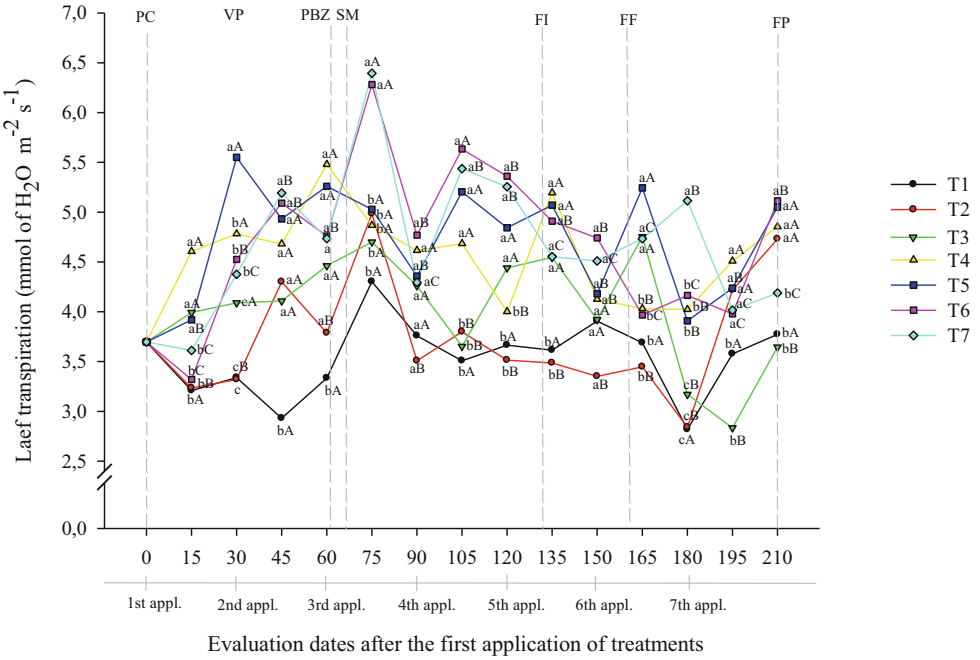

Fig. 4 Leaf transpiration of 'Keitt' mango as a function of different application methods of *Rhodopseudomonas palustris* application and days after the first application of treatments. *PC* plant characterization, *VP* vegetative phase, *PBZ* PBZ application, *SM* shoot maturation, *FI* flowering induction, *FF* full flowering, *FP* fruiting. Means followed by the same capital letters (different application methods of *R. palustris* application treatments) and common lowercase letters (evaluation dates) do not differ according to Scott-Knott's test (5%). *T1* control treatment, *T2* 1.43×10^7 CFU/plant via fertigation, *T3* 2.85×10^7 CFU/plant via fertigation, *T4* 4.27×10^7 CFU/plant via fertigation, *T5* 5.70×10^7 CFU/plant via fertigation, *T6* 1.43×10^7 CFU/plant via fertigation $+1.43 \times 10^7$ CFU/plant via leaf spray, *T7* 2.85×10^7 CFU/plant via fertigation $+1.43 \times 10^7$ CFU/plant via leaf spray

At 15 DAT, the control treatment (T1), 2.85×10^7 CFU/plant via fertigation (T3), and 4.27×10^7 CFU/plant via fertigation (T4) were superior to other treatments with *gs* of 0.14, 0.15, and 0.16 mol $m^{-2} s^{-1}$, respectively. The lowest *gs* values found on this date were recorded for application of 1.43×10^7 CFU/plant via fertigation $+1.43 \times 10^7$ CFU/plant via leaf spray (T6) and 2.85×10^7 CFU/plant via fertigation $+1.43 \times 10^7$ CFU/plant via leaf spray (T7), both with the *R. palustris* application via leaf spraying + fertigation, with a reduction of 24% and 19%, respectively, compared to the control (T1) (Fig. 3).

At 30 DAT *gs* increased in all treatments concerning the previous evaluation date, recording the highest means for control treatment (T1), 2.85×10^7 CFU/plant via fertigation (T3), 4.27×10^7 CFU/plant via fertigation (T4), and 5.70×10^7 CFU/plant via fertigation (T5). Additionally, at 45 DAT there was a *gs* decrease of T1, which was lower than the other treatments, especially with 1.43×10^7 CFU/plant via fertigation, the best treatment on this date, with an increase of 33% in relation to T1. At 90 DAT, only plants from treatments control treatment and 1.43×10^7 CFU/plant via fertigation $+1.43 \times 10^7$ CFU/plant via leaf spray presented higher *gs* values, 0.20 and 0.17 mol $m^{-2} s^{-1}$, respectively (Fig. 3).

