ISAIAS SEVERINO CACIQUE

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

Dissertation submitted to the Federal University of Viçosa, as part of the requirements of the Graduate Program in Plant Pathology, to obtain the title of *Magister Scientiae*.

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APROVADA: 29 de julho de 2014

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Fabrício de Ávila Rodrigues
(Orientador)

Aos meus pais, Otelina Fernandes Cacique e

Avelino Severino Cacique

Aos meus irmãos Mateus, Maria Aparecida,

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A minha estimada namorada Priscilla Aguiar Möller

Aos meus amigos e demais familiares

DEDICO

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BIOGRAFIA

ISAIAS SEVERINO CACIQUE, filho de Otelina Fernandes Cacique e Avelino Severino Cacique, nasceu no dia 17 março de 1976, em Salinas, Minas Gerais. Iniciou o curso de Agronomia no ano de 2007 na Universidade Federal de Viçosa (UFV), e em Janeiro de 2012 graduou-se Engenheiro Agrônomo. Durante a graduação, teve oportunidade de trabalhar como bolsista de Iniciação Científica no Departamento de Fitopatologia sob a orientação do Prof. Fabrício de Ávila Rodrigues. No mês de Novembro de 2012 iniciou o curso de Mestrado no Programa de Pós-Graduação em Fitopatologia da UFV atuando na área da Interação Patógeno-Hospedeiro sob orientação do Prof. Fabrício de Ávila Rodrigues.

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RESUMO

CACIQUE, Isaias Severino, M. Sc., Universidade Federal de Viçosa, Julho de 2014. **Desempenho fotossintético das plantas de manga modulado pelo potássio e infectadas por *Ceratocystis fimbriata***. Orientador: Fabrício de Ávila Rodrigues.

A murcha de Ceratocystis, causada pelo fungo *Ceratocystis fimbriata*, é uma das mais importantes doenças da cultura da manga. Considerando-se os efeitos benéficos proporcionados pelo potássio (K) em culturas rentáveis e a falta de informações sobre o efeito deste macronutriente sobre no desenvolvimento da murcha de Ceratocystis, o presente estudo teve como objetivo avaliar a forma como as plantas de manga respondem fisiologicamente à infecção causada por *C. fimbriata*. Plantas foram cultivadas em vasos plásticos contendo 58 ou 240 mg de K dm^{-3} no substrato . Os sintomas da doença mostraram-se mais pronunciados nas plantas inoculadas e supridas com a menor dose de K, atingindo valores superiores para os índices de lesão URLL (comprimento relativo acima do ponto de inoculação) 79%, RLL (comprimento relativo da lesão) 48% e RFC (colonização radial pelo fungo) 40%, em comparação àquelas que receberam a dose mais elevada (240 mg de K dm^{-3}). Como consequência, declínios substanciais na condutância estomática (g_s) em consonância com reduções na taxa de concentração interna e externa de CO_2 (C_i/C_a) e ausência de alterações detectáveis nos parâmetros de fluorescência da clorofila *a*, sugerem que reduções na taxa fotossintética (*A*) destas plantas deram-se, pelo menos inicialmente, devido a limitações estomáticas. Altas concentrações de potássio, cálcio e manganês foram encontradas nos tecidos do caule das plantas inoculadas e supridas com a maior concentração de K, comportamento provavelmente relacionado ao desenvolvimento local de mecanismos de defesa. Os resultados do presente estudo sugerem que o suprimento de K favorece a resistência das plantas, pois as plantas que receberam a maior dose de K apresentaram menor severidade, levando consequentemente a um melhor desempenho fotossintético.

ABSTRACT

CACIQUE, Isaias Severino, M. Sc.,Universidade Federal de Viçosa, July 2014. **Potassium-modulated photosynthetic performance of mango plants infected by *Ceratocystis fimbriata***. Adviser: Fabrício de Ávila Rodrigues.

The mango wilt, caused by the fungus *Ceratocystis fimbriata*, is one of the most important diseases affecting mango production. Considering the beneficial effects provided by the potassium (K) supply in other profitable crops and the lack of information on the effect of macronutrients in the development of the mango wilt, the present study aimed to evaluate how plants respond physiologically to the infection caused by *C. fimbriata*. Plants were grown in plastic pots containing 58 or 240 mg K dm^{-3} in the substrate. Disease symptoms were more pronounced in plants inoculated and supplied with the lower K rate, reaching higher values for the disease indices URLL (upward relative lesion length) 79%, RLL (relative lesion length) 48% and RFC (radial fungal colonization) 40% when compared to those supplied with the higher rate (240 mg de K dm^{-3}). Consequently, substantial declines in stomatal conductance (g_s), in line with reductions in internal-to-ambient CO_2 concentration ratio (C_i/C_a) and absence of detectable changes in the chlorophyll *a* fluorescence parameters, suggest that the reduction on the net carbon assimilation rate (A) of those plants are, at least initially, due to stomatal limitations. High concentrations of potassium, calcium and manganese were found in the stem tissues of plants inoculated and supplied with the highest concentration of K, most likely involved in the local development of defense mechanisms which possibly hold a higher resistance against pathogen's spread. The results of this study suggest that the supply of K favors the resistance of plants, because the plants that received the higher dose of K showed less severity, leading to better photosynthetic performance.

