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Potassium-modulated physiological performance of mango plants infected by *Ceratocystis fimbriata*

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ABSTRACT: Mango wilt, caused by the fungus *Ceratocystis fimbriata*, is an important disease affecting mango production. In view of the beneficial effects of potassium (K) in other profitable crops and the lack of information about the effect of macronutrients on mango wilt development, the present study aimed to evaluate how mango plants supplied with K respond physiologically when infected by *C. fimbriata*. Mango plants (» 3 years old) from cultivar Ubá were grown in plastic pots containing 58 mg of $K \cdot dm^{-3}$ (original K level based on the chemical analysis of the substrate) or in plastic pots with substrate amended with a solution of 0.5 M potassium chloride (KCl) to achieve the rate of 240 mg $K \cdot dm^{-3}$. Disease symptoms were more pronounced in inoculated plants grown at the lower K level. Substantial declines in stomatal conductance, in line with decreases in the internal-to-ambient CO_2 concentration ratio and the absence of detectable changes in the chlorophyll *a* fluorescence parameters, suggest that the decrease in the net carbon assimilation rate is due, at least initially, to stomatal limitations. High concentrations of K and manganese were found in the stem tissues of inoculated plants and supplied with the highest K rate, most likely due to the involvement of these tissues in the local development of defense mechanisms. The results of this study suggest that the supply of K favored the physiological performance of mango plants and their resistance against *C. fimbriata* infection.

Key words: *Mangifera indica*, gas exchange, host defense, mango wilt, plant nutrition, vascular disease.

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INTRODUCTION

Mango (*Mangifera indica* L.) is one of the most cultivated and traded tropical fruit species worldwide, being mainly produced in Asia, for instance, by China, India and Pakistan, as well as in American countries, such as Brazil and Mexico (FAO 2013). Brazil holds the 17th place among the world's mango producing countries; however, due to territorial extent and the magnitude of the favorable climatic conditions, this crop has great potential for development (FAO 2013). Consumer demand in Brazil for mangos is almost exclusively focused on fresh products (*in natura*), although the interest in fruit processing industries has been growing (Damiani et al. 2011). The industrial processing market has a general preference for mango cultivars with features like high pulp yield, high soluble solids content and lack of fibers (Benevides et al. 2008). Varieties produced in Brazil that emphasize those traits are 'Extrema', 'Haden' and 'Ubá' (Benevides et al. 2008).

Despite the growing interest in the global market and projections for future growth, mango plants are often subjected to several diseases that reduce fruit quality and result in substantial yield losses (Batista et al. 2008). Mango wilt, caused by the fungus *Ceratocystis fimbriata* Ellis & Halsted s.l., is one of the most important diseases of mango, causing substantial yield losses (Batista et al. 2008). Disease symptoms include withered and dried leaves accompanied by internal necrotic lesions in the stem tissues (Viégas 1960). These symptoms begin in the thinner branches and slowly progress throughout the canopy until the death of the entire plant (Batista et al. 2008; Viégas 1960; Ribeiro 2005). At the early stages of fungal infection, mango wilt is extremely difficult to diagnose (Rossetto and Ribeiro 1990). When the symptoms become evident in the trunk, the tree dies rapidly; therefore, cutting and burning the infected plant parts to destroy inoculum and the use of resistant rootstocks are the main measures recommended for management, as no fungicides are registered for disease control (Rossetto and Ribeiro 1990).

Although it is often undervalued in the control of plant diseases, mineral nutrition has shown its importance in empirical tests involving the manipulation of nutrient availabilities to plants and the modification of the integral components of the agricultural soil environment (Huber and Jones 2013). Many physiological processes in plants, such as respiration, water and nutrient translocation, photosynthesis and transpiration, are dramatically altered upon pathogens infection (Lucas 1998). Thus, proper plant nutrition is a cultural practice that greatly contributes to plant health and, consequently, increases the potential of plants to build mechanisms of resistance against pathogens infection (Huber and Jones 2013).

Virtually, all essential nutrients can either decrease or increase host resistance against diseases (Huber and Graham 1999). Among these nutrients, the macronutrient potassium (K) deserves a particular attention because of its crucial roles in many plant physiological processes (Römheld and Kirkby 2010; Zörb et al. 2014). Potassium enrichment strongly facilitates the uptake of water and nutrients by plants and improves the transport of these resources from the source to the sink organs. Additionally, it is the principal cation involved in the establishment of changes in the osmotic potential (Gajdanowicz et al. 2011; Ishizuka 1978; Zörb et al. 2014). Intracellular K homeostasis is of great importance for the good metabolic performance of plants; moreover, the cytosolic concentration of K can be considered as essential for the transition from a normal metabolic state to alterations in plant metabolism due to the occurrence of stresses such as pathogens infection (Shabala and Pottosin 2014). Higher K concentration in the tissues of several plant species represents a key strategy to cope with environmental stresses, including pathogens infection, even though the positive effects of this macronutrient are related to increased plant physiological fitness rather than have a direct effect against the pathogen (Kafkafi 1990; Prabhu et al. 2007). Besides the importance of the K in the growth and development of plants, this macronutrient is strongly linked to signaling mechanisms in response to environmental alterations (Anschütz et al. 2014).

Many studies demonstrated that high levels of K applied to plants reduced disease severity (Prabhu et al. 2007; Wang et al. 2013). Soil amendment with K reduced the severity of sudden death, caused by *Fusarium solani* f. sp. *glycines*, in soybean seedlings, by 36% in comparison with plants not supplied with K (Sanogo and Yang 2001). The level of *Discula destructiva* infection was greatest when there was no K supply for *Cornus florida* L., but it decreased rapidly as the K concentration increased (Holzmueller et al. 2007). However, the effects of K on disease incidence could be affected by the amount and source of this element, plant and pathogen species →

and trial type (Wang et al. 2013). For example, Nam et al. (2006) found that strawberries that were grown with excess K were very susceptible to infection by *Colletotrichum gloeosporioides*, but host resistance was greatly enhanced when no K was supplied. This result was observed because the dose proximal to optimal plant K status induced the synthesis of molecules including reactive oxygen species (ROS) and phytohormones such as auxin, ethylene and jasmonic acid (Wang et al. 2013).

In view of the importance of mango wilt to decrease mango yield, the difficulty to achieve a desiderate level of control, it is urgently needed to search for alternative strategies of control. Thus, considering the beneficial effects of K in reducing the intensities of several foliar and vascular diseases in crops of high economic value (Amtmann et al. 2008; Prabhu et al. 2007) and the lack of information on the effect of this macronutrient on mango wilt development, the present study aimed to evaluate how mango plants grown in soil with low and high K levels would respond to *C. fimbriata* infection at the physiological level.