At 105 and 120 DAT, no significant differences were observed between treatments for *gs*. The evaluations at 135 and 150 DAT occurred during the floral induction phase, but there were differences between treatments only at 135 DAT, in which application of 2.85×10^7 CFU/plant via fertigation and 4.27×10^7 CFU/plant via fertigation were 13% and 19% higher than control, respectively (Fig. 3).

During the full flowering phase, three evaluations were carried out, with no differences among treatments at 165 and 195 DAT (Fig. 3). However, at 180 DAT, full flowering stage, *R. palustris* application methods did not affect *gs* results, although an increase of 55% in T7 plants was recorded, a treatment with applications via fertigation + via leaf spray, even with a total concentration of bacteria lower than T5. This result could be hypothesized that the combined application provided greater comfort to the plants in this treatment, although the stomatal opening patter was not evaluated, just the stomatal conductance.

At 210 DAT, fruiting stage, treatments control (T1), 1.43×10^7 CFU/plant via fertigation (T2), 4.27×10^7 CFU/plant via fertigation (T4), 5.70×10^7 CFU/plant via fertigation (T5), and 1.43×10^7 CFU/plant via fertigation $+1.43 \times 10^7$ CFU/plant via leaf spray were similar (T6) and superior to 2.85×10^7 CFU/plant via fertigation (T3)

and 2.85×10^7 CFU/plant via fertigation $+1.43 \times 10^7$ CFU/plant via leaf spray (T7). T2 had the highest stomatal conductance (Fig. 3) with an increase of 25% as compared to the control (Fig. 2).

Transpiration Rate

For the *E* (Fig. 4), control treatment and 1.43×10^7 CFU/plant via fertigation showed lower results compared to other treatments up to 180 DAT, indicating that plants of both treatments lost less water during the production cycle. This result is a response that may not be interesting since the transpiration process occurs when there is stomatal opening and water is absorbed through the root system, which, consequently, influences the nutrient absorption by the roots to maintain plant metabolism (Taiz et al. 2017).

At 15 DAT, 'Keitt' mango plants that received 2.85×10^7 CFU/plant via fertigation (T3), 4.27×10^7 CFU/plant via fertigation (T4) and 5.70×10^7 CFU/plant via fertigation (T5) showed the highest transpiration rates, with increments of 24%, 43% and 22%, respectively, compared to the control. At 30 DAT, only 4.27×10^7 CFU/plant via fertigation (T5) remained above the values of the other treatments, with a difference of 66% in relation to the control treatment (Fig. 4). T4 and T5 treatments, characterized by the highest *R. palustris* doses supplied only via fertigation, had a greater influence on plant transpiration at the beginning of the vegetative growth phase compared to smaller doses.

In the evaluations carried out at 45 and 60 DAT, vegetative growth phase, all treatments that has *R. palustris* were similar, differing from the control that had the lowest *E*. During that period, the *R. palustris*, regardless of the dose or via of application, affected both *E* (Fig. 4) and *A* (Fig. 1), vital processes for nutrient absorption and photoassimilate synthesis required for the plant growth and vegetative development (Taiz et al. 2017; Yahia et al. 2019).

At the beginning of the branch maturation phase, evaluation at 75 DAT (Fig. 4), *E* increased in plants treated with *R. palustris* via fertigation + via leaf spray, 1.43×10^7 CFU/plant via fertigation $+1.43 \times 10^7$ CFU/plant via leaf spray (T6), and 2.85×10^7 CFU/plant via fertigation $+1.43 \times 10^7$ CFU/plant via leaf spray (T7), reaching the highest averages verified among all evaluation dates. During this phase, the control had the lowest *E* mean value that was 46% and 48% lower than T6 and T7, respectively.