INTRODUCTION

The mango (*Mangifera indica* L.) is among the most produced fruits in the world with India, China, Indonesia, Mexico, Pakistan and Thailand being the major producing countries (FAO, 2013). Brazil is in seventh place among the mango producing countries in the world (FAO, 2013) and among the planted cultivars, Ubá stands out mainly for the juice industry because of the good intrinsic characteristics such as pulp color and excellent brix (Silva *et al*., 2012). The Brazilian production of mango has great potential for improvement in exports and shows increasing competitiveness in terms of prices and quality (Perosa & Pierre, 2002). However, despite the growing interest in the global market and growing incentives and forecasts for production, mango plants are often suffering from the occurrence of several diseases caused by foliar, fruits and soilborne pathogens which reduce fruit quality and leads to substantial yield losses (Batista *et al*., 2008). The mango wilt, caused by the fungus *Ceratocystis fimbriata* Ellis & Halsted, is considered one of the most important diseases causing great yield losses in mango production worldwide (Batista *et al*., 2008). The main symptoms caused by this disease occurs on shoots with withered and dried leaves and internal necrotic lesions in the stem tissues, which are initiated in the thinner branches and slowly progress throughout the canopy until death of the entire plant (Viégas, 1960; Ribeiro, 2005; Batista *et al*., 2008). In the early stages of fungal infection, the mango wilt is quite difficult to be diagnosed and when the symptoms becomes noticeable in the trunk, the tree dies rapidly; therefore, cutting and burning the infected plant parts and the use of resistant rootstocks are the main recommended measures to achieve a better disease control (Rosseto & Ribeiro, 1990).

Although often undervalued in the control of plant diseases, the mineral nutrition shows its importance in empirical tests by the manipulation of nutrients availabilities to plants and the modification of the integral components of the agricultural soil environment (Huber &

Jones, 2013). Many physiological processes on plants such as respiration, water and nutrients 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 possibility of plants to built mechanism of resistance against pathogens infection (Huber & Jones, 2013). Virtually, all essential nutrients can either decrease or increase host resistance against diseases (Huber & Graham, 1999) and, among them, the macronutrient potassium (K) should receive major notability, since it plays crucial roles in many plant physiological process (Zorb *et al*., 2014; Römheld & Kirkby, 2010). The K nourishment favors plants to greatly uptake water and nutrients and improve their transport between the source and the sink organs, besides being the main cation involved in the establishment of changes in the osmotic potential (Ishizuka, 1978). Higher accumulation of K on the tissues of several plant species during their growth stage comprises a key strategy to cope with environmental stresses, including pathogens infection even though the positive effects of this macronutrient are rather related to a physiological effect in improving plant fitness than directly affecting the pathogen itself (Kafkafi, 1990; Prabhu *et al*., 2007). It has been reported that the soil amendment with K reduced the severities of the sudden death, caused by *Fusarium solani* f.sp. *glycines*, on soybean seedlings (Sanogo & Yang, 2001) and the angular leaf spot, caused by *Pseudocercospora griseola*, on beans (Prabhu *et al*., 2007).

Considering the beneficial effects given by K in reducing the intensities of several foliar and vascular diseases in crops of high economic value and the lack of information, to the best of our knowledge, on the effect of this macronutrient on mango wilt development, the present study aimed to evaluate how the mango plants could respond against *C. fimbriata* infection at the physiological level when growing in soil with low and high K levels.

MATERIALS AND METHODS

Plant material. Mango plants from cultivar Ubá (≈ 3 years old), were obtained from a commercial orchard in Dona Euzébia city, Minas Gerais State, Brazil. These plants were grafted onto plants from cultivar Imbú, which is widely used as rootstock in the Zona da Mata region, Minas Gerais State, Brazil. Plants were transplanted into plastic pots containing 8 kg of substrate consisting of a mixture of soil, sand and manure in a 2:1:1 proportion. The plants were grown in plastic pots containing 58 mg of potassium (K) dm^{-3} (original K level based on the chemical analysis of the substrate) and also in plastic pots with substrate amended with a solution of potassium chloride 0.5 M to achieve the rate of 240 mg of K dm^{-3} at five days before the plants were transplanted. The plants were grown in a greenhouse (temperature of 30 ± 2°C and relative humidity of 70 ± 5%) for two months before the beginning of the experiments.

Inoculation procedure. The isolate CEBS15 of *C. fimbriata* was used to inoculate the plants. This isolate was obtained from symptomatic mango plants collected in the city of Brejo Santo, Ceará State (07° 29' 34" S, 38° 59' 06" W), Brazil. The isolate was preserved by Castellani's method (Dhingra & Sinclair, 1995). Plugs of malt extract-agar medium containing fungal mycelia were transferred to Petri dishes containing potato-dextrose-agar (PDA). After three days, the PDA plugs containing fungal mycelia were transferred to new Petri dishes containing the same culture medium and were maintained in an incubator chamber (temperature of 25°C and 12-h photoperiod) 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 width) 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-days-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. Holes on the stems of plants receiving only PDA medium plugs served as the control treatment.