MATERIAL AND METHODS

Plant material and potassium supplement

The 36-month-old plants, with approximately 1.5 m height, from cultivar (cv) Ubá, were obtained from a commercial orchard in Dona Euzébia city, Minas Gerais State, Brazil (lat 21°18′58″S, long 42°48′39″W). The Ubá cv has great commercial importance, especially at the Zona da Mata region, Minas Gerais State, Brazil. These plants were grafted onto plants from the Imbú cv, which is widely used as a rootstock in the Zona da Mata region. The plants were grown into plastic pots containing 8 kg of substrate consisting of a mixture of soil, sand and manure in a proportion of 2:1:1 and pruned when needed. The chemical characteristics of soil were as follows: pH (H_2O) 4.72; phosphorus (P), 176.7 mg·dm^{-3}; calcium (Ca^{2+}), 1.45 cmol$_c$·dm^{-3}; magnesium (Mg^{2+}), 0.54 cmol$_c$·dm^{-3}; organic matter (OM), 5.17 dag·kg^{-1}; and aluminum (Al^{3+}), 0.86 cmol$_c$·dm^{-3}. The concentration of K in the soil was 58 mg·dm^{-3} of soil, which is below the desirable level required by mango plants of 91 to 140 mg·dm^{-3} (Ribeiro et al. 1999). The plants were grown in plastic pots containing 58 mg of K·dm^{-3} (original K level based on the chemical analysis of the substrate) or in pots amended with a solution of 0.5 M potassium chloride (KCl) to achieve the rate of 240 mg K·dm^{-3}. The dose of 240 mg K·dm^{-3} was determined based on a preliminary experiment using different concentrations of KCl on the soil to establish its optimal concentration. The plants were maintained in a greenhouse (30 ± 2 °C and relative humidity of 70 ± 5%) for 2 months before the beginning of the experiments.

Inoculation procedure

The isolate CEBS15 of *C. fimbriata* was obtained from symptomatic mango plants collected in the city of Brejo Santo, Ceará State (lat 07°29′34″S, long 38°59′06″W), Brazil, and stored following Castellani's method (Dhingra and Sinclair 1995). Plugs of malt extract-agar medium containing fungal mycelia were transferred to Petri dishes containing potato-dextrose agar (PDA). After 3 days, freshly colonized PDA plugs were transferred to new PDA Petri dishes and maintained at 25 °C under 12 h photoperiods for 14 days. Plants were inoculated according to Al-Sadi et al. (2010) with a few modifications. Stem disks (10 mm in diameter and approximately 2 mm in depth) were removed from the stems with the aid of a punch at approximately 5 cm above the graft scar. A PDA plug (10 mm in diameter) obtained from a 14-day-old fungal colony was carefully placed in the punch hole. Each hole containing a PDA plug with fungal mycelia was carefully covered with a piece of moistened cotton and then wrapped with parafilm to maintain adequate moisture for fungal infection. The disks used to inoculate each plant were taken from the middle portion of each fungal colony to make the inoculation as homogeneous as possible. Non-inoculated plants received only sterile PDA plugs to serve as the control.

Disease assessments

Disease progress was evaluated at 30, 45 and 60 days after inoculation (dai). The upward, downward and radial colonization of the stem tissues by fungal hyphae was evaluated by measuring the length (in cm) of the internal necrotic tissue using a digital caliper according to Araujo et al. (2014a,b). The upward relative lesion length (URLL) and the downward relative lesion length (DRLL) were determined as the ratio between the →

length from the graft scar to the top of the stem (LGST) and the lesion length (LL) in the same interval (upward and downward) from the inoculation point according to the following formula: URLL or DRLL = LL × 100/LGST. The plants were standardized to the same LGST value (20 cm). Radial fungal colonization (RFC) was determined as the length of the necrotic tissue relative to the total stem diameter × 100. The relative lesion length (RLL) was obtained according to the following formula: RLL = (LL_U + LL_D) × 100/LGST, where LL_U + LL_D is the sum of the lesion lengths above (LL_U) and below (LL_D) the inoculation point, respectively.

Determination of macro and micronutrients

At the end of the experiment, tissues at the point of inoculation and adjacent areas (≈ 4 cm above and below the necrotic area) were carefully removed with a scalpel from the stems of plants of the replications of each treatment, dried at 70 °C for 72 h and grounded with a Thomas Wiley mill (Thomas Scientific, Swedesboro, NJ, USA) to pass through a 40-mesh screen. The powder obtained from the stem tissue was used to determine the concentrations of macro and micronutrients according to Malavolta et al. (1997).

Physiological assessments

The leaf gas exchange parameters were determined with a portable open-flow gas exchange system (LI-6400XT, LI-COR, Lincoln, NE, USA). The net carbon assimilation rate (A), stomatal conductance to water vapor (g_s), internal-to-ambient CO_2 concentration ratio (C_i/C_a) and transpiration rate (E) were measured in fully expanded leaves completely exposed to sunlight. The measurements were conducted at ambient temperature and CO_2 conditions under artificial light (1,000 μmol photons·m^{-2}·s^{-1}) from approximately 8:00 to 12:00 h. The intrinsic (A/g_s) and instantaneous water use efficiency (A/E) at the aforementioned level of irradiance were also calculated. Chlorophyll *a* fluorescence measurements were determined using a portable pulse amplitude modulation fluorometer (MINIPAM, Heinz Walz GmbH, Effeltrich, Germany) on the same leaves used for the gas exchange measurements. Dark-adapted leaf tissues were exposed to a weak modulated measuring beam (0.03 μmol·m^{-2}·s^{-1}) to determine the initial fluorescence (F_0). Next, a saturating white light pulse of 6,000 μmol·m^{-2}·s^{-1} was applied for 0.8 s to ensure maximum fluorescence emission (F_m). From these initial measurements, the maximum quantum efficiency of PSII photochemistry for dark-adapted leaves was calculated as follows: $F_v/F_m = (F_m - F_0)/F_m$. The steady-state fluorescence yield (F_s), the light-adapted maximum fluorescence (F_m'), which was measured after 0.8 s of saturating white light pulse (6,000 μmol·m^{-2}·s^{-1}), and the light-adapted initial fluorescence (F_0'), estimated according to Oxborough and Baker (1997), were determined in light-adapted leaves. From these parameters, the efficiency of excitation energy capture by open PSII reaction centers was calculated: $F_v'/F_m' = (F_m' - F_0')/F_m'$. The estimated fraction of open PSII centers was calculated as $q_L = [(F_m' - F_s) \times F_0']/[(F_m' - F_0') \times F_s]$ (Kramer et al. 2004), and the non-photochemical quenching coefficient was calculated as NPQ = $(F_m/F_m') - 1$ (Bilger and Björkman 1990). The actual quantum yield of PSII electron transport was computed as $\Phi_{PSII} = (F_m' - F_s)/F_m'$, from which the electron transport rate was calculated as $ETR = \Phi_{PSII} \times PPFD \times f \times \alpha$, where PPFD is the photosynthetic photon flux density; f is a factor that represents the partitioning of energy between PSII and PSI and is assumed to be 0.5, indicating that the excitation energy is equally distributed between the 2 photosystems; α is the leaf absorbance by the photosynthetic tissues and is assumed to be 0.84 (Maxwell and Johnson 2000).

