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ORIGINAL ARTICLE

Rhodopseudomonas palustris effects on plant carbohydrate concentrations and production of 'keitt' Mango

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Abstract
The present study aimed to evaluate the effects of *Rhodopseudomonas palustris* on plant carbohydrate concentration and fruit production of 'Keitt' mangoes grown under semi-arid environmental conditions. The experiment was carried out simultaneously in two orchards with the same mango cultivar and crop management practices under semi-arid conditions in Petrolina, Pernambuco, Brazil. The study followed a randomized blocks design with treatments distributed in a factorial arrangement (7 × 8), referring to different use strategies of *R. palustris*: T1) control treatment; T2) 1.43×10^7 CFU/plant via fertigation (colony forming unit); 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; and evaluation days after the first treatment at 0, 30, 60, 90, 120, 150, 180 and 210 days. Each treatment was composed by four replications and each replication by three plants. The use of *R. palustris* increased the total soluble carbohydrates, such as sucrose, in leaves and branches, as well as starch concentration in branches. The application of 11.43×10^7 CFU/plant via fertigation + 1.43×10^7 CFU/plant via leaf spray (T6) increased the production of 'Keitt' mangoes with caliber between 6 and 8, recommended for the European market.

Keywords *Mangifera indica* L. · *Rhodopseudomonas palustris* · Photoassimilates · Abiotic stresses

Introduction

In Brazil, mangoes are produced in about 76.7 thousand hectars, among which 49 thousand hectars are in the Northeast semi-arid region known as the São Francisco Valley that is also reponsable for almost 90% of the Brazilian mango exports (Carvalho et al. 2019). Although the São Francisco Valley is the most important mango growing region in Brazil, it has a tropical semi-arid climate with high air temperature and low relative humidity that is used with water deficit conditions to control flowering, possibly leading to multiple abiotic stresses in the plants (Santos et al., 2016). The water defict condition is imposed from branch maturation phase until flowering and can affect the accumulation of carbohydrates and other plant reserves necessary for uniform flowering and proper fuit set (Cavalcante et al., 2018). Ideed, especifically for 'Keitt' mango, high physiological fruit drop and low yield have been reported under semi-arid conditions, which may be inhibited by crop management approaches focused on hormones, microrganisms or biostimulants (Nkansah et al., 2012).

High temperatures have been reported to reduce photosynthetic activity proportionally to the thermal stress (Chovancek et al., 2019), which could be mitigated by new technologies such as the use of plant biostimulants (Lobo et al., 2019; Silva et al., 2020), especially those based on

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microorganisms that can help increasing photosynthetic metabolism under stress conditions, providing greater synthesis and partitioning of photoassimilates required for growth and development of the whole plant and sink organs (Saad et al. 2020).

Rhodopseudomonas palustris is a phototrophic purple non-sulfur bacterium with multifunctional properties that distinguish it from many traditional plant growth-promoting bacteria (PGPB). In addition to its ability to fix atmospheric nitrogen and synthesize phytohormones such as indole-3-acetic acid, it can improve photosynthetic efficiency, enhance stress tolerance, and increase sugar accumulation in plant tissues. These mechanisms have been described in several crops of economic relevance, including cucumber (Ge et al., 2017), rice (Kantachote et al., 2016), and Chinese dwarf cherry (Yin et al., 2012). Although studies on mango are still lacking, this species is a promising candidate for semi-arid fruit production systems due to its ability to perform well under abiotic stress conditions, such as high irradiance and limited water availability. Compared to other microbial inoculants or microbial consortia, R. *palustris* offers the advantage of combining multiple plant-beneficial traits in a single organism, which simplifies formulation and application (Hsu et al., 2021). Additionally, its scalability is well-documented, with successful commercial production and use in countries like Taiwan and Thailand, where products based on *R. palustris* are used in rice paddies and vegetable crops (Kantachote et al., 2016; Wong et al., 2014). The objectives of this study were to evaluate the effects of *R. palustris* on plant carbohydrate concentration and fruit production of 'Keitt' mangoes grown under semi-arid environmental conditions.

Materials and methods

Plant material and growing conditions

Seven years old mango (*Mangifera indica* L.) plants, cultivar Keitt, with uniform size and vigour in the fifth production cycle were used in this study, which was accomplished from 2019 to 2020 in Petrolina, Pernambuco, Brazil (09°18' S and 40º25' W; altitude of 349 m). The climate is classified as BSh (Köppen), which corresponds to a semi-arid region. During the study, average air temperature and relative humidity ranged from 24.1 ºC to 34.6 ºC and from 54.4% to 79.1%, respectively, with accumulated precipitation of 424 mm $year^{-1}$. The study was composed by two experiments that were simultaneously carried out in two orchards with the same crop management practices and plants spaced with 6.0 m between rows and 2.0 m between plants. Each plant was daily drip irrigated with 1.5 L h^{-1}. All management practices such as pruning, control of weeds, pests and diseases, inhibition of gibberellin synthesis (Cultar®) and dormancy break (calcium nitrate and potassium nitrate) were performed according to the recommendations described by Genú and Pinto (2002). The nutrient management was performed through the fertigation system and tip pruning was performed to synchronize vegetative flush events in the canopy (Genú and Pinto 2002).