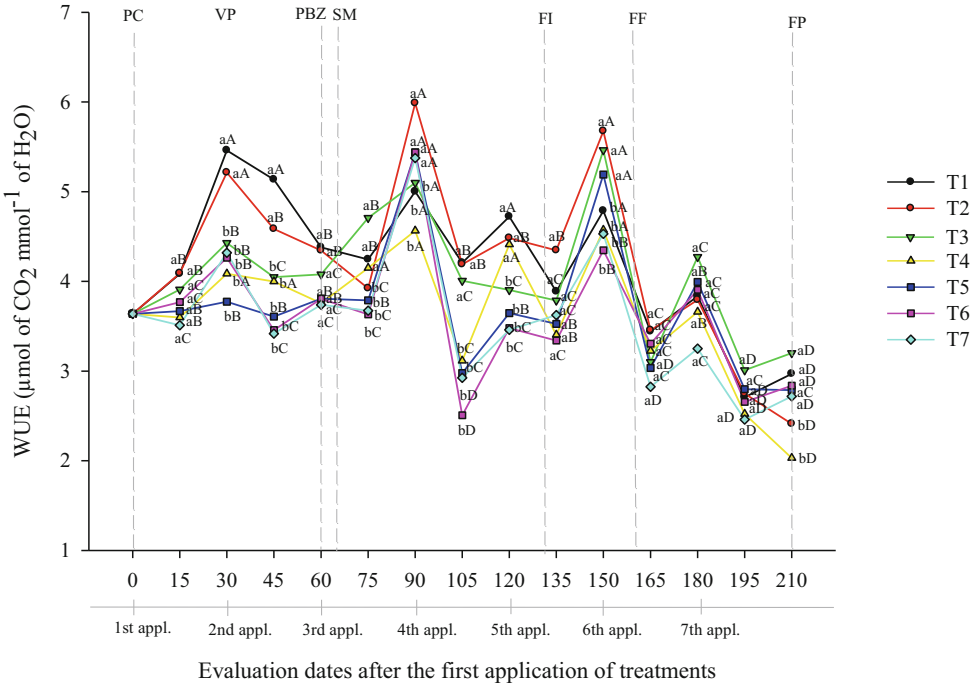

Fig. 5 Water use efficiency of 'Keitt' mango as a function of different application methods of *Rhodopseudomonas palustris* application and days after the first application of treatments. *PC* plant characterization, *VP* vegetative phase, *PBZ* PBZ application, *SM* shoot maturation, *FI* flowering induction, *FF* full flowering, *FP* fruiting. Means followed by the same capital letters (different application methods of *R. palustris* application treatments) and common lowercase letters (evaluation dates) do not differ according to Scott-Knott's test (5%). *T1* control treatment, *T2* 1.43×10^7 CFU/plant via fertigation, *T3* 2.85×10^7 CFU/plant via fertigation, *T4* 4.27×10^7 CFU/plant via fertigation, *T5* 5.70×10^7 CFU/plant via fertigation, *T6* 1.43×10^7 CFU/plant via fertigation $+1.43 \times 10^7$ CFU/plant via leaf spray, *T7* 2.85×10^7 CFU/plant via fertigation $+1.43 \times 10^7$ CFU/plant via leaf spray

Plants with high *E* tend to accumulate more solutes to maintain cell turgor (Taiz et al. 2017), which can benefit the branch maturation process.

At 90 DAT, *E* was not affected by treatments but, on the other hand, in the following evaluations, at 105 and 120 DAT, treatments with 5.70×10^7 CFU/plant via fertigation (T5), 1.43×10^7 CFU/plant via fertigation +1.43×10^7 CFU/plant via leaf spray (T6), and 2.85×10^7 CFU/plant via fertigation +1.43×10^7 CFU/plant via leaf spray (T7) presented the highest *E* values (Fig. 4). During these evaluation dates, the plants were under stress conditions caused by the reduction of water depths, which is a period foreseen during the branch maturation phase. The treatments with the highest *E* were those treated with *R. palustris* through two vias (T6 and T7), and the treatment with the highest *R. palustris* dose applied via fertigation (T5).

From floral induction to half of the full flowering stage, *E* average values of the control treatment and 1.43×10^7 CFU/plant via fertigation were below the others (Fig. 4). The plants of T1 and T2 reduced the photosynthetic and transpiration metabolism to guarantee a better WUE, hence they could tolerate the period of floral induction and full flowering, phases that demand more energy.