The concentrations of chlorophyll (Chl) *a*, Chl *b* and carotenoids were determined using dimethyl sulfoxide (DMSO) as the extractor (Wellburn 1994). Five leaf discs (10 mm diameter) were punched from each leaf used for the determination of the gas exchange and the Chl *a* fluorescence parameters at 30, 45 and 60 dai. The disks were collected in glass tubes containing 6 mL of a saturated solution of DMSO and calcium carbonate (5 g·L^{-1}) (Santos et al. 2008) and kept in the dark for 48 h. The absorbance of the extracts was read at 480, 649 and 665 nm in a spectrophotometer (Thermo Scientific Multiskan GO UV/VIS) using a saturated solution of DMSO and calcium carbonate as a blank.

Experimental design

A 2 × 2 factorial experiment with 5 replications, consisting of 2 K treatments (58 or 240 mg·dm^{-3}) and plants non-inoculated or inoculated with *C. fimbriata*,

was arranged in a completely randomized design. Disease development as well as physiological and biochemical alterations arising from fungal infection were evaluated at 30, 45 and 60 dai. A total of 20 plants were used at each sampling time (5 replicates for each treatment). Each experimental unit corresponded to a plastic pot containing 1 plant. Data from all variables were subjected to analysis of variance (ANOVA). Means from non-inoculated and inoculated plants for each K rate, as well as between K rates, for non-inoculated and inoculated plants at each sampling time were compared with Student's t-test ($p \leq 0.05$) using SAS (Release 8.02 Level 02M0 for Windows, SAS Institute, Inc., 1989, Cary, NC, USA). Correlation analysis was carried out to evaluate the relationships between disease development and physiological parameters.

RESULTS

Disease indices

The KCl treatment was significant for the URLL, RLL and RFC at 30, 45 and 60 dai (Table 1). The URLL, RLL and the RFC significantly decreased by 29.2, 16.4 and 14.4%, respectively (30 dai); by 35.6, 21.8 and 15.6%, respectively (45 dai); and by 44.2, 30.9 and 28.4%, respectively (60 dai), as the K rates increased from 58 to 240 mg·dm^{-3} (Figure 1a,c,d). The DRLL was not affected by the K rates (Figure 1b).

Macro and micronutrients concentrations

Potassium was the only macronutrient that significantly increased in concentration as its rates increased from 58 to 240 mg·dm^{-3} immediately at the point of inoculation (22.9%), above (32.5%) and below (39.2%) (Figure 2a,b,c). The Ca concentration decreased significantly by 29.3% in the symptomatic tissue as the K rates increased from 58 to 240 mg·dm^{-3} (Figure 2a). There was no significant difference between Ca concentration above and below at the point of inoculation when the K rates increased from 58 to 240 mg·dm^{-3} (Figure 2b,c). The manganese (Mn) concentration significantly increased by 39.8, 43.2 and 48%, respectively, at the point of inoculation, above and below, as the K rates increased from 58 to 240 mg·dm^{-3} (Figure 3a,b,c).

Physiological indices

The KCl treatment was significant for A at 30 dai, for A, g_s, E, C_i/C_a and ETR at 45 dai and for g_s, E, C_i/C_a and Chl a/b →

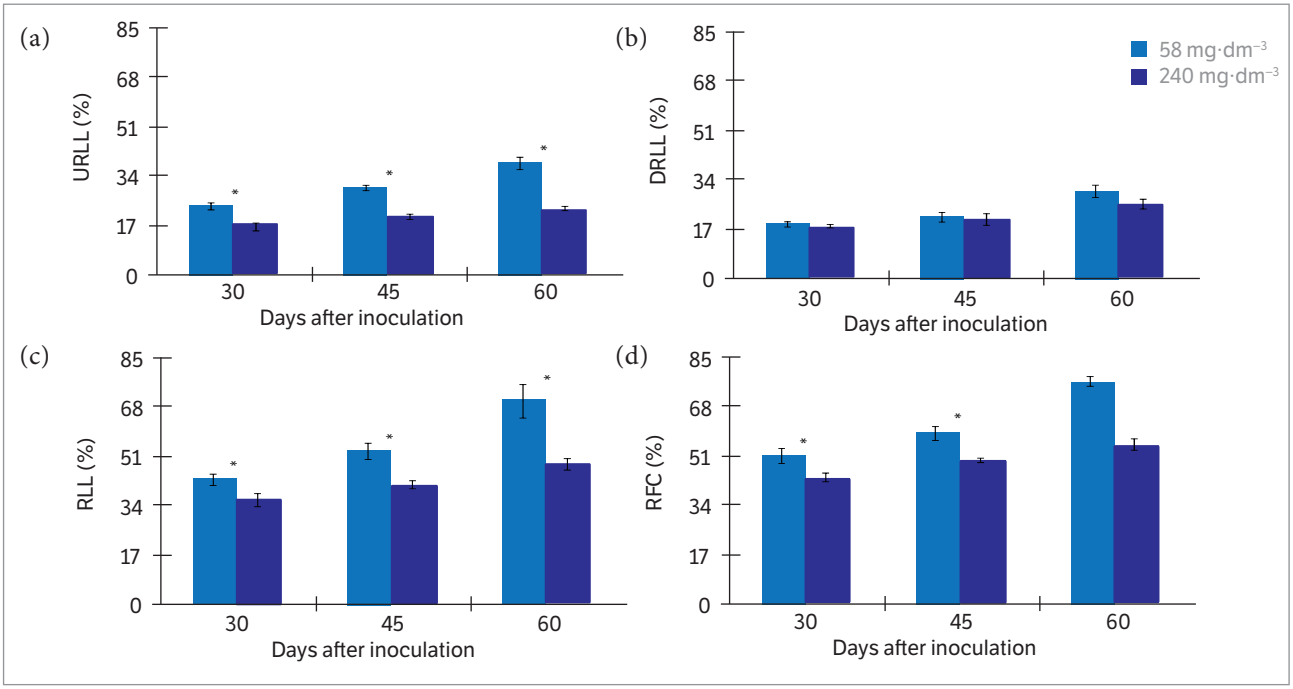

Figure 1. (a) Upward relative lesion length (URLL); (b) Downward relative lesion length (DRLL); (c) Relative lesion length (RLL) and (d) Radial fungal colonization (RFC) determined in the stem tissue of mango plants exposed to potassium (K) application rates of 58 and 240 mg·dm^{-3} and inoculated with *Ceratocystis fimbriata*. The means of the 2 K rates at each evaluation time followed by an asterisk (*) are significantly different according to a Student's *t*-test ($p \leq 0.05$). The error bars represent the standard error of the mean; $n = 5$.

