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Phytopathology/ Original Article

Phytophthora gummosis in citrus scion/rootstock combinations with seedlings from buds challenged by this pathogen

Abstract – The objective of this work was to evaluate the response of citrus seedlings formed from buds challenged with *Phytophthora citrophthora* to the infection caused by this pathogen. For this, 'Pera' orange and 'Tahiti' acid lime scions were grafted on 'Rangpur' lime rootstock. The experiment was carried out in a greenhouse, in a completely randomized design in 2×4 factorial arrangement. Seedlings were challenged by a *P. citrophthora* isolate. Lesion size, plant height, and stem diameter were evaluated, as well as the following physiological attributes: internal CO_2 concentration, transpiration, stomatal conductance, photosynthetic rate, and water use efficiency. In the 'Pera'/'Rangpur' combination, seedlings formed by buds challenged by the pathogen exhibited smaller lesion sizes and higher photosynthetic rates. However, in the 'Tahiti'/'Rangpur' combination, seedlings presented larger lesions, greater stem diameters, lower transpiration rates, and an increased water use efficiency. The challenge with the pathogen and the use of the 'Pera' orange/'Rangpur' lime combination (less sensitive to the disease) shows additive effects in the induction of resistance to gummosis.

Index terms: grafting, inoculation, oomycete, plant immunity.

Gomose causada por *Phytophthora* em combinações copa/porta-enxerto de citros com mudas formadas com borbulhas desafiadas por esse patógeno

Resumo – O objetivo deste trabalho foi avaliar a resposta de mudas de citros formadas a partir de gemas desafiadas por *P. citrophthora* à infecção causada por este patógeno. Para tanto, foram enxertadas laranjeira 'Pera' e limeira ácida 'Tahiti' sobre porta-enxerto de limoeiro 'Cravo'. O experimento foi realizado em casa de vegetação, em delineamento inteiramente casualizado, em arranjo fatorial 2x4. As mudas foram desafiadas com um isolado de *P. citrophthora*. Foram avaliados o tamanho da lesão, a altura da planta e o diâmetro do caule, além dos seguintes atributos fisiológicos: concentração interna de CO_2, transpiração, condutância estomática, taxa fotossintética e eficiência no uso da água. Na combinação 'Pera'/'Cravo', as mudas desafiadas pelo patógeno apresentaram menor tamanho de lesão e maior taxa de fotossíntese. No entanto, na combinação 'Taiti'/'Cravo', as mudas apresentaram maior tamanho de lesão, maior diâmetro do caule, menor taxa de transpiração e maior eficiência no uso da água. O desafio com o patógeno e o uso da combinação laranja 'Pera'/ limão 'Cravo' (menos sensível à doença) apresenta efeitos aditivos na indução de resistência à gomose.

Termos para indexação: enxertia, inoculação, oomiceto, imunidade vegetal.

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Introduction

Most citrus orchards are established by combining the favorable characteristics of both scion and rootstock. This combination can contribute to increase the yield and quality of fruit, as well as to extend the harvest period (Tietel et al., 2020), as well as to enhance the resistance to pests and pathogens, and undergo adverse conditions and other physiological disorders (Ribeiro et al., 2019).

In citrus crops, root rot and gummosis caused by *Phytophthora* are among the most significant diseases worldwide (Das et al., 2019). Several species of *Phytophthora* are associated with these diseases in citrus crops, from which the most widespread are: *P. citrophthora* (R. E. Sm. & E. H. Sm.) Leonian, *P. nicotianae* Breda de Haan (synonym of *P. parasitica* Dastur), and *P. palmivora* (E. J. Butler) E.J. Butler (Hao et al., 2018; Das et al., 2019).

Among the scion varieties, 'Tahiti' acid lime [*Citrus* × *latifolia* (Yu. Tanaka) Tanaka] has emerged as an alternative for sweet orange growers, due to its good adaptation to tropical climate conditions and high economic value (Rodrigues et al., 2016). In Brazil, lime and lemon crops heavily rely on the use of the 'Rangpur' lime rootstock [*Citrus* × *limon* (L.) Osbeck] (Cunha Sobrinho et al., 2013). The use of 'Rangpur' lime rootstock are more frequent in Brazil, exhibiting exceptional yield performance when associated with 'Pera' orange (*Citrus* × *aurantium* var. *sinensis* L.). The 'Rangpur' rootstock induces great vigor, early production, and good tolerance to water stress, as well as resistance to the *Citrus tristeza virus* (CTV) (Carvalho et al., 2016). However, the 'Rangpur' lime is considered susceptible to gummosis caused by *Phytophthora citrophthora* and *Phytophthora parasitica*, which may reduce plant longevity (Carvalho et al., 2016).