At 135 DAT, floral induction phase, *E* increased 26%, 44%, 40%, 36%, and 26% with 2.85×10^7 CFU/plant via fertigation (T3), 4.27×10^7 CFU/plant via fertigation (T4), 5.70×10^7 CFU/plant via fertigation (T5), 1.43×10^7 CFU/plant via fertigation +1.43×10^7 CFU/plant via leaf spray (T6), and 2.85×10^7 CFU/plant via fertigation +1.43×10^7 CFU/plant via leaf spray (T7) plants, respectively, compared to control treatment (T1). It demonstrates that *R. palustris* doses have a rapid mitigating action against environmental stresses, promoting maintenance of gas exchange and greater comfort for plants in phases that demand more energy. This fact was not observed in $1.43\times10^{7\ CFU}$/plant via fertigation (T2), which had the lowest *R. palustris* dose applied via fertigation (Fig. 4).

At 165 DAT, beginning of full flowering, the treatments with 2.85×10^7 CFU/plant via fertigation (T3), 5.70×10^7 CFU/plant via fertigation (T5), and 2.85×10^7 CFU/plant via fertigation +1.43×10^7 CFU/plant via leaf spray (T7) promoted the highest *E*, with increases of 29%, 42%, and 28%, respectively, concerning with control treatment (T1). Only T7 remained superior to the others at 180 DAT, with a difference of 82% in comparison with the control (Fig. 4).

From 195 DAT onwards, leaf transpiration increased in the application of 1.43×10^7 CFU/plant via fertigation plants (T2), a different result from that observed in previous evaluations, showing its late action. On this date, T2 was similar to with application of 4.27×10^7 CFU/plant via fertigation (T4), 5.70×10^7 CFU/plant via fertigation (T5), 1.43×10^7 CFU/plant via fertigation +1.43×10^7 CFU/plant via leaf spray (T6) and, 2.85×10^7 CFU/plant via fertigation +1.43×10^7 CFU/plant via leaf spray but it differed from control treatment and 2.85×10^7 CFU/plant via fertigation (T7). On the subsequent date, at 210 DAT, the fruiting stage, treatments T2, T4, T5, and T6 were similar among them and superior to the other treatments. At both dates mentioned above, 2.85×10^7 CFU/plant via fertigation (T3) had the lowest *E* means, with values 21% and 3% lower than T1 at 195 and 210 DAT, respectively (Fig. 4).

Table 3 Nitrate reductase enzyme activity in leaves and roots of mango 'Keitt' as a function of different application methods of *R. palustris* applied (R) and days after the first application of treatments (DAT)

	Nitrate reductase activity (aRN)	
	Leaf	Root
Application methods of *R. palustris* (R)		
Value 'F'	23.29**	19.11**
Evaluation dates after the first application of treatments (DAT)		
Value 'F'	189.49**	264.67**
	R × DAT	
Value 'F'	10.93**	9.12**
CV (%)	11.40	11.18

CV (%) Coefficient of variation, *DAT* days after treatments
Means with the same letters do not differ by Scott-Knott test at 1% (**) probability error

Water Use Efficiency

Regarding WUE (Fig. 5), the control treatment and 1.43×10^7 CFU/plant via fertigation (T2) were superior to the other treatments during the vegetative growth phase, with a marked increase at 30 and 45 DAT. Soon after this period, there was no statistical differences observe at 60 DAT.

In the branch maturation phase, at 90 DAT, there was an increase in WUE for all treatments, with emphasis on T2 which had the highest mean on all evaluation dates. At 90 DAT, the WUE increase of T2 concerning the control (T1) was 20%, followed by treatments on the application of 5.70×10^7 CFU/plant via fertigation, 1.43×10^7 CFU/plant via fertigation +1.43×10^7 CFU/plant via leaf spray, and 2.85×10^7 CFU/plant via fertigation +1.43×10^7 CFU/plant via leaf spray, with increments of 9%, 9%, and 7.5% as compared to the control, respectively (Fig. 5).