at 60 dai (Table 1). Plant inoculation factor was significant for *A* at 30 dai, for g_s, *E* and C_i/C_a at 45 dai and for *A*, g_s, *E* and C_i/C_a at 60 dai. The K rate × plant inoculation interaction was significant only for C_i/C_a at 60 dai (Table 1). For the non-inoculated plants at 45 dai, *A*, g_s and *E* increased significantly by 17.3, 28.6 and 43.4%, respectively, as the K rate increased from 58 to 240 mg·dm^{-3} (Table 2). At 60 dai, *A*, g_s, *E* and C_i/C_a increased significantly by 5.5, 33.3, 27.1 and 18.5%, respectively, for the non-inoculated plants as the K rate increased from 58 to 240 mg·dm^{-3} (Table 2). Significant increases of 14.7, 20, 34.5 and

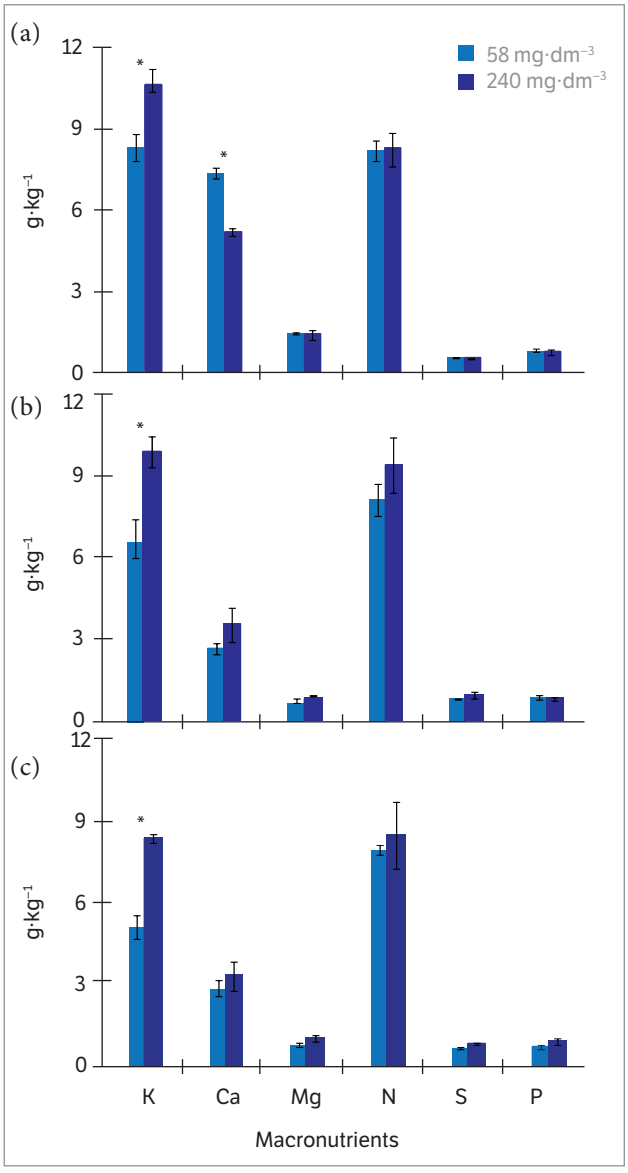

Figure 2. Concentrations of macronutrients in the symptomatic stem tissue (a) as well as above (b) and below (c) the symptomatic tissue in the stem tissue of mango plants exposed to potassium (K) application rates of 58 and 240 mg·dm^{-3} and inoculated with *Ceratocystis fimbriata*. The means of the 2 K rates at each evaluation time followed by an asterisk (*) are significantly different according to Student's *t*-test ($p \leq 0.05$). The error bars represent the standard error of the mean; $n = 5$.

Table 1. Analysis of variance for the effects of K rates, plant inoculation and their interaction for the net CO_2 assimilation rate, stomatal conductance, internal-to-ambient CO_2 concentration ratio, transpiration rate, instantaneous water use efficiency, intrinsic water use efficiency, maximum quantum efficiency of PSII photochemistry in dark-adapted leaves, the efficiency of excitation energy capture by open PSII reaction centers, electron transport rate through PSII, non-photochemical quenching, the fraction of open PSII reaction centers, total chlorophyll, carotenoids, Chl *a*/*b* ratio, upward relative lesion length, downward relative lesion length, the relative lesion length and the radial fungal colonization at 30, 45 and 60 days after inoculation.

Parameters /Variables	Sources of variation								
	K rates			PI			K rates × PI		
	30 dai	45 dai	60 dai	30 dai	45 dai	60 dai	30 dai	45 dai	60 dai
A	**	**	ns	*	ns	**	ns	ns	ns
g_s	ns	*	*	ns	*	*	ns	ns	ns
E	ns	*	*	ns	*	*	ns	ns	ns
C_i/C_a	ns	*	*	ns	*	*	ns	ns	**
A/*E*	ns	**	ns	ns	**	**	ns	**	ns
A/g_s	ns	ns	ns	*	**	**	*	ns	ns
F_v/F_m	ns	ns	ns	ns	ns	ns	ns	ns	*
F_v'/F_m'	ns	ns	ns	ns	ns	ns	ns	ns	ns
NPQ	ns	ns	ns	ns	ns	ns	ns	ns	ns
ETR	ns	*	ns	ns	**	ns	ns	ns	ns
q_L	ns	ns	ns	ns	ns	ns	ns	ns	ns
Total chlorophyll	ns	ns	ns	ns	ns	ns	ns	ns	ns
Chl *a*/*b*	ns	ns	**	ns	ns	ns	ns	ns	ns
Car	ns	ns	ns	ns	ns	ns	ns	ns	ns
URLL	**	**	**	*	*	*	*	*	*
DRLL	ns	ns	ns	*	*	*	ns	ns	ns
RLL	**	**	**	**	**	**	**	**	**
RFC	*	**	**	*	*	*	**	*	*
df	1			1			1		

The results are presented as non-significant or significant at $^{*}p \leq 0.05$ or $^{**}p \leq 0.01$; ^{ns}Non-significant. PI = Plant inoculation; dai = Days after inoculation; *A* = Net CO_2 assimilation rate; g_s = Stomatal conductance to water vapor; *E* = Transpiration rate; C_i/C_a = Internal-to-ambient CO_2 concentration ratio; F_v/F_m = Maximum quantum efficiency of PSII photochemistry in dark-adapted leaves; F_v'/F_m' = Efficiency of excitation energy capture by open PSII reaction centers; NPQ = Non-photochemical quenching; ETR = Electron transport rate through PSII; q_L = Fraction of open PSII reaction centers; Car = Carotenoids; URLL = Upward relative lesion length; DRLL = Downward relative lesion length; RLL = Relative lesion length; RFC = Radial fungal colonization; df = Degrees of freedom.