The initial perception of pathogens by plants can induce a state of enhanced activation of defense responses to subsequent pathogen challenges. This priming of defense mechanisms is linked to what is known as the “systemic acquired resistance” (SAR) (Mauch-Mani et al., 2017).

Defense priming requires immunological memory to retain the changes or information acquired during the initial detection of pathogens, subsequently recalling this information during later pathogen challenges (Ramirez-Prado et al., 2018). Studies have shown that plants challenged with primary stimuli can exhibit physiological, molecular, or epigenetic alterations within seconds or hours after the challenge. These changes can either be transient or persist throughout the plant life cycle, and they can also be inherited by subsequent generations (Mauch-Mani et al., 2017; Bertini et al., 2018; Meller et al., 2018). When challenged by stress, plants activate specific molecules, which rapidly become available to prevent or hinder pathogen attacks (Bertini et al., 2018).

The objective of this work was to evaluate the response of citrus seedlings formed from buds challenged with *P. citrophthora* to the infection caused by this pathogen.

Material and Methods

The experiment was carried out in greenhouse maintained at 25°C, at Embrapa Mandioca e Fruticultura, in the municipality of Cruz das Almas, in the state of Bahia, Brazil (12º40'39"S, 39º06'23"W, at 225 m altitude). 'Rangpur' lime seed were sown in seedling plugs. After six months, the rootstocks were transplanted into plastic bags (28 × 28 cm) containing washed sand, commercial substrate (Plantmax Citrus, Brazil) consisting of vermiculite, *Pinus* sp. bark, and organic matter, and soil at 1:1:2 proportion, respectively. Following transplantation into bags, these rootstocks were used for grafting buds of 'Pera' orange and 'Tahiti' acid lime scions, which were joined with the 'Indio' citrandarin rootstock, known to be less sensitive to *Phytophthora* (Lima et al., 2018); this grafting was performed to induce a possible acquired resistance from the first challenge event.

Seedlings were placed on suspended benches, receiving daily irrigation and weekly fertilization with 125mL soil SS 220 nutrient solution (Solo Sagrado, Brandt, SP, Brazil), containing nitrogen, magnesium, boron, manganese, molybdenum and zinc. The grafted seedlings were challenged with the isolate LRS 45/17 of *P. citrophthora*, using the mycelial disk inoculation method applied under the bark (Siviero et al., 2002).

A completely randomized design was used in a 2 × 4 factorial arrangement, with the two scion genotypes (GEN - 'Pera' orange and 'Tahiti' acid lime), and four challenge levels (control, inoculated, unchallenged, and challenged). Physiological evaluations were conducted with five replicates, while phenotypic evaluations had nine replicates.

The plants were subjected to inoculation by removing a bark disk from the rootstock, using an iron boring tool at about 10 cm above the soil level. Over the exposed cambium was placed a mycelium disk of colonies of *P. citrophthora* in carrot-agar medium (Siviero et al., 2002) for seven days of growth. The inoculation site was covered with a separated bark disk, protected with moistened cotton, and covered with adhesive tape. This tape remained in place for 15 days after inoculation (DAI). In the control plants, culture medium disks were placed without the pathogen, following the same protective procedure.

Two months after the initial inoculation in the 'Indio' citrandarin rootstock, buds from the scion varieties were removed and grafted onto 'Rangpur' lime rootstock. Three months after the new graft, a second challenge was conducted by inoculating the *P. citrophthora* isolate in the stem of the new combinations, following the same procedure used in the 'Indio' citrandarin rootstock. Each scion/rootstock combination was divided into four groups: control (no inoculation in challenges I and II); inoculated (inoculation only in challenge I); unchallenged (inoculation only in challenge II); and challenged (inoculation in challenges I and II), as shown in Figure 1.

Evaluations were performed at 30, 60, and 90 DAI from the second challenge. Plant height (cm) was measured with a measuring tape, from the root collar to the tip of the plant, and stem diameter was measured (mm) using a digital caliper rule at 10 cm from the base of the plants.