Treatments and experimental design

The experiments followed a randomized blocks design with treatments distributed in a factorial arrangement (7 × 8), referring to different use strategies 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 + 1.43×10^7 CFU/plant via leaf spray; T7) 2.85×10^7 CFU/plant via fertigation + 1.43×10^7 CFU/plant via leaf spray; and evaluation days after the first treatment (DAT) at 0, 30, 60, 90, 120, 150, 180 and 210 days. Each treatment was composed by four replications and each replication by three plants. The source of *R. palustris* used was Bioavance (Biotrop®) which contains 750.000 CFU/ml of *R. palustris*, with density of 1.0 g cm^{-3}, based on studies of Kantachote et al. (2016) and Ge et al. (2017). Treatments were applied every 30 days after the production pruning until the beginning of the fruit set.

Physicochemical and statistical analyses

Thirty days after applying each treatment, branch and leaf samples were collected for analyses of total soluble carbohydrates, sucrose and starch concentrations. Four season branches with four recently fully expanded leaves were collected in the middle of the canopy. A two-leaf sample without necrotic areas due to pests and diseases were collected from the apex of each branch. Leaf samples were analysed without the leaf midrib. Both leaf and branch (without leaves) samples were subjected to total soluble carbohydrates, starch, and sucrose analyses. The total soluble carbohydrates concentration was quantified following the methodology described by Dubois et al. (1956). Starch content was determined based on the approach described by Hodge and Hofreiter (1962). Sucrose was analysed following the method described by Van Handel et al. (1968). The number of panicles per plant was quantified by counting all panicles in each plant. After fruit physiological drop, all fruit were counted in each plant and fruit retention per panicle was estimated by the ratio between the total number of fruit per plant and the total number of panicles emitted per plant.

Harvest was accomplished when the fruit reached the maturity stage 2, characterized by the cream-yellowed flesh colour (Filgueiras et al. 2000). After harvest, fruit were weighed to determine the fruit yield (kg per plant) and were separated based on size according to the Normative Instruction of the Ministry of Agriculture, Livestock and Supply (Brasil 2012), which determines fruit caliber based on the number of fruit required to fill a commercial box with 6 kg. Based on the caliber, fruit were then classified for the potential market based on each market preferences such as fruit with quality for Brazilian market (calibers 4 and 5), fruit with quality for European market (calibers 6 to 8), and low quality fruit that do not fit in the aforementioned calibers. The data obtained were subjected to the analysis of variance (ANOVA). Statistical analyses were performed with the software 'R' (R Core Team, 2019), using combined data of both experimental orchards. The averages were compared with $p<0.05$ and $p<0.01$. Figures were generated by the software SIGMAPLOT 11.0.

Results

According to the results, there is a significant interaction between the *R. palustris* application and evaluation dates for leaf and branch total soluble carbohydrates and sucrose contents, as well as branch starch concentrations (Table 1).

During the vegetative growth phase (phase after production pruning), the total soluble carbohydrates were higher in leaves, compared to the branches (Fig. 1). In this phase, 30 days after treatments (the first foliar spray - DAT), the control treatment (T1) had the highest total soluble carbohydrates with 80.12 µmol·g^{-1} of FM and 38.82 µmol·g^{-1} of FM in leaf and branch, respectively.

After the vegetative phase, i.e., during the branch maturation phase, total soluble carbohydrates in both leaves and branches increased and reached a peak at the floral induction phase (Fig. 1). Thirty days after the paclobutrazol (PBZ) treatment, T2 reached the highest average of leaf total soluble carbohydrates (103.85 µmol·g^{-1} of FM), compared to all other treatments and evaluation dates, which corresponds to 73% higher total soluble carbohydrates than the control treatment. Leaves and branches had higher total soluble carbohydrates during the floral induction phase,

Table 1 Total soluble carbohydrates, starch, and sucrose contents in leaves and branches of 'keitt' Mango trees as influenced by different *R. palustris* application strategies

	Total soluble carbohydrates µmol·gFM^{-1}		Starch mg·gFM^{-1}		Sucrose mg·gFM^{-1}	
	Leaf	Branch	Leaf	Branch	Leaf	Branch
Strategies of *R. palustris* application (B)						
Value 'F'	1.49^{ns}	4.13**	1.71^{ns}	3.29**	0.52^{ns}	1.79^{ns}
T1	63.2	30.4 a	0.85	0.71 b	1.33	1.33
T2	70.3	24.2 b	0.84	0.70 b	1.32	1.53
T3	62.6	22.2 b	0.89	0.71 b	1.30	1.53
T4	65.2	27.7 a	0.89	0.75 a	1.26	1.71
T5	70.3	27.4 a	0.87	0.79 a	1.34	1.55
T6	67.3	26.6 a	1.00	0.71 b	1.24	1.44
T7	66.1	29.6 a	0.89	0.77 a	1.21	1.83
Evaluation dates after the first treatment (D)						
Value 'F'	8.61**	27.9**	1.7^{ns}	14.3**	41.3**	24.9**
0	57.2 d	29.6 b	0.82	0.85 a	0.85 e	0.99 d
30	67.2 c	20.0 d	0.96	0.68 c	1.37 c	1.34 c
60	58.9 d	17.2 d	0.99	0.68 c	1.20 d	0.80 d
90	67.6 c	21.4 d	0.87	0.65 c	0.73 e	1.25 c
120	71.6 b	26.7 c	0.89	0.73 b	1.58 b	1.26 c
150	82.0 a	31.6 b	0.87	0.70 c	0.88 e	1.82 b
180	60.8 d	25.9 c	0.86	0.74 b	1.81 a	2.58 a
210	66.1 c	42.6 a	0.85	0.83 a	1.88 a	2.45 a
B x D						
Value 'F'	1.99**	1.60*	1.17^{ns}	2.46**	2.77**	2.14**
CV (%)	18.7	25.8	22.7	12.2	24.7	38.8

ns: not significant by the Scott-Knott test (5%); CV%: Coefficient of variation. Means followed by the same letter do not differ by Scott-Knott test at 5% (*) or 1% (**) probability error. 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