10.8% at 45 dai and of 32.9, 57.1, 48.7 and 36.2% at 60 dai occurred for A, g_s, E and C_i/C_a, respectively, for the inoculated plants as the K rate increased from 58 to 240 mg·dm^{-3} (Table 2). At 45 dai, g_s, E and C_i/C_a significantly decreased by 20.0, 29.4 and 15.4% and by 28.6, 38.9 and 15.6%, respectively, at the K rates of 58 and 240 mg·dm^{-3} for the inoculated plants in comparison with the non-inoculated counterparts (Table 2). At 60 dai, A, g_s, E and C_i/C_a decreased significantly by 29.0, 62.5, 54.5 and 30.2%, respectively, and g_s, E and C_i/C_a decreased significantly by 41.7, 35.2 and 10.8%, respectively, at the K rates of 58 and 240 mg·dm^{-3} for the inoculated plants in comparison with the non-inoculated counterparts (Table 2).

The factor K rates was significant for A/E only at 45 dai (Table 1). Plant inoculation factor was significant for A/g_s at 30, 45 and 60 dai and for A/E at both 45 and 60 dai (Table 1). The interaction K rates × plant inoculation was significant for A/g_s at 30 dai and for A/E at 45 dai (Table 1). The A/E significantly decreased by 28.1 and 20.3%, respectively, for the non-inoculated and inoculated plants as the K rates increased from 58 to 240 mg·dm^{-3} at 45 dai (Figure 4). At the K rate of 58 mg·dm^{-3}, A/E (Figure 4b) significantly increased by 30.3 and 49.6% and A/g_s (Figure 5) by 22.1 and 52.5% at 45 and 60 dai, respectively, for the inoculated plants in comparison with

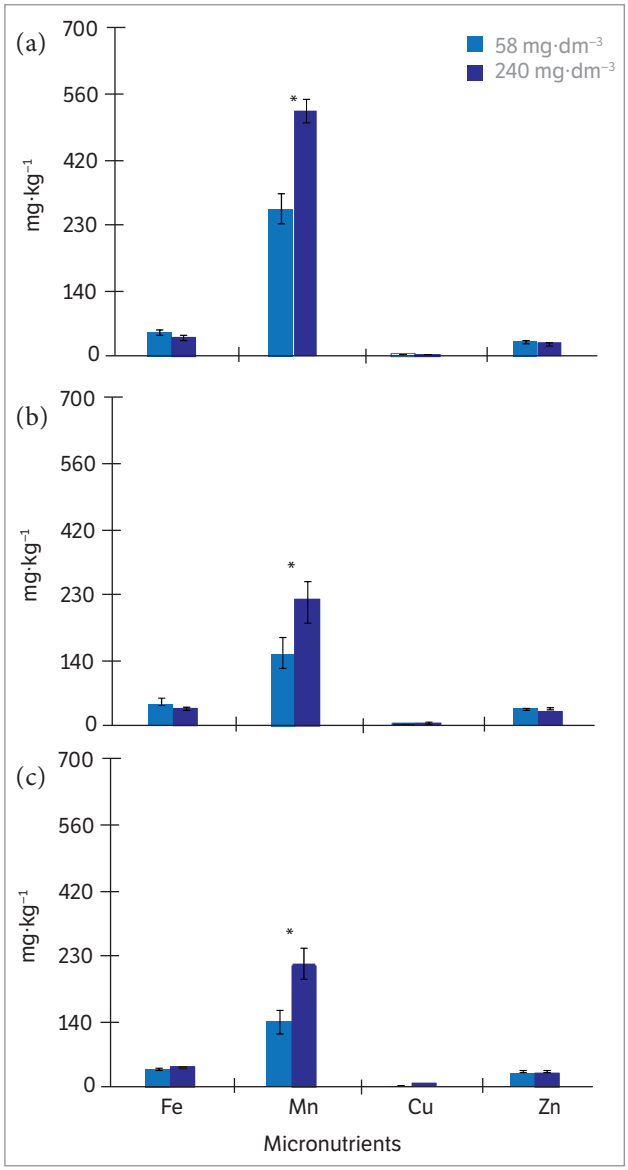

Figure 3. Concentrations of micronutrients in the symptomatic stem tissue (a) as well as above (b) and below (c) the symptomatic tissue in the stem tissue of mango plants exposed to potassium (K) application rates of 58 and 240 mg·dm^{-3} and inoculated with *Ceratocystis fimbriata*. The means of the 2 K rates at each evaluation time followed by an asterisk (*) are significantly different according to Student's *t*-test ($p \leq 0.05$). The error bars represent the standard error of the mean; $n = 5$.

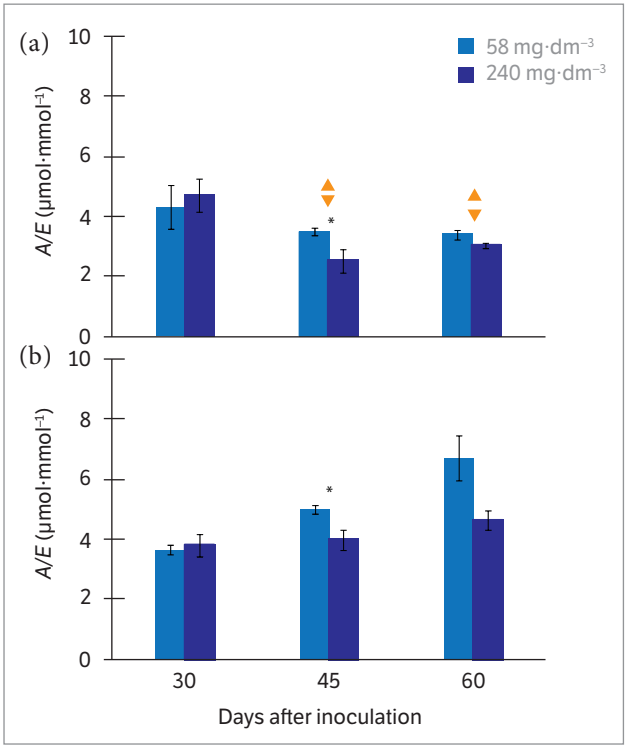

Figure 4. Instantaneous water use efficiency (A/E) determined in the stem tissue of mango plants exposed to potassium (K) application rates of 58 and 240 mg·dm^{-3} and non-inoculated (a) or inoculated (b) with *Ceratocystis fimbriata*. The means of the 2 K rates at each evaluation time followed by an asterisk (*) are significantly different according to Student's *t*-test ($p \leq 0.05$). The symbols ▼ and ▲, when shown, indicate differences between non-inoculated and inoculated plants, respectively, for the K rates of 58 and 240 mg·dm^{-3} at each evaluation time. The error bars represent the standard error of the mean; $n = 5$.