The size of the lesion caused by *P. citrophthora* on the stems was evaluated at 90 DAI from the second challenge. This evaluation involved removing the bark from the stem surface near the inoculation site. The areas with lesions (mm²) were plotted on transparent

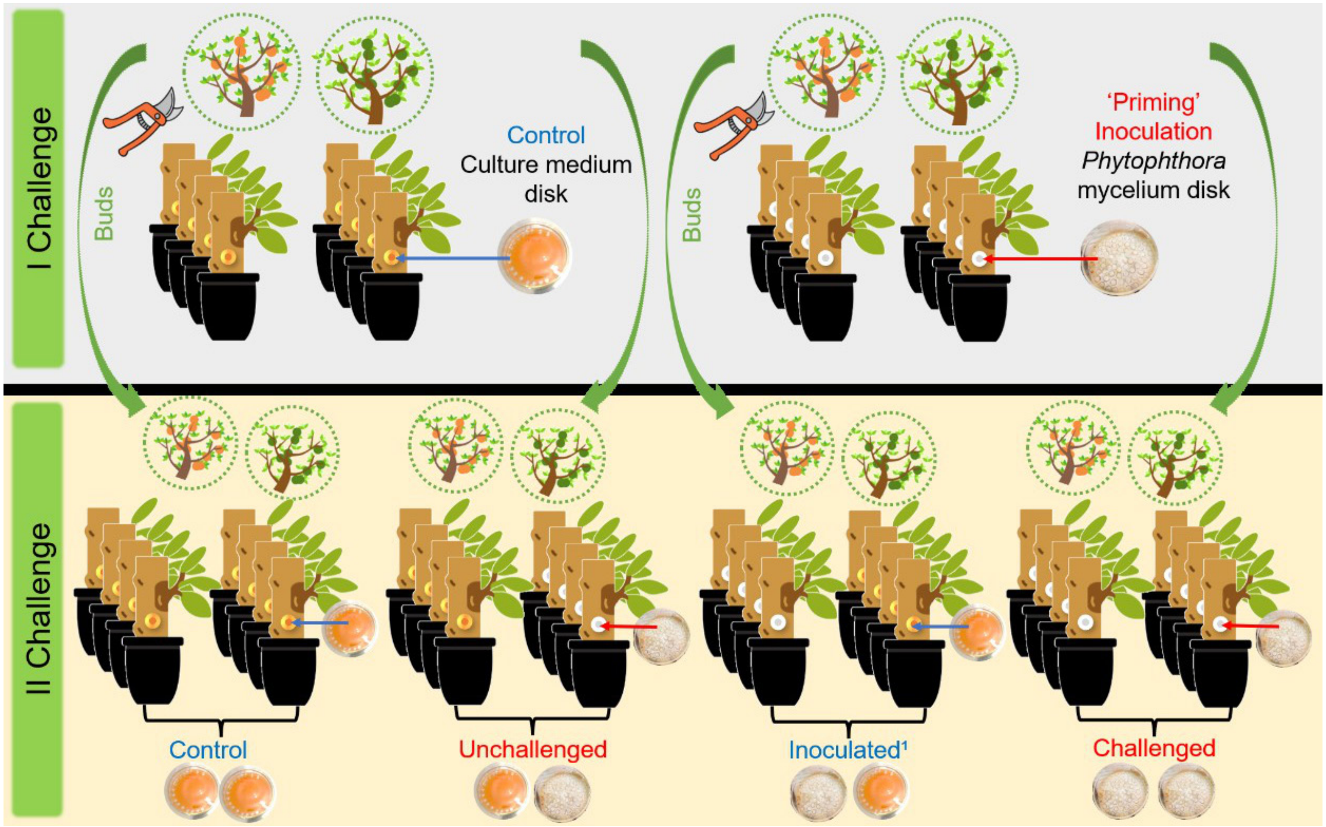

Figure 1. Schema of the challenges with *Phytophthora citrophthora* in combinations of 'Pera' orange and 'Tahiti' acid lime scions on 'Indio' citrandarin rootstock in challenge I and grafting with buds of the scion varieties from challenge I onto 'Rangpur' lime rootstock in challenge II.

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paper and measured (pixels) using the ASSESS software (Lamari, 2002).