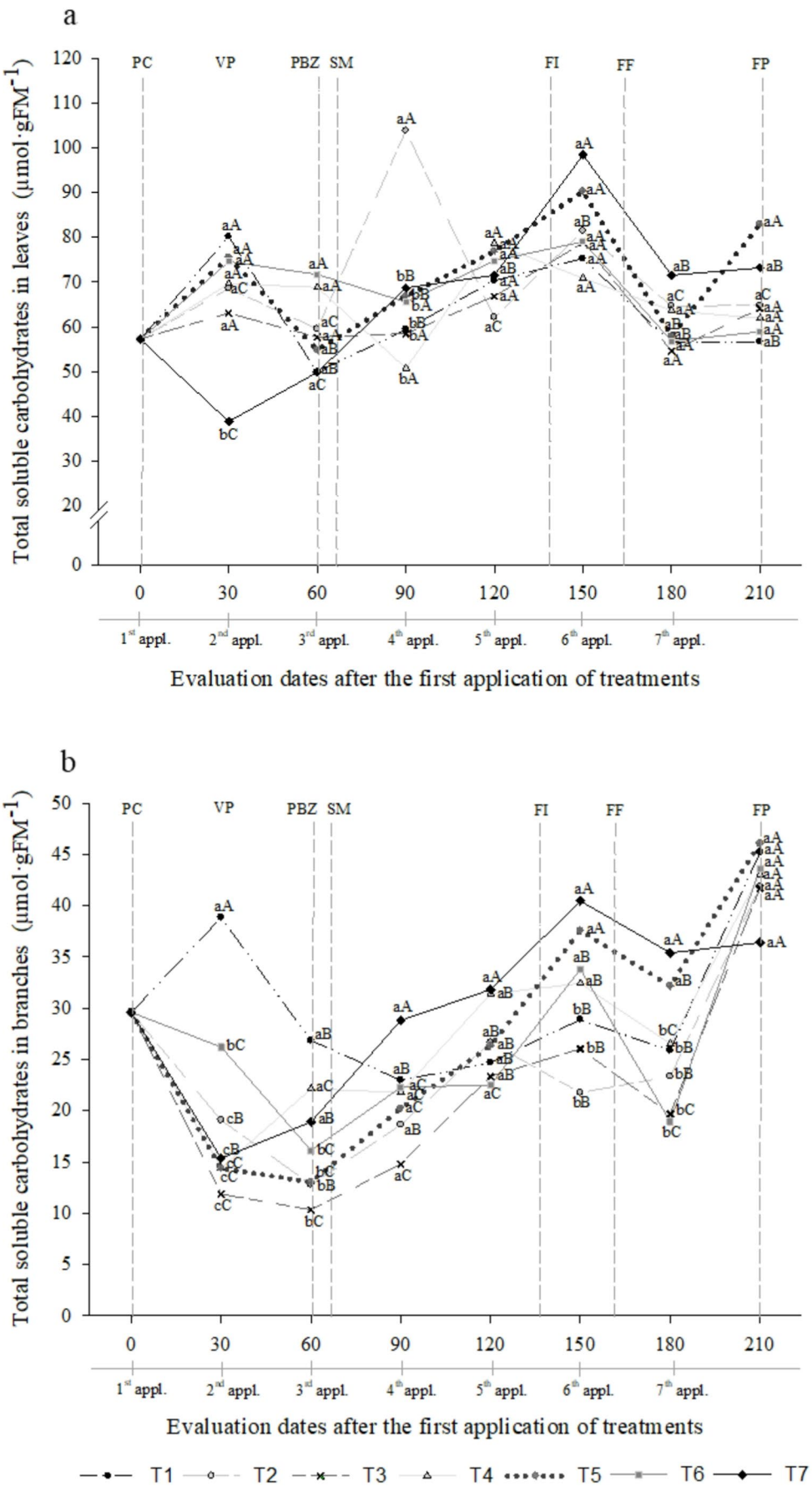
a
Total soluble carbohydrates in leaves (µmol·gFM-1)
PC
VP
PBZ
SM
FI
FF
FP
0
30
60
90
120
150
180
210
1st appl.
2nd appl.
3rd appl.
4th appl.
5th appl.
6th appl.
7th appl.
Evaluation dates after the first application of treatments
b
Total soluble carbohydrates in branches (µmol·gFM-1)
Evaluation dates after the first application of treatments
T1
T2
T3
T4
T5
T6
T7

Fig. 1 Total soluble carbohydrates concentrations in leaves (**a**) and branches (**b**) of 'Keitt' mango as a function of different strategies of *R. palustris* application and days after the first treatment. *PC*: plant carachterization; *VP*: vegetative phase; *PBZ*: PBZ application; *SM*: shoot maturation; *FI*: flowering induction; *FF*: full flowering; *FP*: fruiting. Averages followed by the same capital letter (strategy of *R. palustris* application) or lowercase letter (evaluation dates) do not differ according to the 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

compared to the previous phase, but treatments do not differ for leaf carbohydrates. However, the treatments T4, T5, T6 and T7 differed from the others for total soluble carbohydrates in branches, presenting 32.40, 33.80, 37.54 and 40.45 $\mu mol \cdot g^{-1}$ of FM, respectively (Fig. 1). Treatments T4 and T5 had the highest doses of the bacteria applied through fertigation, while treatments T6 and T7 received the bacteria by fertigation and leaf spray.