Table 2. Net carbon assimilation rate, stomatal conductance to water vapor, internal-to-ambient CO_2 concentration ratio, transpiration rate, total chlorophyll and carotenoid concentrations as well as the Chl *a*/*b* ratio determined in the leaves of mango plants exposed to potassium (K) application rates of 58 and 240 mg·dm^{-3} and non-inoculated or inoculated (45 and 60 days after inoculation) with *Ceratocystis fimbriata*.

Parameters / Variables	45 dai				60 dai			
	NI		I		NI		I	
	58	240	58	240	58	24	58	240
	mg·dm^{-3}							
A	6.2 ± 0.11*	7.5 ± 0.29	6.4 ± 0.07*	7.5 ± 0.08	6.9 ± 0.03*▼	7.3 ± 0.13	4.9 ± 0.31*	7.3 ± 0.60
g_s	0.10 ± 0.01*▼	0.14 ± 0.01▲	0.08 ± 0.01*	0.10 ± 0.01	0.08 ± 0.01*▼	0.12 ± 0.02▲	0.03 ± 0.01*	0.07 ± 0.01
E	1.80 ± 0.03*▼	3.18 ± 0.38▲	1.27 ± 0.03*	1.94 ± 0.20	1.78 ± 0.11*▼	2.44 ± 0.09▲	0.81 ± 0.14*	1.58 ± 0.15
C_i/C_a	0.69 ± 0.02▼	0.77 ± 0.04▲	0.58 ± 0.01*	0.65 ± 0.01	0.53 ± 0.01*▼	0.65 ± 0.01▲	0.37 ± 0.03*	0.58 ± 0.01
Car	5.47 ± 0.44	5.29 ± 0.43	5.14 ± 0.16	4.55 ± 0.03	5.20 ± 0.54	6.33 ± 0.45	5.33 ± 0.48	5.78 ± 0.37
Chl *a*/*b*	4.37 ± 0.19	4.22 ± 0.05	4.11 ± 0.16	4.27 ± 0.07	4.68 ± 0.10*	3.83 ± 0.19	4.60 ± 0.21	4.21 ± 0.18
Total chlorophyll	22.6 ± 2.20	22.9 ± 1.03	21.2 ± 0.80	21.8 ± 0.91	22.9 ± 1.51	27.9 ± 2.59	21.7 ± 2.10	23.4 ± 1.25

Means between the 2 K rates, at each evaluation time, followed by an asterisk (*) are significantly different according to Student's *t*-test ($p \leq 0.05$). The symbols ▼ and ▲, when shown, indicate difference between non-inoculated (NI) and inoculated (I) plants, respectively, for the K rates of 58 and 240 mg·dm^{-3} at each evaluation time. Values are means ± standard error; $n = 5$. dai = Days after inoculation; *A* = Net CO_2 assimilation rate; g_s = Stomatal conductance to water vapor; *E* = Transpiration rate; C_i/C_a = Internal-to-ambient CO_2 concentration ratio; Car = Carotenoids.

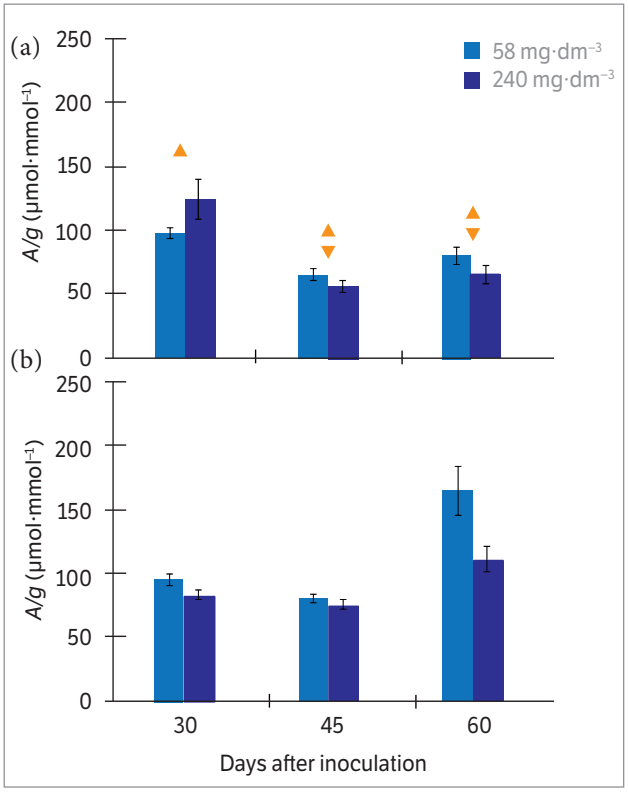

Figure 5. Intrinsic water use efficiency (A/g_s) determined in the stem tissue of mango plants exposed to potassium (K) application rates of 58 and 240 mg·dm^{-3} and non-inoculated (a) or inoculated (b) with *Ceratocystis fimbriata*. The symbols ▼ and ▲, when shown, indicate differences between non-inoculated and inoculated plants, respectively, for K application rates of 58 and 240 mg·dm^{-3} at each evaluation time. The error bars represent the standard error of the mean; $n = 5$.

the non-inoculated counterparts (Figures 4, 5). Significant increases of 37.1 and 34.9% occurred for A/E and of 29 and 43.5%, for A/g_s at the K rate of 240 mg·dm^{-3}, respectively, at 45 and 60 dai, for the inoculated plants in comparison with the non-inoculated counterparts (Figures 4, 5). The A/g_s significantly decreased by 31% at the K rate of 240 mg·dm^{-3} at 30 dai for the inoculated plants in comparison with the non-inoculated counterparts (Figure 5).

The factors K rates and plant inoculation had no significant effect on the photosynthetic parameters at 30 dai (data not shown). The K rates × plant inoculation interaction was significant only for F_v/F_m at 60 dai (Table 1). The value of q_L increased significantly by 69.3% as the K rates increased from 58 to 240 mg·dm^{-3} at 60 dai for inoculated plants (Table 3). At 45 dai, ETR significantly decreased by 28.7 and 25.4%, respectively, at the K rates of 58 and 240 mg·dm^{-3} for the inoculated plants in comparison with the non-inoculated counterparts (Table 3).

The K rate factor was significant only for Chl *a*/*b* at 60 dai (Table 1). For the non-inoculated plants at 60 dai, the Chl *a*/*b* concentration decreased significantly by 18.2% as the K rate increased from 58 to 240 mg·dm^{-3} (Table 2).

There were inverse relationships between *A*, *E*, g_s or C_i/C_a and the RFC (Table 4). The correlations of the K concentration with *A*, g_s, E and C_i/C_a, of C_i/C_a with g_s and *E*, of *E* with *A* and g_s and of *A* with g_s were significantly positive (Table 4).