At 105 DAT, the water use efficiency of 'Keitt' mango plants showed superiority in the control treatment (T1), 1.43×10^7 CFU/plant via fertigation (T2); and at 210 DAT in control treatment, 2.85×10^7 CFU/plant via fertigation (T4), and 4.27×10^7 CFU/plant via fertigation (T3). T1 and T2 plants presented *gs* similar to the other treatments (Fig. 3), and even so, they transpired less (Fig. 4) and were more efficient in using water (Fig. 5). The *E* reduction, that is, resistance to water leakage by diffusion, is a mechanism

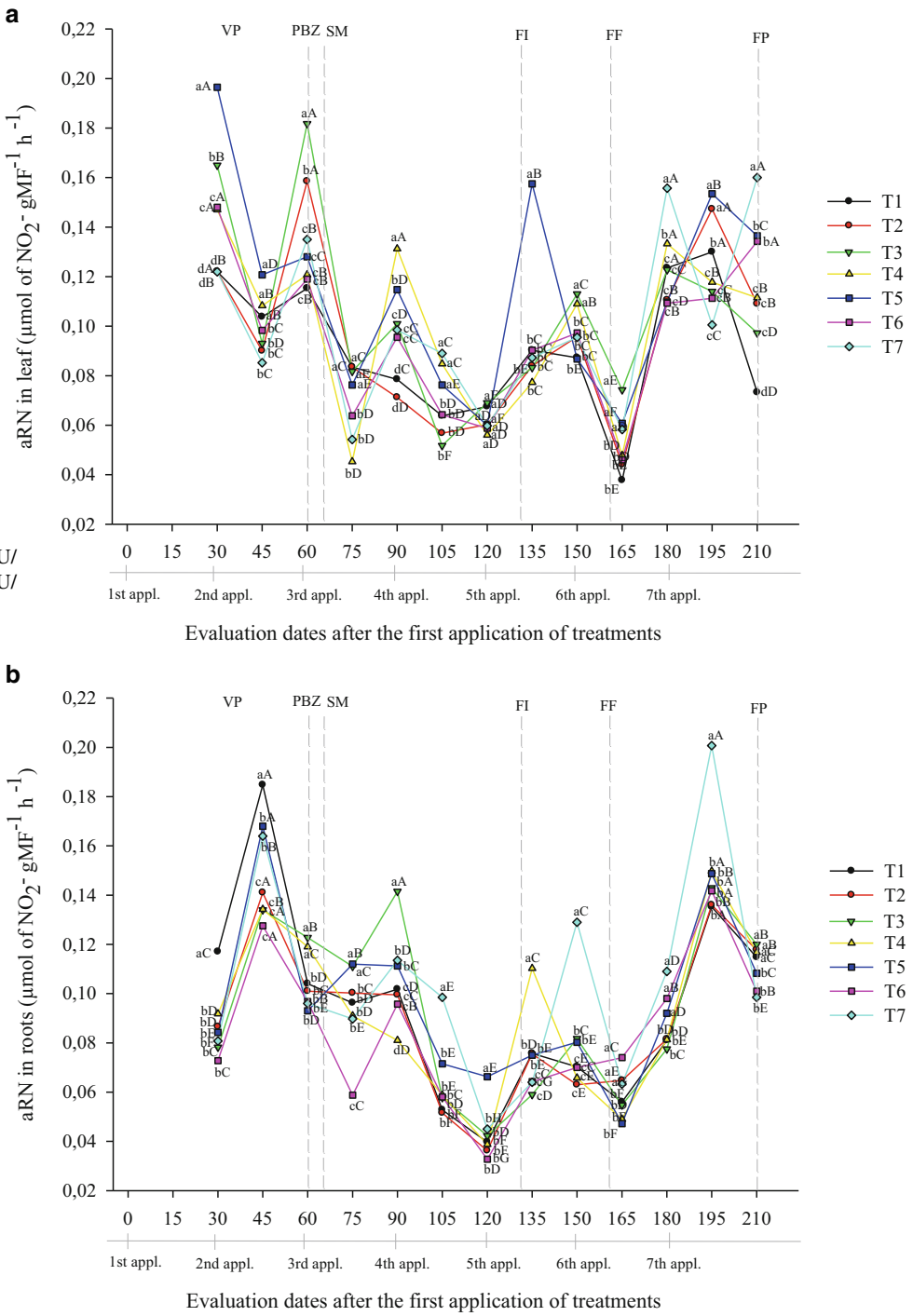

Fig. 6 Activity of nitrate reductase in leaves (a) and roots (b) of 'Keitt' mango as a function of different application methods of *Rhodopseudomonas palustris* application and days after the first application of treatments. *VP* vegetative phase, *PBZ* PBZ application, *SM* shoot maturation, *FI* flowering induction, *FF* full flowering, *FP* fruiting. Means followed by the same capital letters (different application methods of *R. palustris* application treatments) and common lowercase letters (evaluation dates) do not differ according to Scott-Knott's test (5%). *T1* control treatment, *T2* 1.43×10^7 CFU/plant via fertigation, *T3* $2.85 \times 10^{7\,CFU}$/plant via fertigation, *T4* 4.27×10^7 CFU/plant via fertigation, *T5* 5.70×10^7 CFU/plant via fertigation, *T6* 1.43×10^7 CFU/plant via fertigation + 1.43×10^7 CFU/plant via leaf spray, *T7* $2.85 \times 10^{7\,CFU}$/plant via fertigation + 1.43×10^7 CFU/plant via leaf spray