Relative lesion indices. 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. 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 a length of 20 cm (the distance from the graft scar to the top of the stem). The radial fungal colonization (RFC) was determined as the length of the necrotic tissue in relation 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 lesions lengths above (LL_U) and below (LL_D) the inoculation point, respectively.

Leaf gas exchange and chlorophyll *a* fluorescence measurements. The leaf gas exchange parameters were determined by using 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 (1000 µmol photons m^{-2} s^{-1}) from approximately 0800 to 1200 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. After 40 min of dark adaptation, the leaf tissue was 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 & Baker (1997) were determined in light-adapted leaves. From these parameters, the efficiency of excitation energy capture by open PSII reaction centers (F_v'/F_m') was calculated [(F_m' - F_0'/F_m')]. The estimated fraction of open PSII centers (q_L) was calculated as [(F_m' - F_s) $*F_0$'/ (F_m' - F_0')$*F_s$] (Kramer *et al.*, 2004) and the non-photochemical quenching coefficient (NPQ) was calculated as [(F_m/F_m') - 1)] (Bilger & Bjorkman, 1990). The actual quantum yield of PSII electron transport (Φ_{PSII}) was computed as [(F_m' -F_s)/F_m'], from which the electron transport rate (ETR) was calculated as (Φ_{PSII}*PPFD$*f*$*α$), where f is a factor that accounts for the partitioning of energy between PSII and PSI and is assumed to be 0.5, which indicates that the excitation energy is equally distributed between the two photosystems; α is the leaf absorbance by the photosynthetic tissues and is assumed to be 0.84 (Maxwell & Johnson, 2000).

Determination of the concentrations of nutrients on stem tissue. At the end of the experiments carried out to evaluate the disease indices, the diseased tissue was carefully removed with a scalpel from the stems of plants of the replications of each treatment as well as the non-diseased tissue above and below the diseased stem tissue, dried at 70°C for 72 h and ground to pass through a 40-mesh screen with a Thomas Wiley mill (Thomas Scientific, Swedesboro, NJ, USA). The powder obtained from the stem tissue was used to determine the concentrations of macro and micronutrients according to Malavolta *et al*. (1997).

Determination of photosynthetic pigments. 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) (Santos *et al.*, 2008) and kept in the dark for 48 h. The absorbance of the extracts were read at 480, 649.1 and 665.1 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 five replications, consisting of two K rates (58 and 240 mg dm^{-3}) and non-inoculated or inoculated plants arranged in a completely randomized design was carried out to evaluate the URLL, DRLL and RFC as well as the concentrations of macro and micronutrients on the stem tissue. A 2 × 2 factorial experiment with five replications, consisting of two K rates and plant inoculation (non-inoculated or inoculated plants) with a completely randomized design, was carried out to obtain samples for the biochemical analysis. The ANOVA for the experiment used to evaluate the URLL, DRLL

and RFC as well as the concentrations of macro and micronutrients on the stem tissue tested 2 × 3 factors consisting of two K rates and three sampling times (30, 45 and 60 dai). The analysis of variance (ANOVA) for the experiment used to evaluate the biochemical variables tested 2 × 2 × 2 factors consisting of two K rates, both non-inoculated and inoculated plants and two sampling times (45 and 60 dai). Each experimental unit consisted of one plastic pot with one plant with a total of five plants at each sampling time. Data from all variables were analyzed by ANOVA and means between the two K rates at each evaluation time and between non-inoculated and inoculated plants for each K rate at each evaluation time were compared by *t*-test ($P \leq 0.05$) using SAS (version 6.12; SAS Institute, Inc., Cary, NC).

RESULTS

URLL, DRLL, RLL and RFC. The factor K rates 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 41, 55 and 79%, by 20, 28 and 48% and by 17, 19 and 40%, respectively, at 30, 45 and 60 dai as the K rates increased from 58 to 240 mg dm^{-3} (Fig. 1a, c and d). The DRLL was not affected by the K rates (Fig. 1b).

Nutrients concentrations of the stem tissue. The K was the only macronutrient that significantly increased in concentration as the K rates increased from 58 to 240 mg dm^{-3} at above (48%) and below (64%) of the diseased tissue and also at the diseased tissue (30%) (Fig. 2a-c). The Ca concentration significantly decreased by 41% at the diseased tissue as the K rates increased from 58 to 240 mg dm^{-3} (Fig. 2a). The Mn concentration significantly increased by 66% at the diseased tissue as the K rates increased from 58 to 240 mg dm^{-3} (Fig. 3a).