At 180 DAT (Fig. 1), 30 days after applying the 6th treatment, a period that comprises the full flowering phase, leaf and branch total soluble carbohydrate levels decreased. Regarding the soluble carbohydrate concentrations in branches, treatments T5 and T7 had higher values with averages of 32.16 and 35.40 $\mu mol \cdot g^{-1}$ of FM, corresponding to an increase of 24% and 37% in relation to control treatment, respectively. There was a significant interaction between treatments and evaluation dates for branch starch concentration (Table 1). At 30 DAT branch starch concentrations decreased in all treatments, except for T7 (Fig. 2), which presented 0.88 $mg \cdot g^{-1}$ of FM that is 33.3% higher than the control (T1). From 30 to 60 DAT, T5 branch starch concentration was significantly increased, reaching 1.07 $mg \cdot g^{-1}$ of FM, which is equivalent to an increase of 74% in relation to the control.

At 60 DAT, PBZ was applied to all treatments and, after that, the same trend of branch starch concentration was verified, i.e. no differences among treatments were recorded until the last evaluation date (Fig. 2). However, at 150 DAT, the control treatment had the lowest starch concentration, compared to the other treatments, with 0.60 $mg \cdot g^{-1}$ of FM (Fig. 2). A significant interaction between the studied factors was recorded for sucrose concentrations in leaves and branches. At 30 DAT (Fig. 3), during the vegetative growth phase, T5 leaf sucrose (2.14 $mg \cdot g^{-1}$ of FM) and T7 branch sucrose (2.90 $mg \cdot g^{-1}$ of FM) increased, compared to the other treatments, representing 96% and 46% higher sucrose levels, respectively. At 60 DAT, PBZ was applied and from that date on, leaf sucrose reduced in parallel with branch sucrose increase at 90 DAT. During this evaluation, the plants were in the branch maturation stage, which possibly resulted in the translocation of sucrose from the leaves to synthetized starch in the branches (reserve carbohydrate).

At 120 DAT (30 days after applying the 4th treatment), leaf sucrose increased in all treatments (Fig. 3A), concomitantly with a decrease of this sugar in branches (Fig. 3B), except for the T4 that showed a higher average than the other treatments, with 2.66 $mg \cdot g^{-1}$ of FM. Our results also show a similar trend for leaf sucrose content in all treatments between 60 and 120 DAT (Fig. 3A), with no statistical differences among treatments. Based on the evaluation after applying the 5th treatment, at 150 DAT, representing the floral induction phase, sucrose concentrations increased in branches and decreased in leaves, with no differences observed among treatments (Fig. 3A and B). However, at 180 DAT (full flowering phase), leaf sucrose increased, mainly in the T6 and T7 that have *R. palustris* applied through leaf spray and fertigation, showing 7% and 24% higher leaf sucrose than the other treatments, respectively (Fig. 3A).

During fruit development, at 30 DAT, the reduction in sucrose levels can be explained by the sugar translocation to the fruit, where sucrose is used as a source of carbon for fruit structure, storage and energy requirements. *R. palustris* applications through fertigation + foliar (T6 and T7) showed the same trend of sucrose reduction in both leaf and branch, differing from all other treatments for leaf sucrose (Fig. 3A) and from T3 and T4 for branch sucrose concentrations (Fig. 3B). In our study, the treatments affected the number of fruit per plant, as well as the amount of fruit with quality for the Brazilian market, European market and low-quality fruit (Table 2). However, the treatments had no significant effects on the number of panicles per plant and fruit retention per panicle (Table 2).

The treatments T2, T4 and T6 produced more fruit per plant than all other treatments, resulting in 125, 111.2 and 114.4 fruit per plant, respectively (Table 2). The T2 plants had on average 25.9 more fruit than T7 plants that showed the lowest number of fruit per plant.

In our study, the treatments that reached the highest production of fruit with caliber that attend the European market were T2, T4, T6 and T7, with averages of 48.57, 51.06, 48.71 and 50 kg per plant, respectively (Fig. 4). Therefore, the same treatments that resulted in the highest number of fruit per plant (Table 2) were also more efficient to promote fruit caliber for the European market, except for T7.

The European market requires mangoes to be sized by weight into specific codes: Code A (100–350 g), B (351–550 g), C (551–800 g), and D (> 800 g), following UNECE standards (CBI 2024). Typically, mangoes are packed in categories B or C, equivalent to 7–8 fruits per 4 kg carton, as this size range (especially 351–550 g) offers optimal visual appeal, handling convenience, and shelf-life (CBI 2024).