used by plants to ensure survival under water stress conditions (Ryan 2011; Ferraz et al. 2012), which possibly contributes to the increase in WUE.

At 150 DAT, WUE increased with application of *R. palustris* via fertigation at 1.43×10^7 CFU/plant, 2.85×10^7 CFU/plant, and 5.70×10^7 CFU/plant and showed superiority to the control treatment, with differences of 19%, 14%, and 8%, respectively (Fig. 5). No differences were observed between treatments in the full flowering and fruiting phases (Fig. 5).

Nitrate Reductase Activity

The R × DAT interaction had a significant effect on the enzyme nitrate reductase (aRN) in leaves and roots (Table 3). Nitrate reductase is the key enzyme in the nitrogen cycle because it is the first in the chain of reactions in the cycle,

catalyzing the reduction of nitrate (NO_3^-) to nitrite (NO_2^-), which will be reduced to ammonia (NH_3^+) and translocated via xylem for use by the plant (Santos et al. 2021).

All treatments presented a similar aRN data distribution, with a peak in leaves at 30 DAT, except for control treatment (Fig. 6a). At 30 DAT there was a difference among treatments for leaf aRN (Fig. 6a) especially for 5.70×10^7 CFU/plant via fertigation, with a mean of 0.20 µmol of $NO_2^- g^{-1}$ FM h^{-1}, which was 66% higher than control. Treatments control, 1.43×10^7 CFU/plant via fertigation, and 2.85×10^7 CFU/plant via fertigation $+1.43 \times 10^7$ CFU/plant via leaf spray did not differ from each other, showing the lowest means at 30 DAT, with a mean of 0.12 µmol of $NO_2^- g^{-1}$ FM h^{-1}. In the same evaluation, for root aRN (Fig. 6b), all plants that received treatment *R. palustris* reduced the aRN.

At 60 DAT leaf aRN increased, a result also repeated at 30 DAT, but not at 120 DAT. The bacterium affects leaf aRN due to the increase plant photosynthetic rates, which are essential for increasing aRN (Hunter and Ruffner 1997). At 60 DAT, the application of 2.85×10^7 CFU/plant via fertigation showed superiority both in leaf and root, with an increase of 57% and 17%, respectively, in relation to control (T1) (Fig. 6a and b).

At 90 DAT, leaf aRN increased for almost all treatments, except control treatment (T1) and 1.43×10^7 CFU/plant via fertigation. In this evaluation, 4.27×10^7 CFU/plant, which is applied via fertigation, differed from the other treatments, with increase of 67% compared to T1. It should be noted that on this date, T1 had also the lowest *A* compared to the other treatments (Fig. 1).

At 105 and 120 DAT, aRN in leaves and roots decreased in all treatments (Fig. 6a and b). During this period, the plants were under water stress, which is adopted during the management of floral induction in the semiarid region to stimulate the production of ethylene, responsible for aiding in bud differentiation and flowering uniformity in mango (Davenport 2007; Cavalcante et al. 2018). This way, plants subjected to water limitation tend to close the stomata, reducing the flow of water through the transpiration stream and, consequently, the absorption of nitrate, which is the substrate of the nitrate reductase enzyme (Oliveira et al. 2011).

At 135 and 150 DAT, the plants were in the floral induction phase, which includes the foliar spray with nitrates to stimulate blooming after branch maturation. The nitrates used for flowering induction are mainly calcium [$Ca(NO_3)_2$] and potassium (KNO_3), which are applied via the leaves, at concentrations of 1.5%–2% and 2%–4%, respectively (Mouco 2015).

After nitrates spraying, aRN increased, mainly in leaves, in relation to the previous evaluation date (120 DAT). At 135 DAT, highest leaf aRN occurred in the application of 5.70×10^7 CFU/plant via fertigation, with superiority of 74% (Fig. 6a), while in root tissue, the greatest increase was verified for application of 4.27×10^7 CFU/plant via fertigation, with 46%, both compared to control treatment (Fig. 6b).