During the second challenge, physiological characteristics were assessed, including the internal concentration of CO_2 in the leaf (Ci, µmol of CO_2 m^{-2} s^{-1}), stomatal conductance (gs, mmol m^{-2} s^{-1}), transpiration rate (E, µmol de H_2O m^{-2} s^{-1}), photosynthetic rate (A, µmol m^{-2} s^{-1}), and water use efficiency (WUE, mmol CO_2 mol H_2O^{-1}), calculated by the ratio between A/E. These measurements were taken at 1, 2, 3, 10, 30, 60, and 90 DAI. Evaluations were performed on fully expanded leaves located in the middle third of the plants, during the morning period between 09:00 and 11:00 h, using an infrared gas analyzer LCpro-SD IRGA (ADC Bioscientific Limited, Hoddesdon, England, UK).

The statistical analysis of variance was carried for the data obtained in the phenotypic and physiological evaluations, employing the ExpDes.pt package within the R software (R Core Team, 2020). When significant differences were observed, means were compared using the Tukey's test, at 5% probability.

Results and Discussion

Plant height remained unaffected by the pathogen challenges, as there was a significant difference only for the scion source of variation at 30, 60, and 90 DAI (Table 1). Concerning stem diameter of the rootstock, significant differences in the challenge factor were observed for 'Tahiti' acid lime at 30 DAI (Table 2). In this case, plants formed by both challenged and unchallenged buds by this pathogen exhibited a greater diameter than control and inoculated plants. At 60 DAI, plants formed from challenged and unchallenged buds of both scion/rootstock combinations showed a greater diameter than those of the control and inoculated plants.

Depending on the grafted scion variety, the 'Rangpur' lime rootstock induced different responses in the phenotypic characteristics of plant height, stem diameter, and in the size of the lesion caused by *P. citrophthora*. A smaller stem diameter was observed in the combination with the 'Pera' orange scion, while a greater plant height was observed in the 'Tahiti' acid lime scion on the same rootstock (Table 1). This result corroborates that from the evaluation of 'Tahiti' acid lime performance on rootstocks in the field, showing that 'Rangpur' lime induced a greater height, canopy volume, and yield in this scion variety (Morais et al., 2020).

The decomposition of the challenge within each scion level showed differences in the response of the plants to pathogen attacks, depending on the combination of the scion with the 'Rangpur' lime rootstock (Table 1). In the combination with the 'Pera' orange scion, plants formed by challenged buds exhibited a smaller lesion size than those formed by unchallenged buds. However, in the combination with 'Tahiti' acid lime scions, there was no statistical difference for the lesion size in the stem of plants formed by challenged and unchallenged buds (Figure 2).

Mandarin and their hybrids are less sensitive than oranges, which in turn are less sensitive than lemons and limes (Fawcett & Bitancourt, 2013). However, all commercial citrus scion cultivars are susceptible to *Phytophthora* spp. infection, although they become moderately susceptible to bark infection when grafted onto specific rootstocks (Graham & Feichtenberger, 2015).

In the combination of 'Pera' orange grafted on 'Rangpur' lime, which includes cultivars less or more

Table 1. Analysis of variance for plant height, stem diameter, and size of the lesion of the 'Rangpur' lime rootstock with 'Pera' orange and 'Tahiti' acid lime scion in plants formed with buds challenged and not challenged by *Phytophthora citrophthora*.

Source of variation[1]	Plant height (cm)			Stem diameter (mm)			Lesion (mm^2)
	30 DAI	60 DAI	90 DAI	30 DAI	60 DAI	90 DAI	90 DAI
Scion	0.0000**	0.0000**	0.0000**	0.0314*	0.1270^{ns}	0.0683^{ns}	0.2369^{ns}
Challenge	0.7240^{ns}	0.2993^{ns}	0.6725^{ns}	0.0107*	0.0045**	0.4641^{ns}	0.7854^{ns}
Scion x challenge	0.9509^{ns}	0.8357^{ns}	0.9756^{ns}	0.0324*	0.3986^{ns}	0.4665^{ns}	0.0092*
CV (%)	23.2	19.91	19.01	7.56	9.07	11.35	18.27

[1]Scion: 'Pera' orange and 'Tahiti' acid lime; challenge: control, inoculated, unchallenged, and challenged plants; x, interaction between the sources of variation. * and **Significant at 5 and 1% probability, respectively. ^{ns}Nonsignificant. CV, coefficient of variation.