***A*/*E* and *A*/g_s parameters.** The factor K rates was significant for *A*/*E* only at 45 dai (Table 1). The factor plant inoculation was significant for *A*/g_s at 30 dai and for *A*/*E* and *A*/g_s at both 45 and 60 dai. 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 39 and 25%, respectively, for the non-inoculated and inoculated plants as the K rates increased from 58 to 240 mg dm^{-3} at 45 dai (Fig. 4). At the K rate of 58 mg dm^{-3}, *A*/*E* significantly increased by 43 and 98% and *A*/g_s by 28 and 110%, respectively, at 45 and 60 dai for the inoculated plants (Figs. 4b and 5b) in comparison to the non-inoculated counterparts (Figs. 4a and 5a). Significant increases of 59 and 54% occurred for *A*/*E* and of 45 and 77% 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 to the non-inoculated

counterparts (Figs. 4 and 5). The A/g_s significantly decreased by 31% at the K rate of 240 mg dm^{-3} at 30 dai for the non-inoculated plants in comparison to the inoculated counterparts (Fig 5).

Leaf gas exchange parameters. The factor K rates was significant for A at 30 dai, for A, g_s, E and C_i/C_a at 45 dai and for g_s, E and C_i/C_a at 60 dai (Table 1). The factor plant inoculation 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 interaction K rates × plant inoculation was only significant for C_i/C_a at 60dai (Table 1). For the non-inoculated plants at 45 dai, A, g_s and E significantly increased by 21, 40 and 77%, respectively, as the K rates increased from 58 to 240 mg dm^{-3} (Table 3). At 60 dai, A, g_s, E and C_i/C_a significantly increased by 6, 50, 37 and 23%, respectively, for the non-inoculated plants as the K rate increased from 58 to 240 mg dm^{-3}. Significant increases of 17, 25, 53 and 12% at 45 dai and of 49, 133, 95 and 57% at 60 dai occurred, respectively, for A, g_s, E and C_i/C_a for the inoculated plants as the K rates increased from 58 to 240 mg dm^{-3}(Table 3). At 45 dai, g_s, E and C_i/C_a significantly decreased by 25, 42 and 19% and by 40, 64 and 18%, respectively, at the K rates of 58 and 240 mg dm^{-3} for the inoculated plants in comparison to the non-inoculated counterparts (Table 3). At 60 dai, A, g_s, E and C_i/C_a significantly decreased by 41, 167, 120 and 43% and g_s, E and C_i/C_a by 71, 54 and12%, respectively, at the K rates of 58 and 240 mg $dm^{-3}$for the inoculated plants in comparison to the non-inoculated counterparts (Table 3).

Photosynthetic parameters: There was no significant effect of the factors K rates and plant inoculation for the photosynthetic parameters at 30 dai (data not shown). The interaction K rates × plant inoculation was significant only for F_v/F_m at 60 dai, (Table 1). The q_L significantly increased by 69% as the K rates increased from 58 to 240 mg dm^{-3}(Table 4). At

45 dai, ETR significantly decreased by 40 and 34%, respectively, at the K rates of 58 and 240 mg dm^{-3} for the inoculated plants in comparison to the non-inoculated counterparts (Table 4).

Pigments concentration. The factor K rates 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 significantly decreased by 22% as the K rates increased from 58 to 240 mg dm^{-3} (Table 3).

Pearson correlation. The correlation of *A*, *E*, g_s and C_i/C_a and K concentration with the RLL was significantly negative (Table 2). The correlation 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 2).

DISCUSSION

The present study provides, to the best of the author's knowledge, novel information on the role played by the macronutrient K on mango resistance against *C. fimbriata* infection. The mango wilt symptoms on plants supplied with the basal level of K in the substrate, based on the disease indices URLL, RLL and RFC, were more pronounced in constrast to plants supplied with the highest K rate. The RFC has proved to be a variable of utmost importance in studying the progress of mango wilt because it indicates the colonization of the inner stem tissues by *C. fimbriata*, including the vascular system (Araújo *et al*., 2014a,b). According to Harrington (2000), *Ceratocystis* spp. is primarily a xylem pathogen, thus the vessels colonization and the development of internal tissue necrosis may provoke the disruption of sap flow leading, therefore, to the development of leaf water shortages and, consequently, the wilt symptoms. The impairment of the regular flow of water throw the soil-plant-atmosphere continuum generally leads to the mediation 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 rates. This finding corroborates with the harmful effects of *C. fimbriata* infection on mango physiology, which can also be demonstrated by the negative correlations found for RLL and the gas exchange parameters studied. Moreover, the decrease in g_s in consonance with reductions in the C_i/C_a ratio suggest that the decreases in A were, at least initially, related to an increase on stomatal resistance to CO_2 intake reducing, therefore, its availability at the carboxylation sites and, consequently, reducing the photosynthetic performance of the mango plants. This fact is also corroborated by the absence of any detectable changes in the parameters related to the photochemical activity (e.g. F_v/F_m), suggesting a minor role in the impairment of CO_2 fixation at the biochemical level. Reduce healthy green leaf tissue was also not a major factor contributing to reduce A since, in general,

no differences were found between non-inoculated and inoculated plants regardless of the K rates for the concentration of photosynthetic pigments. Although K fertilization results in the upgrade of the plants water-use efficiency (Ashraf *et al*., 2001), in the present study, increases in both A/g_s and A/E ratios were found for the inoculated plants regardless of the K rate, which implies that rather than an effect of K, this amelioration is better linked to the higher influence of fungal infection on the parameters g_s and E than on A.