With the advance of the evaluations up to 150 DAT, still, in the floral induction phase, the leaf aRN was higher for application of 2.85×10^7 and 4.27×10^7 CFU/plant via fertigation, with increments of 29% and 25% in relation to control treatment (Fig. 6a); in roots, the highest aRN was observed for T7, with an increase of 84% compared to the control (Fig. 6b). Nitrate reductase is a key enzyme in the nitrate assimilation pathway for the synthesis of amino acids, such as methionine, a precursor of ethylene, which is the hormone inducing the differentiation of mango floral buds (Sudha et al. 2012; Coutinho et al. 2016; Anusuya et al. 2018).

In the beginning of flowering, at 165 DAT, there was a decrease in aRN, mainly in leaves, with higher leaf aRN values for 2.85×10^7 and 5.70×10^7 CFU/plant via fertigation, and 2.85×10^7 CFU/plant via fertigation $+1.43 \times 10^{7\ CFU}$/plant via leaf spray, with a difference of 96%, 61% and 54% in comparison the control, which reached the lowest value among all other treatments and evaluation dates (Fig. 6a). Root aRN was higher for treatments with application of 1.43×10^7 CFU/plant via fertigation, 1.43×10^7 CFU/plant via fertigation $+1.43 \times 10^7$ CFU/plant via leaf spray and 2.85×10^7 CFU/plant via fertigation $+1.43 \times 10^7$ CFU/plant via leaf spray with increments of 15%, 32%, and 12%, respectively, compared to the control (Fig. 6b). It is notable that on this date (165 DAT) the *A* was lower for treatments control and 1.43×10^7 CFU/plant via fertigation (Fig. 1), which may influence the lower aRN.

The aRN reduction at the beginning of flowering may have occurred as a result of the greater amount of energy that is made available for the formation of panicles and fruits, which are stronger drains than leaves and roots during this phase (Lu et al. 2012; Taiz et al. 2017). In addition, the nitrogen content is higher in the floral induction phase, while the lowest levels are found in flowering (Nascimento et al. 2005).

At 180 and 195 DAT, there was aRN increased both in leaf and root. At 180 DAT, a treatment that had *R. palustris* application with 2.85×10^7 CFU/plant via fertigation $+1.43 \times 10^7$ CFU/plant via leaf spray, was 26% higher than T1 in leaf aRN; in the roots, aRN values of 5.70×10^7 CFU/plant via fertigation (T5), 1.43×10^7 CFU/plant via fertigation $+1.43 \times 10^7$ CFU/plant via leaf spray (T6) and 0.85×10^7 CFU/plant via fertigation $+1.43 \times 10^7$ CFU/plant via leaf spray (T7) increased 13%, 20%, and 34%, respectively, in relation to the control (T1). In the next evaluation, 195 DAT, a superiority was reported for T2 and T5, both with applications only via fertigation in leaf aRN, with

an increase of 13% and 18% concerning the control (T1) (Fig. 6a); in the root, there was a higher enzyme activity in T7 plants, with an increase of 48% compared to the control (Fig. 6b).

In the productive phase, at 210 DAT, there was a difference in leaf aRN and root aRN, with an increase of 118% in leaf aRN for the T7 treatment compared with the control. It is noteworthy that this was the largest increase verified between a treatment and the control among all the evaluated dates, detaching that T7 is composed by application via foliar and via fertigation, which may have favored the greater aRN of this treatment.

Conclusions

R. palustris affects stomatal conductance, gas exchange, and nitrate reductase enzyme activities in mango cv. 'Keitt' grown in Brazilian semiarid, but the effects depend on the phenological phase evaluated. The application of *R. palustris* at 1.43×10^7 CFU/plant via fertigation $+1.43 \times 10^7$ CFU/plant via leaf spray (T6) provides a greater increase in the photosynthetic activity of mango cv. 'Keitt,' reaching 35% more net photosynthesis than control treatment.

Conflict of interest J. de Oliveira Siqueira Lino, L. E. Delmondes Mudo, J. Texeira Lobo, Í. H. Lucena Cavalcante, A. G. de Luna Souto, L. Guimarães Sanches and V. Borges de Paiva Neto declare that they have no competing interests.

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Further Reading

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