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sensitive to the pathogen, plants formed from buds challenged with the pathogen displayed a greater stem diameter and a limited damage to a small area, resulting in smaller lesions. This suggests that the first challenge with *P. citrophthora* may have contributed to an improved response in the second challenge. An opposite reaction was observed in 'Tahiti' acid lime on 'Rangpur' lime, for which plants formed by buds challenged with the pathogen exhibited a greater stem diameter and no significant difference for lesion size, in comparison with plants formed by unchallenged buds. This suggests that, in this combination, it was not possible to limit the pathogen´s development in the second challenge (Table 1).

Table 2. Challenge factor within the 'Tahiti' acid lime scion level at 30 and 60 days after inoculation (DAI) for stem diameter (mm) of the 'Rangpur' lime rootstock, in plants formed with buds challenged and unchallenged by *Phytophthora citrophthora*(1).

Challenge(2)	30 DAI	60 DAI
Control	5,8800c	6,9854ab
Inoculated	6,0050bc	6,6183b
Unchallenged	6,4458ab	7,1571a
Challenged	6,6383a	7,2554a

(1)Means followed by equal lowercase letters, in the lines, do not differ by the Tukey's test, at 5% probability. (2)Challenged: inoculation in challenges I (bud initial inoculation) and II (inoculation in new scion-rootstock combination); unchallenged: inoculation only in challenge II; control (no inoculation in challenges I and II); and inoculated: inoculation only in challenge I.

The subsequent inoculation of the pathogen triggered varying defense responses among the scion/rootstock combinations, although some studies have shown that plants challenged or prepared through "priming" respond more rapidly and robustly to subsequent pathogen attack (Mauch-Mani et al., 2017; Bertini et al., 2018; Meller et al., 2018). The priming effect of defense through buds challenged with the pathogen activated the immune system in the rootstock combination of 'Pera' orange and 'Rangpur' lime, resulting in enhanced protection during the second challenge, reducing the infection propagation, showing smaller lesion sizes (Figure 2) and higher photosynthetic rates (Figure 3 E).

However, in the rootstock combination of 'Tahiti' acid lime and the 'Rangpur' lime, buds challenged with the pathogen did not induce resistance to *P. citrophthora*. In this combination, larger lesion sizes were observed (Figure 2), suggesting that the induced biotic stress memory from the first inoculation was not activated or