Plants supplied with the highest K rate that consequently presented the lowest RLL and RFC values showed an enhancement in the photosynthetic performance. According to Marschner (1995) and Jin *et al*. (2011), K affects the process of photosynthesis in many ways such as in the ATP synthesis, activation of enzymes involved in photosynthesis, balance of electric charges required for photophosphorylation and acting as counterion to the light-induced H^+ flux across thylakoid membranes. In addition, stomatal closure is a common and well documented response to K deprivation often considered a major factor contributing to decrease the net photosynthesis (Thiel & Wolf, 1997). The light-dependent uptake of K into the guard cells is a critical step in stomatal opening (Shavala, 2003) and is likely that the stomatal limitations for the plants infected by *C. fimbriata* may have been overcome in some extent at the highest K rate. Accordingly, in the present study, as K supply increased, g_s increased coupled with both A and C_i/C_a. The results obtained by Jin *et al*. (2011) also suggest that low leaf K concentrations limit A and this relative limitation is defeated by increasing K supply that results in increased g_m and g_s. Conversely, leaf K concentration did not significantly influence stomatal conductance implying, therefore, that the effects of K deficiency on plant photosynthesis remain elusive (Basile *et al*., 2003; 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 the

highest K rate may be also due to an effect of this macronutrient at the infection site contributing, therefore, to reduce disease development.

Among all the essential nutrients necessary for a better plant development, K is most often associated with reducing diseases intensities without being discarded the participation of other nutrients (Lopes, 1998). In fact, in the present study, it was observed the accumulation of Ca and Mn together with K in the stem tissue of plants supplied with the highest K rate and colonized by *C. fimbriata*. The accumulation of Ca in the stem tissues of plants infected by *C. fimbriata* was also detected by x-ray microanalysis (Araújo *et al*., 2014a). Indeed, it is known that Ca availability allows plants to fix up and structure cell walls through calcium bridges, which might increase their strength (Willats, 2001; Cantu *et al*., 2008). The effect of K on increasing the resistance of plants to diseases has been attributed to the reduction of the competition between pathogen and its host for nutritional resources (Holzmueller *et al*., 2007). This condition greatly favors the allocation of resources by the plants, which will be used, for example, on the fortification of cell walls that contribute to reduce tissue colonization by the pathogen and on the potentiation of other host defense responses (Mengel, 2001). The K is also essential for the maintenance of cellular osmotic potential allowing greater stomatal opening and consequently greater $C0_2$influx to the internal spaces of the mesophyll cells (Mengel, 2001; Marschner, 2012). Adequate K supply also increases the concentration of phenolic compounds on infected plant tissues contributing to increase the resistance against diseases (Prasad *et al*., 2010). Phenolics were highlighted to be important for mango resistance against *C. fimbriata* infection (Araújo *et al*., 2014a,b).

The increased Mn concentration in tissues infected by *C. fimbriata* may be related to a reduction of disease severity. There are reports of the influence of manganese on plant diseases and the lower concentration of this micronutrient in the tissues of plants from susceptible cultivars. However, its concentration increases in localized areas near to the point

of pathogen infection (Huber & Wilhelm, 1988). Many fungal diseases are reduced with increasing concentration of Mn in plant tissues such as wilting caused by *Fusarium oxysporum* f.sp. *vasinfectum* and *Verticillium albo-atrum* in cotton and tomato, respectively (Fahim *et al*., 1971; Mandal & Sinha, 1992; Shao & Foy, 1982; Dutta & Bremner, 1981).

It is known that mango wilt is a very assertive disease that affects mango plants at different phenological stages and may lead to the fast decay of affected trees and the death of entire plants in the orchards in a short time (Batista *et al*., 2008). Mango wilt control consist in preventing the introduction of diseased seedlings in the orchards, the cutting and burning of already infected plant parts and the use of resistant rootstocks since no fungicides are registered for disease control (Rosseto & Ribeiro, 1990). In this way, is highly advisable the find alternative strategies for mango wilt control to reduce disease development and yield losses.

The results of the present study suggest that mango plants containing high K concentration on the stem tissue became more resistant to mango wilt probably through the occurrence of host defense responses at infection sites that indirectly favored the photosynthetic performance of the infected plants. Thus, keeping high levels of K in the stem tissue of mango plants becomes a useful tool for the reduction of mango wilt severity