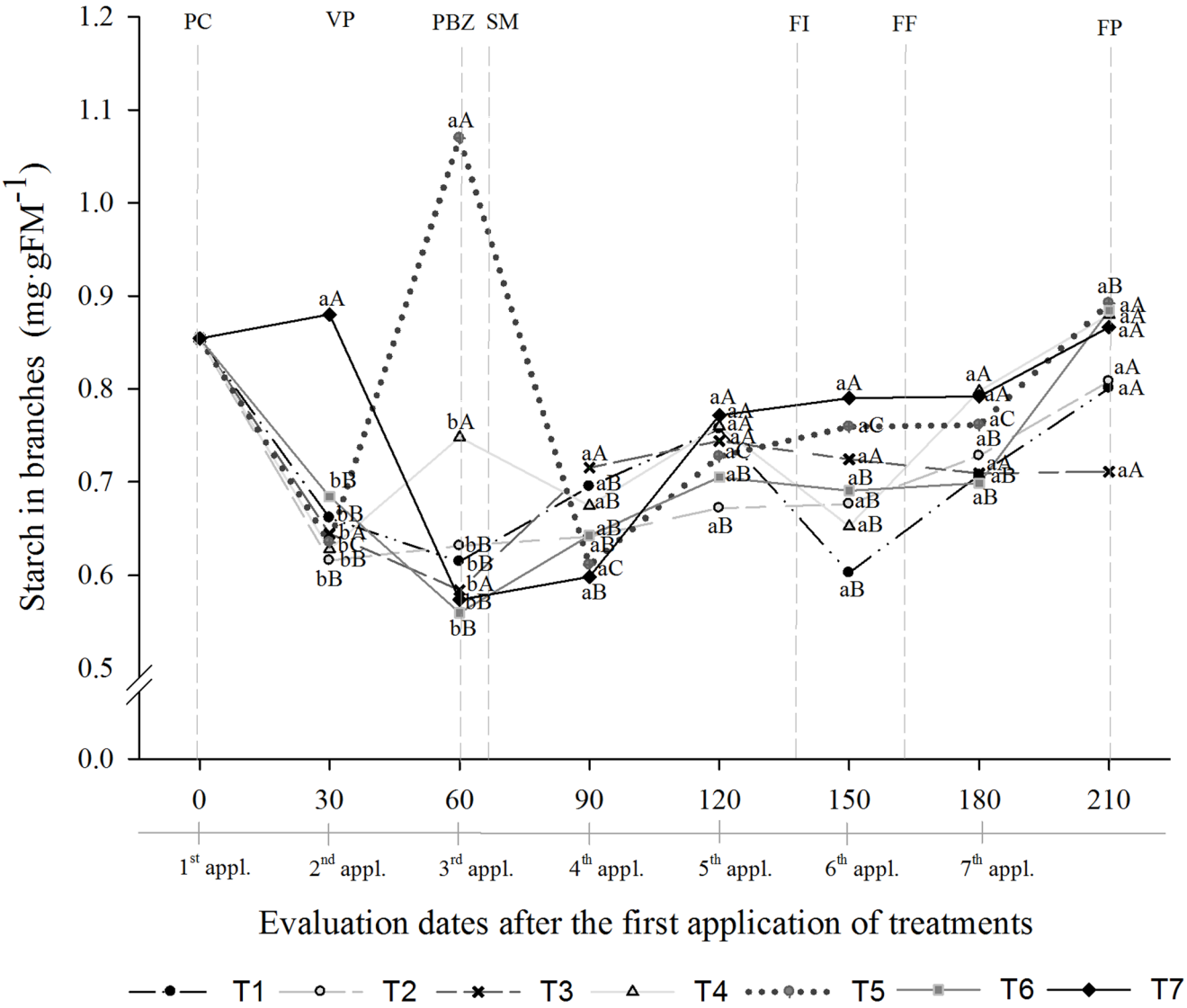

Fig. 2 Starch concentrations in branches of 'Keitt' mango as a function of different strategies of *R. palustris* application and days after the first treatment. *PC*: plant carachterization; *VP*: vegetative phase; *PBZ*: PBZ application; *SM*: shoot maturation; *FI*: flowering induction; *FF*: full flowering; *FP*: fruiting. Averages followed by the same capital letter (strategy of *R. palustris* application) or lowercase letter (evaluation dates) do not differ according to the 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

Additionally, a minimum weight of 200 g per fruit is mandatory for European commercialization (Kader, 2008). These standards reflect clear market preferences for medium to large calibers, justifying our focus on yield per plant in terms of fruit size suitable for European export.

The control treatment (T1) resulted in the lowest average fruit production with the caliber for the European market, which was 26.5% lower than the T4 that had the highest average (Fig. 4). However, T1 produced more fruit with caliber for the Brazilian market, which was statiscally equal to T5 and T6. This result can be attributed to the lower number of fruit per plant, which promoted fruit growth and size, leading to fewer fruit with an ideal caliber for the European market. Treatment 2 had the highest production of low-quality fruit, compared to all other treatments, resulting in an average of 16.7 kg of low-quality fruit per plant, which is 154% higher than the control. The fruit classified as low-quality are those that do not reach the ideal size for the Brazilian and European markets, and then are sold at prices that do not cover the production costs. Although T2 had the highest production of low-quality fruit, this treatment was also efficient in the production of fruit with caliber for the European market, showing that it has the potential for increasing the production of commercial fruit. Even with

a number of fruit per plant equal to T2 and higher than the control, T6 had the lowest low-quality fruit production, with 4.67 kg per plant (Fig. 4), approximately 29% less than the control.