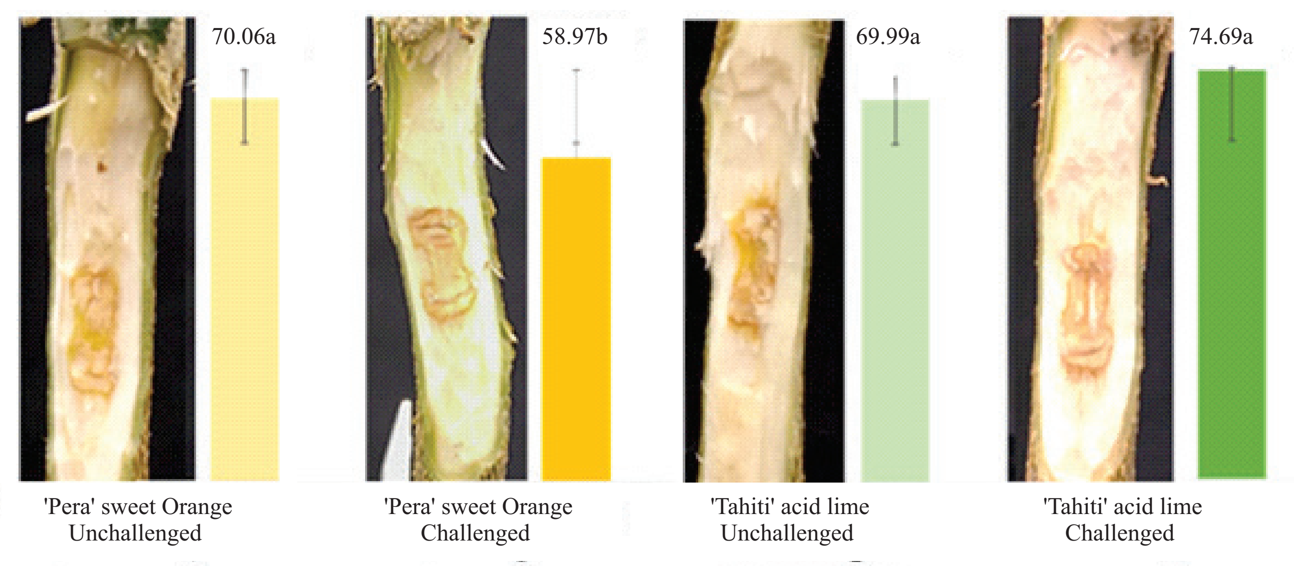

Figure 2. Area size (mm^2) of the lesion in the stem of the 'Rangpur' lime rootstock with 'Pera' orange and 'Tahiti' acid lime scions evaluated at 90 days after inoculation with *Phytophthora citrophthora*. Means followed by equal lowercase letter do not differ by the Tukey's test, at 5% probability. Challenged: inoculation in challenges I (bud initial inoculation) and II (inoculation in new scion-rootstock combination). Unchallenged: inoculation only in challenge II.

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transmitted to the plants during the second pathogen challenge.

Differences were observed for Ci and WUE in all sources of variation, in gs and A for scion cultivar and pathogen challenge, and in E only for scion (Table 3). These differences indicate that the scion/rootstock combination and the challenge with inoculation influenced the plant defense responses against *P. citrophthora*. These results open up new perspectives regarding the use of defense primings in the disease control of grafted plants. At 3 and 10 DAI, the 'Tahiti' acid lime plants formed by challenged buds and the inoculated plants exhibited higher Ci than the plants formed from unchallenged buds and the control plants. However, at 60 DAI, plants formed by unchallenged buds of this combination had lower Ci than plants in the other groups (Figure 3 A).