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TABLES AND FIGURES

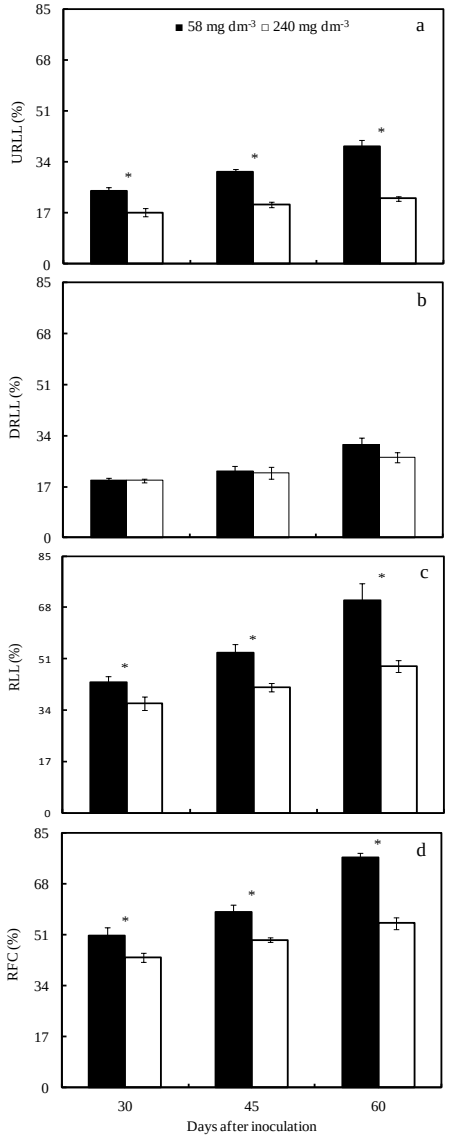

Figure 1. Upward relative lesion length (URLL), downward relative lesion length (DRLL), relative length of the lesion (RLL) and radial fungal colonization (RFC) determined on the stem tissue of mango plants exposed to the potassium (K) rates of 58 and 240 mg dm^{-3} and inoculated with *Ceratocystis fimbriata*. Means between the two 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. $n = 5$.

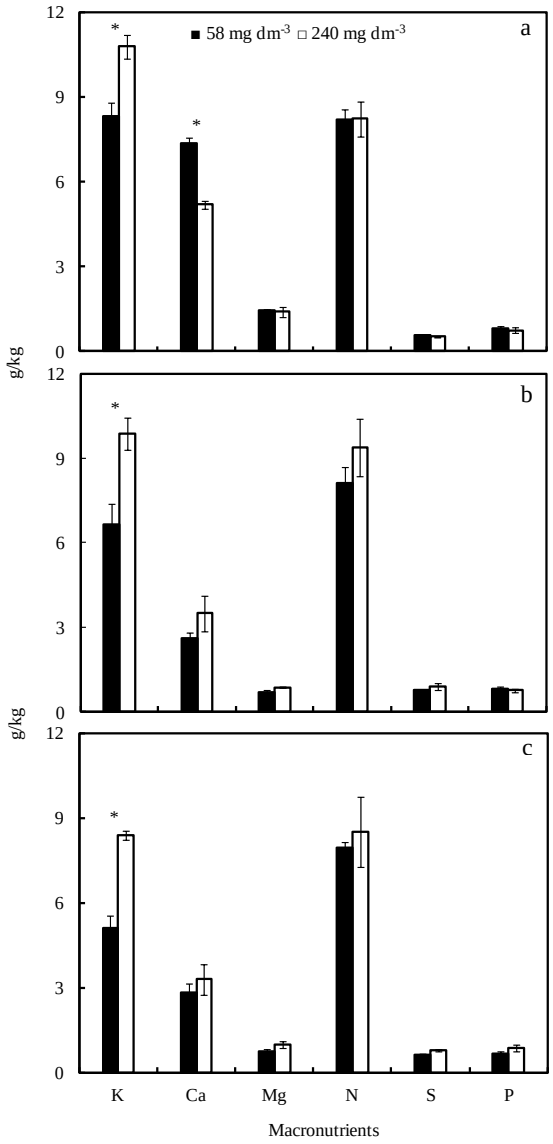

Figure 2. Concentrations of macronutrients in the diseased stem tissue (a) and at above (b) and below (c) the diseased tissue in the stem tissue of mango plants exposed to the potassium (K) rates of 58 and 240 mg dm^{-3} and inoculated with *Ceratocystis fimbriata*. Means between the two K rates at each 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. $n = 5$.