Table 3. Maximum quantum efficiency of PSII photochemistry in dark-adapted leaves, the efficiency of excitation energy capture by open PSII reaction centers, non-photochemical quenching, electron transport rate through PSII and fraction of open PSII reaction centers determined in the leaves of mango plants exposed to potassium application rates of 58 and 240 mg·dm^{-3} as well as non-inoculated or inoculated (45 and 60 days after inoculation) with *Ceratocystis fimbriata*.

Parameters	45 dai				60 dai			
	NI		I		NI		I	
	58	240	58	240	58	240	58	240
	mg ·dm^{-3}							
F_v/F_m	0.78 ± 0.01	0.79 ± 0.03	0.78 ± 0.02	0.79 ± 0.03	0.82 ± 0.003	0.83 ± 0.03	0.83 ± 0.01	0.80 ± 0.01
F_v'/F_m'	1.50 ± 0.23	2.24 ± 0.51	2.06 ± 0.26	1.67 ± 0.39	2.71 ± 0.51	2.96 ± 0.64	2.96 ± 0.64	2.75 ± 0.48
NPQ	0.60 ± 0.02	0.55 ± 0.06	0.54 ± 0.04	0.59 ± 0.06	0.56 ± 0.04	0.60 ± 0.07	0.62 ± 0.05	0.53 ± 0.04
ETR	86.9 ± 5.10▼	71.0 ± 5.06▲	62. 0 ± 8.89	53.0 ± 5.48	54.91 ± 23.8	82.4 ± 12.76	80.2 ± 8.94	84.1 ± 0.03
q_L	0.16 ± 0.02	0.17 ± 0.04	0.13 ± 0.02	0.11 ± 0.04	0.11 ± 0.06	0.17 ± 0.04	0.13 ± 0.01*	0.22 ± 0.03

t-test ($p \leq 0.05$). The symbols ▼ and ▲, when shown, indicate difference between non-inoculated (NI) and inoculated (I) plants, respectively, for the K rates of 58 and 240 mg·dm^{-3} at each evaluation time. Values are means ± standard error; $n = 5$. F_v/F_m = Maximum quantum efficiency of PSII photochemistry in dark-adapted leaves; F_v'/F_m' = Efficiency of excitation energy capture by open PSII reaction centers; NPQ = Non-photochemical quenching; ETR = Electron transport rate through PSII; q_L = Fraction of open PSII reaction centers. Means between the 2 K rates, at each evaluation time, followed by an asterisk (*) are significantly different according to Student's

Table 4. Pairwise Pearson correlations of the net carbon assimilation rate, stomatal conductance, transpiration rate, internal-to-ambient CO_2 concentration ratio, the radial fungal colonization and the potassium concentration in diseased stem tissue in which measurements were made of the upward relative lesion length, the downward relative lesion length and the relative lesion length for mango plants exposed to potassium application rates of 58 and 240 mg·dm^{-3} and inoculated with *Ceratocystis fimbriata*.

Parameters/Variables	Net CO_2 assimilation rate	g_s	Transpiration rate	C_i/C_a	Radial fungal colonization	Potassium
Net CO_2 assimilation rate	-	13.79*	11.10*	0.30^{ns}	−2.73*	3.03*
g_s	0.89	-	55.74*	3.49*	−3.06*	3.20*
Transpiration rate	0.84	0.99	-	4.39*	−3.41*	3.56*
C_i/C_a	0.04	0.45	0.54	-	−1.80*	1.69*
Radial fungal colonization	−0.37	−0.40	−0.44	−0.26	-	−5.03*
Potassium	0.40	0.42	0.46	0.24	−0.59	-

The values above and below the diagonal are, respectively, the Pearson's correlation coefficients and their t-values. The asterisk (*) indicates significance at 5% of probability according to the Student's *t*-test; ^{ns}Non-significant. g_s = Stomatal conductance to water vapor ; C_i/C_a = Internal-to-ambient CO_2 concentration ratio.

DISCUSSION

The present study provides new information on the role of KCl in enhancing mango resistance to mango wilt. Potassium fertilizer is widely reported to decrease insect infestation and disease incidence in many plant species (Wang et al. 2013). Williams and Smith (2001) found a positive correlation between the high percentage of K in leaf blades and reduced stem rot (*Sclerotium oryzae*) and aggregate sheath spot (*Rhizoctonia oryzae–sativae*) severities in rice plants supplied with K. Araujo et al. (2015) reported that the foliar spray of potassium phosphite reduced the internal necrosis and mango wilt development of mango plants. In the present study, mango plants that received no supplemental KCl became more susceptible to disease. In many cases, K-deficient plants tend to be more susceptible to infection than those with an adequate K supply (Wang et al. 2013). Thus, potassium supplement seems to be a promising strategy to control mango wilt.

Ceratocystis fimbriata are primarily xylem pathogens (Harrington 2000), thus vessel colonization and the development of internal tissue necrosis may provoke the disruption of sap flow, leading to the development of leaf water shortages and, consequently, wilt symptoms (Al-Sadi et al. 2010; Park et al. 2013). The impairment of the regular flow of water throw the soil-plant-atmosphere continuum generally leads to the initiation of adaptive responses, such as stomatal closure, in order to minimize the water loss by transpiration (Christmann et al. 2013). In fact, when compared to the non-inoculated plants, substantial →

declines in g_s and E were observed for inoculated plants, regardless of the K supply to which plants were subjected. This finding is consistent with the harmful effects of *C. fimbriata* infection on mango physiology, which can also be demonstrated by the negative correlations found for RFC and the gas exchange parameters.

The decrease in g_s in consonance with decreases in C_i/C_a ratio suggests that the decreases in A were, at least initially, related to an increased stomatal resistance to CO_2 intake, thus reducing its availability at carboxylation sites and, consequently, reducing the photosynthetic performance of the mango plants subjected to the KCl treatment. Strict diffusive limitations were also supported by the absence of any detectable changes in the parameters related to photochemical activity (e.g., F_v/F_m), suggesting a minor role in the impairment of CO_2 fixation at the biochemical level. Decreases in healthy green leaf tissue were also not a major factor contributing to the decreases in A because, in general, no differences in the concentration of photosynthetic pigments were found between the non-inoculated and the inoculated plants regardless of the KCl treatment.

It should be note that, although KCl fertilization results in an increase in the water-use efficiency of the plants (Ashraf et al. 2001), increases in the A/g_s and A/E ratios were found for the inoculated plants in the present study, regardless of the KCl treatment. This finding implies that this amelioration is not an effect of KCl. Rather, the increases in both ratios reflect the higher influence of fungal infection on g_s and E than on A.