Discussion

Indeed, Moldal et al. (2020) reported that during the vegetative growth there is a high demand for soluble carbohydrates, as they are related to the plant photosynthetic efficiency and, consequently, growth and development of vegetative flushes. Paclobutrazol is known to inhibit gibberellins biosynthesis, reducing vegetative growth, and influencing the synthesis and partitioning of carbohydrates in mango (Prasad et al., 2014; Silva et al., 2021). In addition, during branch maturation, foliar sprays with potassium sulfate (K_2SO_4) are performed, which increases the production and translocation of carbohydrates, and the K/N ratio, further restricting vegetative growth and thus improving the bud fertility (Coutinho et al., 2016).

The mango plant maturation phase is essential for uniform flowering and higher fruit production, as during this phase plants are exposed to the stress caused by high temperatures and water deficit conditions (Ramírez & Davenport, 2016; Cavalcante et al., 2018), inducing a greater production and accumulation of carbohydrates, since high sugar levels can stimulate flowering (Silva, 2018). The soluble carbohydrates accumulated during this phase possibly have mitigated plant stress by modulating the osmotic adjustment and promoting resistance to cell dehydration, which is expected at low water potentials (Gurrieri et al., 2020).

Prasad et al. (2014) have also found the highest carbohydrate concentration during the pre-flowering phase for 'Totapuri' (67.09 $mg \cdot g^{-1}$ of FM) and 'Royal Special' (67.58 $mg \cdot g^{-1}$ of FM) mangoes, with a decrease throughout the panicle development, as observed in our study (Fig. 1). Davenport (2007) reported that ideal amounts of leaf carbohydrates provide the necessary energy for proper reproductive development, especially for panicle formation. In addition, carbohydrates ensure the supply of energy such as ATP, as well as reduction agents and intermediate compounds that increase the assimilation of nitrate (NO_3) and other nutrients during flowering (Phavaphutanon & Krisanapook, 2000). No differences were observed among treatments for leaf total soluble carbohydrates during the full flowering phase, corroborating with the data obtained by Lobo et al. (2019), who studied the action of biostimulants on 'Kent' mango cultivated under semi-arid environmental conditions. During the flowering stage, the demand for carbohydrates often surpasses the daily production capacity, leading to a reduction in the carbohydrate reserves within the leaves. This dynamic is directly correlated with enhanced reproductive activity, characterized by longer panicles and a higher number of flowers. Previous studies have demonstrated that this physiological shift is not only a consequence of increased demand by the reproductive organs but also a strategic allocation of assimilates towards the most energy-demanding organs (Prasad et al., 2014; Cavalcante et al., 2018).

As such, carbohydrate levels fluctuate within the leaves as a result of the balance between their synthesis in the source organs, such as the leaves, and their distribution to sink organs, like the reproductive tissues. This allocation is influenced by a variety of factors, including the plant's metabolic efficiency, the availability of nutrients, and environmental conditions that regulate photosynthetic activity. Silva et al. (2020) emphasize the role of this sink-source relationship in modulating the growth and development of reproductive structures, where the coordination between carbohydrate production and the physiological demands of flowering is critical for optimal fruit set. Moreover, the timing and intensity of flowering are closely linked to the plant's ability to mobilize stored carbohydrates from other tissues, such as stems and roots, to meet the increased energy needs during this period. This process is particularly important in species like mango, where flowering is a highly energy-intensive process. The redistribution of carbohydrates during flowering, therefore, reflects the plant's overall physiological strategy to balance reproductive success with the maintenance of vegetative growth, ensuring survival and reproduction under varying environmental conditions. This intricate balance between carbohydrate availability, storage, and mobilization plays a key role in determining not only the intensity of flowering but also the subsequent fruit set and development. Understanding these physiological mechanisms can help improve agricultural practices aimed at optimizing fruit production by manipulating factors that influence carbohydrate availability during critical stages of reproductive development.

Santos-Villalobos et al. (2013) evaluated the carbohydrates levels in 'Ataulfo' mango and observed a reduction in such compounds at the end of the production cycle, suggesting that these were highly consumed by developing panicles and fruit. However, in this study, there was not difference among treatments at 210 DAT for both leaf and branch, but it was possible to notice that the carbohydrate content in the branch was higher at the fruit development stage, compared to all other the evaluation stages. Upreti et al. (2014) studied the PBZ effect on carbohydrate levels and alpha-amylase enzyme activity in 'Totapuri' mango and found that the flowering induced by PBZ is accompanied by an increase in leaf starch levels, concomitant with the