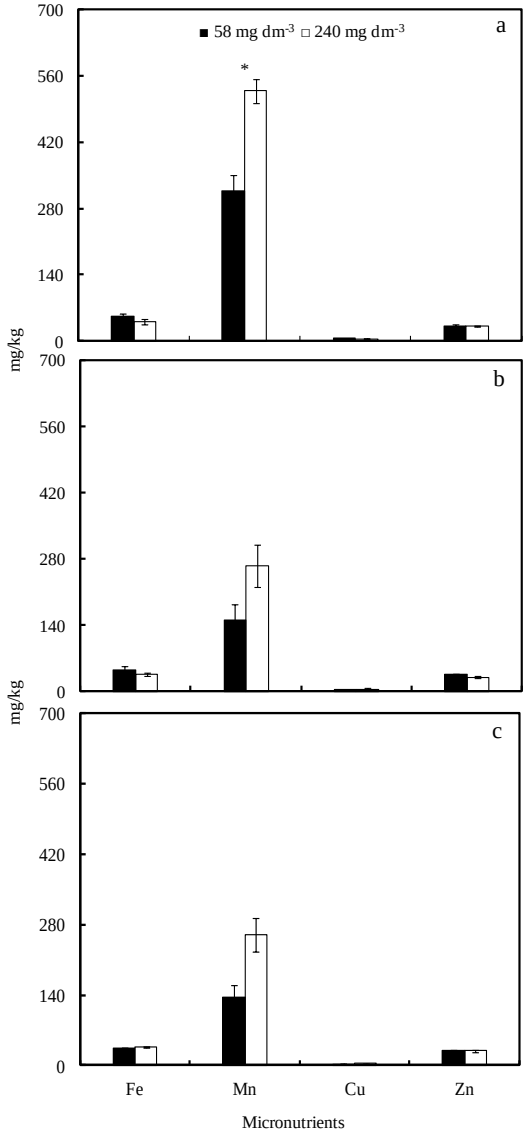

Figure 3. Concentrations of micronutrients in the diseased stem tissue (a) and at above (b) and below (c) the diseased tissue in the stem tissue of mango plants exposed to the potassium (K) rates of 58 and 240 mg dm^{-3} and inoculated with *Ceratocystis fimbriata*. Means between the two K rates at each 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. $n = 5$.

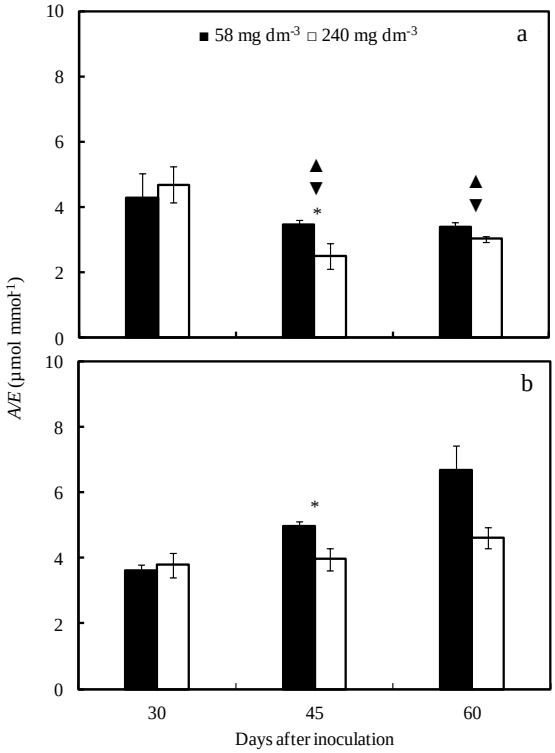

Figure 4. Instantaneous water use efficiency (*A*/*E*) determined on the stem tissue of mango plants exposed to the potassium (K) rates of 58 and 240 mg dm^{-3} and non-inoculated (a) or inoculated (b) with *Ceratocystis fimbriata*. Means between the two K rates at each evaluation time followed by an asterisk (*) are significantly different according to Student's *t* test ($P \leq 0.05$). The symbols ▼ and ▲, when shown, indicate difference between non-inoculated 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. $n = 5$.