Despite the negative effects arising from inoculation, when isolating the effect of the KCl treatment on the inoculated plants, it was observed that there was an enhancement in photosynthetic performance with KCl treatment. According to Jin et al. (2011) and Marschner (2012), K influences the process of photosynthesis in many ways, e.g. in ATP synthesis, in the activation of enzymes, balance of electric charges required for photophosphorylation and in stomatal opening/closure regulation. Various yields components are strongly linked to nutrition with K favoring the photoassimilates transport from the source to the sink (Gajdanowicz et al. 2011; Zörb et al. 2014). Since K uptake into guard cells is a critical step in stomatal opening (Thiel and Wolf 1997; Shabala 2003), the diffusive limitations brought by the plant inoculation with *C. fimbriata* may have been overcome in some extent in mango plants supplied with the KCl treatment. Accordingly, in the present study, as K supply increased from 58 to 240 mg·dm^{-3}, g_s increased coupled with both A and C_i/C_a in inoculated plants.

The results obtained by Jin et al. (2011) also suggest that low leaf K concentrations limit A, and this relative limitation is defeated with increasing supplies of K, which results in increased g_m and g_s. Conversely, other reports such as Basile et al. (2003) showed that leaf K concentration did not significantly influence stomatal conductance, implying that the effects of K deficiency on plant photosynthesis remain elusive (Jin et al. 2011). Thus, the non-categorical way of stating the involvement of K directly in the photosynthetic process gives the loophole to assume that, beyond a supposed direct effect of mineral nutrient at leaf level, the resulting best photosynthetic performance of inoculated plants supplied with greater K rate may be also due to an effect of K directly at the site of infection, reducing disease severity.

The effect of K on increasing the resistance of plants to diseases has been attributed to the reduction of the competition between the pathogen and its host for nutritional resources (Holzmueller et al. 2007). This condition greatly favors the allocation and availability of resources by the plants, which may be used in a myriad of strategies for protection and repair of damages (Mengel 2001). Among all the essential nutrients necessary for better plant development, K is most often associated with reducing disease intensities; nevertheless, the participation of other nutrients must be likewise acknowledged (Lopes 1998) and probably linked in a synergistic relationship.

In the present study, the accumulation of Mn, together with K, was observed in the stem tissues of inoculated plants supplied with the higher K rate. In contrast, the Ca concentration decreased in the point of inoculation of mango plants supplied with the higher K rate. X-ray microanalysis revealed a higher accumulation of K in the pith, secondary xylem and phloem that were in close contact with hyphae of *Phytophthora sojae* in soybean (Sugimoto et al. 2010). According to Sugimoto et al. (2010), the K accumulation around the penetration sites of *P. sojae* may be a part of soybean resistance against pathogen infection. X-ray microanalysis observations of bean leaves also demonstrated that →

the increased K content might be effective to decrease anthracnose severity (Cruz et al. 2014). Sugimoto et al. (2010) reported that marked K accumulations inside of penetration-stopping sites of fungal hyphae are due to host defense responses. Although the physiological function of K in host resistance against disease is not well understood, nutritional factors favoring host resistance have been attributed to alterations in protein or amino acid availability, decreased cell permeability and reduced susceptibility of tissue to maceration and penetration (Prabhu et al. 2007). In the present study, high K concentration at the point of fungal inoculation and adjacent areas indicated that this macronutrient contributed for mango resistance against infection by *C. fimbriata*.

An adequate K supply frequently increases the concentration of phenolic compounds in infected plant tissues, contributing to increase the resistance against disease (Prasad et al. 2010). Phenolic accumulation at the sites of infection has been previously highlighted as an important component of mango resistance against *C. fimbriata* infection (Araujo et al. 2014a,b). According to Araujo et al. (2015), mango plants with resistance induced by potassium phosphite showed reduced mango wilt development and microscopic defense responses against fungal infection, such as the accumulation of phenolic-like compounds, formation of an antifungal barrier and quick deposition of tyloses impregnated with phenolics. In another study, Araujo et al. (2016) showed that 6 phenolic compounds (caffeic acid, *p*-coumaric acid, gallic acid, protocatechuic acid, catechin and epicatechin) played an important role in mango resistance against *C. fimbriata* infection. In the present study, is it plausible to postulate that plants exposed to the highest KCl doses showed reduced mango wilt development due to a potentiation on the accumulation of phenolics in the sites of fungal infection.

Higher concentrations of phenolic compounds may also be related to an increase in local availability of Mn, as observed in the present study in conjunction with the increase in K concentration. It is known that Mn acts directly in the activation of the enzyme phenylalanine ammonia lyase (PAL), a key enzyme in the phenylpropanoid route, which allows reactions leading to the production of various phenolic compounds (Hammerschmidt 1999). Araujo et al. (2015) associated the reduced internal stem necrosis and mango wilt development with an induction of the phenylpropanoid pathway by potassium phosphites. Mn is also a cofactor of peroxidases, associated with the formation of lignin (Leina et al. 1996) and is also a key component of the enzyme superoxide dismutase (SOD), involved in the defense of tissues against oxidative stress that may arise from pathogen infection (García-Limones et al. 2002). Bispo et al. (2015) reported that mango plants exhibited an increase in the activities of enzymes and in the concentration of metabolites related to the oxidative stress responses after inoculation with *C. fimbriata*. Many fungal diseases decrease with increasing concentrations of Mn in plant tissues (Huber and Wilhelm 1988). Examples of such diseases are wilting caused by *F. oxysporum* f. sp. *vasinfectum* and *Verticillium albo-atrum* in cotton and tomato, respectively (Dutta and Bremner 1981; Fahim et al. 1973; Mandal and Sinha 1992; Shao and Foy 1982). According to Huber and Wilhelm (1988) and in accordance with our findings, the concentration of Mn generally increases in localized areas near the point of pathogen infection.

The K and Ca concentrations increased and decreased, respectively, in the diseased tissue as the K rates increased. Some factors such as other cations and pH can affect the availability of Ca to the roots (Prabhu et al. 2007). Cations in the soil compete with one another for a place on the cation exchange capacity; however, some are attracted more strongly than others (Benton Jones 2014). The monovalent cations (e.g. K^+) are more readily absorbed by roots than the divalent ones (e.g. Ca^{2+} and Mg^{2+}) (Benton Jones 2014). Changes in the balance between K and Ca can alter the susceptibility of plants to pathogens (Prabhu et al. 2007). The increased severity of black shank (*P. parasitica* var. *nicotianae*) with high levels of K may be related to the effect of an altered K:Ca ratio on the differential permeability of cell membranes (Prabhu et al. 2007). However, Araujo et al. (2014b), using X-ray microanalysis, reported that Ca accumulation in stem tissues of mango plants contributed to the strength of the cell walls which hampered *C. fimbriata* colonization. In the present study, even though the K supply probably affected the K:Ca ratio, due the Ca concentration decrease in the inoculation point, the susceptibility of mango plants against infection by *C. fimbriata* did not increase.

CONCLUSION

The results of the present study suggest that mango plants subjected to higher KCl rates became more resistant to the mango wilt, most likely through fostering a better physiological performance and consequently favoring the mounting of host defense responses at the infection sites. Thus, the development of management strategies that favor the increase of KCl supply may be used as a useful tool for the reduction of mango wilt severity.

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