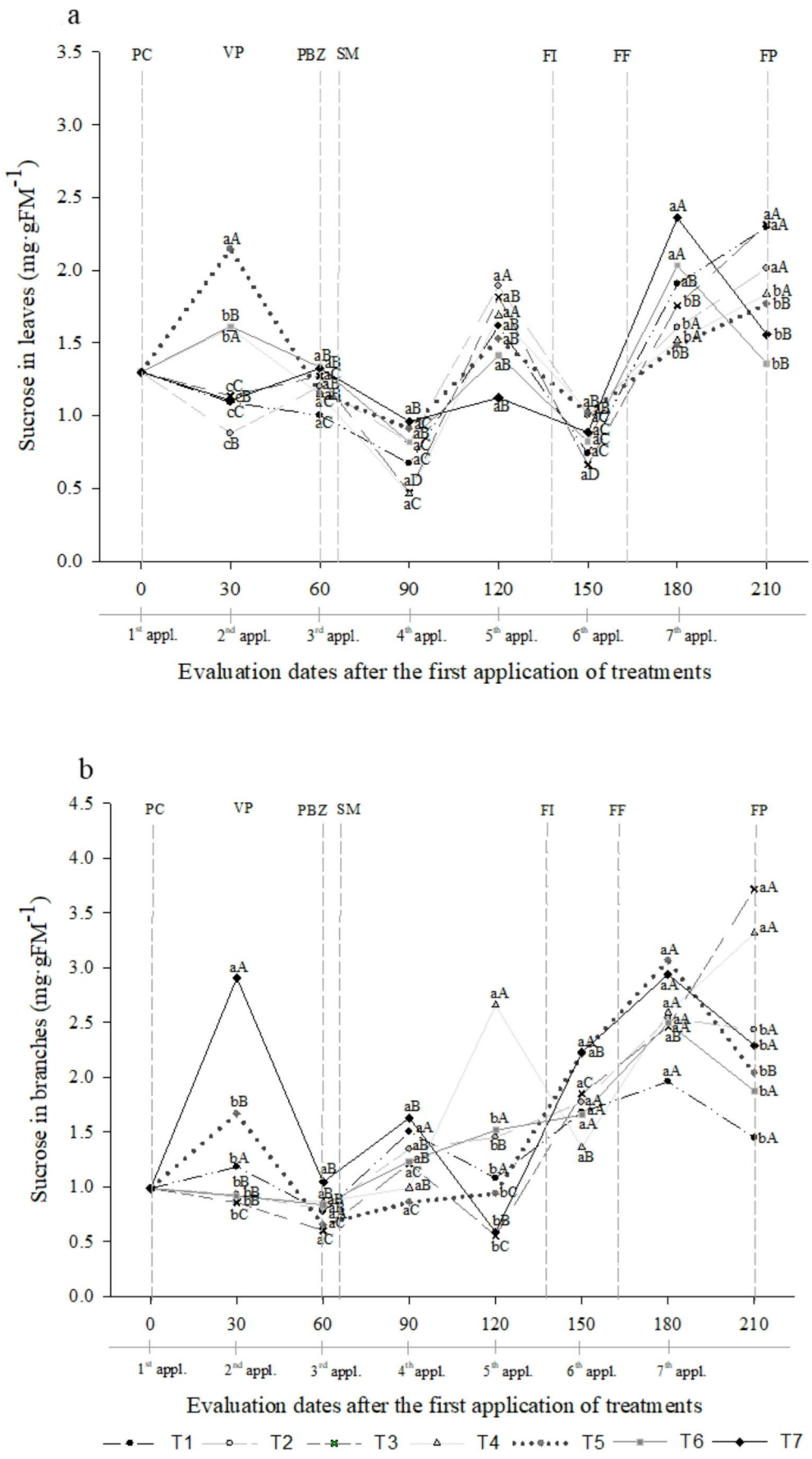
a
PC
VP
PBZ
SM
FI
FF
FP
Sucrose in leaves (mg·gFM-1)
0.0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
0
30
60
90
120
150
180
210
1st appl.
2nd appl.
3rd appl.
4th appl.
5th appl.
6th appl.
7th appl.
Evaluation dates after the first application of treatments
b
Sucrose in branches (mg·gFM-1)
0.0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
4.0
4.5
T1
T2
T3
T4
T5
T6
T7

Fig. 3 Sucrose concentrations in leaves (**a**) and branches (**b**) of 'Keitt' mango as a function of different strategies of *R. palustris* application and days after the first treatment. *PC*: plant carachterization; *VP*: vegetative phase; *PBZ*: PBZ application; *SM*: shoot maturation; *FI*: flowering induction; *FF*: full flowering; *FP*: fruiting. Averages followed by the same capital letter (strategy of *R. palustris* application) or lowercase letter (evaluation dates) do not differ according to the 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

inhibition of amylase activity. In the present study, the leaf starch concentrations did not increase, but branch starch concentrations increased after PBZ application. According to Yahia et al. (2019) starch is the main carbohydrate reserve in plants, being surpassed only by cellulose as the most abundant polysaccharide in plants.

Sucrose is produced in leaves, specifically in the cytosol and is translocated through the phloem to sink organs in the plant. Because sucrose is the main product of photosynthesis, it is the carbon source used as an energy carrier in plants, representing an important substrate for plant metabolism by assisting plants in physiological events and regulating the import of carbon into the metabolically active sinks (Lu et al., 2012). During this phase (branch maturation), plants are exposed to a reduced irrigation, so sucrose also modulates plant development and its response to stress, directly or indirectly, through interactions with other signaling pathways, including processes mediated by hormones and redox (Ruan, 2014).

Sucrose synthesis is more intense during phenological phases that require higher carbohydrate and energy input, such as flowering, where flower abortion must be minimized. During this stage, the photosynthetically fixed carbon, which could otherwise be used for starch synthesis in the chloroplasts, is redirected to supply carbon and energy to other vital metabolic processes. Specifically, during flowering, this carbon is primarily allocated to sucrose production in the leaves, which is then translocated to the developing flowers, organs with high energy demands. This process ensures that the plant meets the energy needs of its reproductive organs, promoting successful flower development and minimizing abortion, a key factor in determining fruit set (Paul & Foyer, 2001). The balance between carbon allocation for vegetative and reproductive growth during this critical phase is essential for optimal reproductive success.