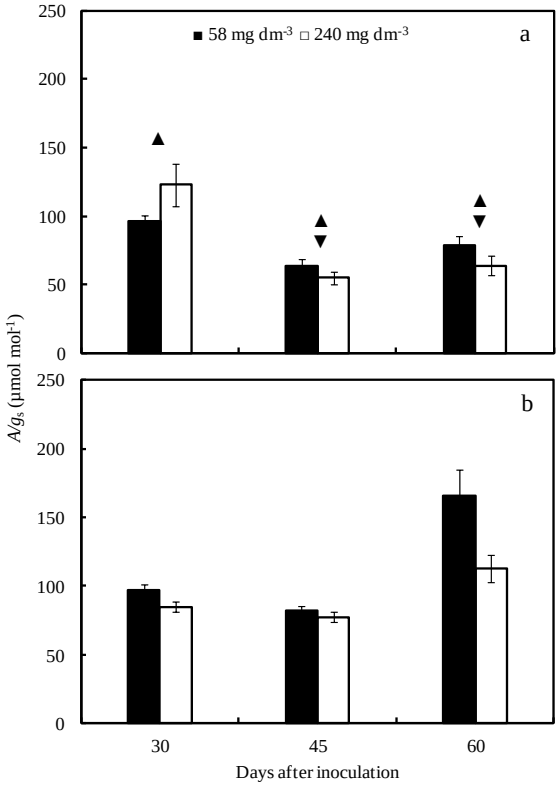

Figure 5. Intrinsic water use efficiency (A/g_s) determined on the stem tissue of mango plants exposed to the potassium (K) rates of 58 and 240 mg dm^{-3} and non-inoculated (a) or inoculated (b) with *Ceratocystis fimbriata*. Means between the two K rates at each evaluation time followed by an asterisk (*) are significantly different according to Student's *t* test ($P \leq 0.05$). The symbols ▼ and ▲, when shown, indicate difference between non-inoculated 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 1. Analysis of variance for the effects of K rates, plant inoculation (PI) and their interaction for the net CO_2 assimilation rate (A), stomatal conductance (g_s), internal-to-ambient CO_2 concentration ratio (C_i/C_a), transpiration rate (E), instantaneous water use efficiency (A/E), intrinsic water use efficiency (A/g_s), maximum quantum efficiency of PSII photochemistry in dark-adapted leaves (F_v/F_m), the efficiency of excitation energy capture by open PSII reaction centers (F_v'/F_m'), electron transport rate through PSII (ETR), non-photochemical quenching (NPQ), the fraction of open PSII reaction centers (q_L), total chlorophyll (Chl) [Chl(a+b)], carotenoids (Car), Chl a/b ratio, upward relative lesion length (URLL), downward relative lesion length (DRLL) and the radial fungal colonization (RFC) at 30, 45 and 60 days after inoculation (dai). The results are presented as non significant (ns) or significant at $P \leq 0.05$(*) or $P \leq 0.01$ (**).The symbol (-) and the letters (df) means, respectively, not determined data and degrees of freedom.

Parameters	Sources of variation[Z]								
	K rates			Plant inoculation (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 Chl	ns	ns	ns	ns	ns	ns	ns	ns	ns
Chla/b	ns	ns	**	ns	ns	ns	ns	ns	ns
Car	ns	ns	ns	ns	ns	ns	ns	ns	ns
URLL	**	**	**	-	-	-	-	-	-
DRLL	ns	ns	ns	-	-	-	-	-	-
RLL	**	**	**	-	-	-	-	-	-
RFC	*	**	**	-	-	-	-	-	-
df	1			1			1		

Table 2. The pairwise Pearson correlations of the net carbon assimilation rate (*A*), stomatal conductance (g_s), internal-to-ambient CO_2 concentration ratio (C_i/C_a), transpiration rate (*E*), the relative lesion length (RLL) and the potassium (K) concentration on the diseased stem tissue used to assess the upward relative lesion length, the downward relative lesion length and the relative length of the lesion for mango plants exposed to the potassium rates of 58 and 240 mg dm^{-3} and inoculated with *Ceratocystis fimbriata*.

Parameters	*A*	g_s	*E*	C_i/C_a	RLL	K
A	---	13.79*	11.10*	0.30^{ns}	-2.86*	3.03*
g_s	0.89	---	55.74*	3.49*	-3.29*	3.20*
E	0.84	0.99	---	4.39*	-3.70*	3.56*
C_i/C_a	0.04	0.45	0.54	---	-2.11*	1.69*
RLL	-0.38	-0.43	-0.47	-0.29	---	-5.36*
K	0.4	0.42	0.46	0.24	-0.61	---

The values above and below the diagonal are, respectively, the Pearson's correlation coefficients and their *t* values. The symbols * and ns indicate significance at 5% of probability ($P \leq 0.05$) according to the Student's *t* test.

Table 3. Net carbon assimilation rate (*A*), stomatal conductance to water vapor (g_s), internal-to-ambient CO_2 concentration ratio (C_i/C_a), transpiration rate (*E*), total chlorophyll (Chl) and carotenoids (Car) concentrations and the (Chl *a*/*b*) ratio determined on the leaves of mango plants exposed to the potassium (K) rates of 58 and 240 mg dm^{-3} and non-inoculated (NI) or inoculated (I) (45 and 60 days after inoculation (dai) with *Ceratocystis fimbriata*.

Parameters	45 dai				60 dai			
	NI		I		NI		I	
	58 mg dm^{-3}	240 mg dm^{-3}	58 mg dm^{-3}	240 mg dm^{-3}	58 mg dm^{-3}	240 mg dm^{-3}	58 mg dm^{-3}	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 Chl	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 two 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 and inoculated plants, respectively, for the K rates of 58 and 240 mg dm^{-3} at each evaluation time. Values are means ± standard error. $n = 5$.

Table 4. Maximum quantum efficiency of PSII photochemistry in dark-adapted leaves (F_v/F_m), the efficiency of excitation energy capture by open PSII reaction centers (F_v'/F_m'), non-photochemical quenching (NPQ), electron transport rate through PSII (ETR) and fraction of open PSII reaction centers (q_L) determined on the leaves of mango plants exposed to the potassium (K) rates of 58 and 240 mg dm^{-3} and non-inoculated (NI) or inoculated (I) (45 and 60 days after inoculation(dai) with *Ceratocystis fimbriata*.

Parameters	45 dai				60 dai			
	NI		I		NI		I	
	58 mg dm^{-3}	240 mg dm^{-3}	58 mg dm^{-3}	240 mg dm^{-3}	58 mg dm^{-3}	240 mg dm^{-3}	58 mg dm^{-3}	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

Means between the two 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 and inoculated plants, respectively, for the K rates of 58 and 240 mg dm^{-3} at each evaluation time. Values are means ± standard error. $n = 5$.