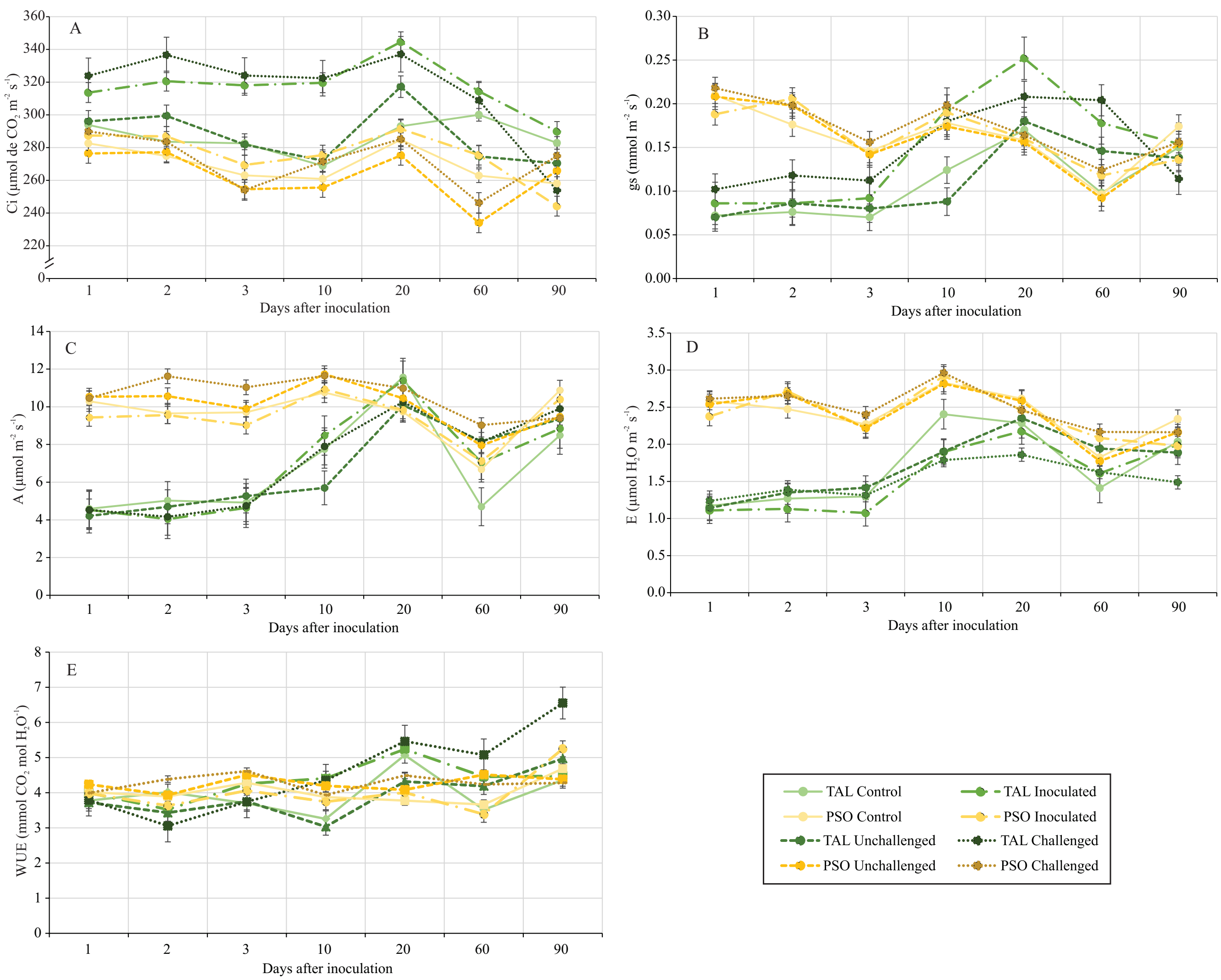

Figure 3. Physiological responses in 'Pera' orange (PSO) and 'Tahiti' acid lime (TAL) leaves grafted on the 'Rangpur' lime rootstock, in plants formed with buds challenged and not challenged by *Phytophthora citrophthora*, as follows: A, internal concentration of CO_2 in the leaf (Ci, µmol of CO_2 m^{-2} s^{-1}); B, stomatal conductance (gs, mmol m^{-2} s^{-1}); C, photosynthetic rate (A, µmol m^{-2} s^{-1}); D, transpiration rate (E, µmol of H_2O m^{-2} s^{-1}); E, water use efficiency (WUE, mmol CO_2 mol H_2O^{-1}) ratio between A/E. Challenged: inoculation in challenges I (buds initial inoculation) and II (inoculation in a new scion-rootstock combination). Unchallenged: inoculation only in challenge II. Control (no inoculation in challenges I and II). Inoculated: inoculation only in challenge I.

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At 10 DAI, the plants formed by unchallenged buds showed a reduction of gs than the other plants (Figure 3 B), and A at 60 DAI was higher in plants formed by challenged buds of 'Pera' orange (Figure 3 C). At 20 and 90 DAI, the plants formed by challenged buds of 'Tahiti' acid lime exhibited a lower E value (Figure 3 D). At 60 DAI, plants formed by challenged buds had higher WUE than the control plants (Figure 3 E).

Several studies have reported that pathogen infections can lead to modifications in the photosynthetic system, primarily resulting in a decrease in A and gs (Berger et al., 2007; He et al., 2007; Grimmer et al., 2012). In the present study, the gs values were influenced by the challenge with *P. citrophthora*, in plants formed by unchallenged buds showing lower gs values. Stomatal closure is a protection mechanism of plants that can be altered by biological and adaptive factors. The presence of molecules derived from pathogens can lead to a decline in gs (He et al., 2007; Grimmer et al., 2012). Pathogen infections have led to a reduction of A, which may have resulted from a reduction of gs or from a direct damage to the photosynthetic apparatus, causing the metabolic inhibition of photosynthesis (Berger et al., 2007).

Table 3. Analysis of variance for gas exchanges in 'Pera' orange and 'Tahiti' acid lime leaves grafted on the 'Rangpur' lime rootstock, in plants formed with buds challenged and unchallenged with *Phytophthora citrophthora*, as follows: internal concentration of CO_2 in the leaf (Ci); stomatal conductance (gs); transpiration rate (E); photosynthetic rate (A); and efficiency of water use (WUE) ratio between A/E.