Sucrose is a key signaling molecule that regulates the partitioning of carbon between source and sink tissues (Taiz et al., 2017), which is also an important source of structural carbon that makes up about 90% of plant biomass, making this sugar a determining factor in crop yields (Ruan, 2014). The higher yield promoted by *R. palustris* has also been reported by Kantachote et al. (2016), who studied biofertilizers containing this bacterium in field-trials to enhance rice yields and reduce CH4 emissions in both organic and saline flooded rice fields. Accordingly, previous studies have also described positive effects of plant biostimulants on mango production, as observed for 'Haydi', 'Naomi', and 'Tommy Atkins' mangoes (Mouco et al., 2009; Abd Ellatif et al., 2019). In addition, Lobo et al. (2019) have also registered an increase in the number of 'Kent' mangoes per plant in response to biostimulants, especially the ones containing soluble nutrients, free amino acids and *Lithothamnium* seaweed extract, which resulted in 54.37 more fruit per plant, compared to control untreated plants.

According to our results and previous studies, the positive effects of *R. palustris* on fruit yield could be attributed to the increase in microbial activity and other key bacteria involved into C and nutrient cycling, both of which can potentially contribute to the improved plant growth and development, as it has also been suggested by Xu et al. (2016). It is also possible that carbohydrate accumulation in sink organs could be limited by the activity of source organs in the plant. Therefore, when the number of fruit per plant is high, the available leaf area per fruit is often insufficient to maintain high fruit growth (Taiz et al., 2017). In that case, a positive effect of *R. palustris* on plant nutrient uptake can help boosting photosynthetic rates and carbohydrates translocation into the fruit, resulting in mangoes with ideal sizes for different markets.

Conclusions

The application of *Rhodopseudomonas palustris* enhanced carbohydrate metabolism in mango plants by increasing the levels of total soluble carbohydrates and sucrose in leaves and branches, as well as starch accumulation in the branches — a key physiological indicator associated with floral induction. These biochemical responses suggest a positive effect of *R. palustris* on source–sink dynamics and carbohydrate allocation.

Moreover, the combined use of *R. palustris* via fertigation and foliar spray at 1.43×10^7 CFU/plant each resulted in higher yields of 'Keitt' mango fruits within the preferred commercial calibers (6–8) for the European market, while reducing the proportion of undersized fruits. These findings support our initial hypothesis that *R. palustris* can act as a plant biostimulant capable of improving both physiological performance and commercial fruit quality in mango cultivation under semi-arid conditions.

Table 2 Number of panicles (NP), number of fruits (NF), fruit retention (FR), fruit production with quality for Brazilian market (BMF), fruit production with quality for European market (EMF) and low-quality fruit (LQF) of 'keitt' Mango as a function of different strategies of *R. palustris* application

	NP	NF	FR	BMF	EMF	LQF
				Kg per plant		
Strategy of *R. palustris* application						
Value 'F'	2.21^{ns}	4.03^{**}	1.52^{ns}	9.73^{**}	2.37^{*}	56.7^{**}
T1	71.1	100 b	1.62	18.8 a	40.4 b	6.57 d
T2	102	125 a	1.20	12.1 b	48.6 a	16.7 a
T3	75.1	100 b	1.57	11.9 b	43.8 b	8.77 c
T4	86.6	111 a	1.31	10.9 b	51.1 a	11.2 b
T5	92.5	105 b	1.16	19.3 a	44.6 b	7.08 d
T6	85.8	114 a	1.46	19.7 a	48.7 a	4.67 e
T7	64.0	99.1 b	1.41	11.4 b	50.0 a	6.20 d
CV (%)	21.61	19.6	20.6	39.9	24.0	27.7

ns: not significant by the Scott-Knott test (5%); CV%: Coefficient of variation. Means followed by the same letter do not differ by Scott-Knott test at 5% (*) or 1% (**) probability error. 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

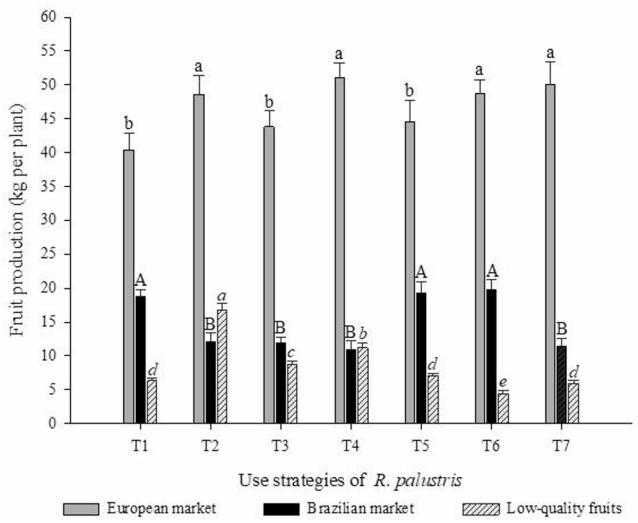

Fig. 4 Fruit production with quality for Brazilian market (BMF), European market (EMF) and low-quality fruit (LQF) of 'Keitt' mango as a function of different strategies of *R. palustris* application. Bars followed by the same lowercase letter (European market), capital letter (Brazilian market) or italic letter (low-quality fruits) do not differ according to the 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

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Data availability The data presented in this study are available on request from the corresponding author.

Declarations

Competing interests The authors declare no conflicts of interest related to the content of this article.

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