Source of variation[1]	Pr>Fc						
	Days after inoculation						
	1	2	3	10	20	60	90
	Internal concentration of CO_2 in the leaf (Ci, µmol of CO_2 m^{-2} s^{-1})						
Scion	0.0003**	0.0000**	0.0000^{ns}	0.0000**	0.0185*	0.0000**	0.0849^{ns}
Challenge	0.0395*	0.0018**	0.0053^{ns}	0.0000**	0.0036**	0.0123*	0.9529^{ns}
Scion x challenge	0.5293^{ns}	0.0576^{ns}	0.0113*	0.0304*	0.0067**	0.6653^{ns}	0.0263*
CV (%)	5.98	6.03	6.14	6.41	8.56	9.35	8.98
	Stomatal conductance (gs, mmol m^{-2} s^{-1})						
Scion	0.0000**	0.0000**	0.0000**	0.0104*	0.0011**	0.0045**	0.0854^{ns}
Challenge	0.4428^{ns}	0.2640^{ns}	0.1498^{ns}	0.0104*	0.0719^{ns}	0.0274*	0.2245^{ns}
Scion x challenge	0.5969^{ns}	0.6186^{ns}	0.5573^{ns}	0.1386^{ns}	0.1127^{ns}	0.3732^{ns}	0.1422^{ns}
CV (%)	24.3	24.8	22.7	26.98	20.97	38.40	19.39
	Transpiration rate (E, µmol of H_2O m^{-2} s^{-1})						
Scion	0.0000**	0.0000**	0.0000**	0.0000**	0.0000**	0.0647^{ns}	0.0006**
Challenge	0.4583^{ns}	0.7089^{ns}	0.4092^{ns}	0.4233^{ns}	0.3231^{ns}	0.6284^{ns}	0.0290^{ns}
Scion x challenge	0.9180^{ns}	0.6248^{ns}	0.5538^{ns}	0.1752^{ns}	0.3760^{ns}	0.4142^{ns}	0.0429^{ns}
CV (%)	14.12	17.42	16.09	15.88	10.58	28.89	12.74
	Photosynthetic rate (A, µmol m^{-2} s^{-1})						
Scion	0.0000**	0.000^{0}**	0.0000**	0.0000**	0.2705^{ns}	0.3585^{ns}	0.1816^{ns}
Challenge	0.7813^{ns}	0.4568^{ns}	0.2395^{ns}	0.5190^{ns}	0.9463^{ns}	0.0443*	0.9913^{ns}
Scion x challenge	0.6163^{ns}	0.2542^{ns}	0.2727^{ns}	0.1337^{ns}	0.1991^{ns}	0.7197^{ns}	0.4004^{ns}
CV (%)	16.73	21.11	15.79	18.79	15.32	31.54	21.59
	Efficiency of water use (WUE, mmol CO_2 mol H_2O^{-1})						
Scion	0.2525^{ns}	0.0224*	0.0116**	0.2915^{ns}	0.3560^{ns}	0.3508^{ns}	0.1815**
Challenge	0.9759^{ns}	0.7170^{ns}	0.9406*	0.0399*	0.0861^{ns}	0.0122*	0.1324^{ns}
Scion x challenge	0.8337^{ns}	0.0965*	0.1782*	0.0022**	0.2878^{ns}	0.0930^{ns}	0.0035^{ns}
CV (%)	16.72	17.04	13.86	14.63	14.74	20.86	19.08

[1]Scion: 'Pera' orange and 'Tahiti' acid lime; challenge: control, inoculated, non-challenged, and challenged plants; x, interaction between the sources of variation. * and ** Significant at 5% and 1% probability, respectively. ^{ns}Nonsignificant.

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There was likely no induction of SAR in plants formed from buds challenged with the pathogen, from the combination with 'Tahiti' acid lime scion, since they did not exhibit lower gs than plants formed by unchallenged buds by the pathogen. In plants induced by SAR, there is a reduction in A in noninoculated distal leaves, both on a transcriptional and physiological level. This reduction of water loss in leaves suggests a decline in leaf E and gs, when SAR is established (Bernsdorff et al., 2016).

Pathogens can cause various types of damage to plants, with specific damage to plant physiology being particularly noteworthy, as it results in changes in the photosynthetic processes (Berger et al., 2007). Plants with a 'Tahiti' acid lime scion formed from unchallenged buds significantly increased the absorption of Ci, in comparison with plants formed by buds challenged by the pathogen, which may have adversely affected the photosynthetic rates. This fact suggests that *P. citrophthora* infections impacted the stem tissues of the citrus rootstock, leading to an inability to take up sufficient water and nutrients to support their development (Hao et al., 2018).

Conclusions

1. The challenge with *Phytophthora citrophthora* results in an induction effect of resistance in the combination of 'Pera' orange and 'Rangpur' lime.
2. Challenged 'Pera'/'Rangpur' plants are more efficient than 'Tahiti'/'Rangpur' in the control of *Phytophthora* gummosis, as the pathogen challenge and the use of cultivars less sensitive to *P. citrophthora* showed additive effects.
3. The combination 'Tahiti' acid lime and 'Rangpur' lime does not show any effect of inductive resistance.

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