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Andean Solanaceae species with resistance to biotic factors, such as tree tomato (*Solanum betaceum* Cav.) rootstocks

Especies de Solanáceas Andinas con resistencia a factores bióticos, como portainjerto de tomate de árbol (*Solanum betaceum* Cav.)

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ABSTRACT

The infestation of the root system by nematodes (*Meloidogyne incognita*) and *Fusarium solani* to the rootneck hinders the production of tree tomato (*Solanum betaceum* Cav.), an Andean native fruit consumed in Ecuador and other countries. This paper evaluates the potential of different Ecuadorian Andean Solanaceae species (*Solanum auriculatum*, *Solanum asperolanatum*, *Solanum arboreum* and *Nicotiana glauca*), such as tree tomato rootstocks towards Fusarium and nematode resistance through controlled inoculation trials. The experimental design used was complete randomized in factorial arrangement with three factors. The variables were: fungus incubation time, incidence and lesion size, increase in nematode population, plant height increase and plant fresh weight. The most promising results for an extended open field evaluation were *N. glauca* (no incidences of Fusarium and 0.36 times increase in nematode population), followed by *S. auriculatum*. Fruit of these plants were assessed for chaconine and solanine content. The results indicated that the two rootstocks did not induce toxic substances in the fruits, they are suitable for commercial production zones, enhance crop yield, increase productive plant life and use fewer chemicals to control soil pathogens.

Keywords: Meloidogyne; Fusarium; rootstock; tomato; grafted plant.

RESUMEN

La infestación del sistema radicular por nematodos (*Meloidogyne incognita*) y *Fusarium solani* al cuello radicular dificulta la producción de tomate de árbol (*Solanum betaceum* Cav.), una fruta nativa andina consumida en Ecuador y en otros países del mundo. Este trabajo evalúa el potencial de diferentes especies de Solanáceas Andinas ecuatorianas (*Solanum auriculatum, Solanum asperolanatum, Solanum arboreum* y *Nicotiana glauca*), como portainjertos de tomate de árbol, frente a Fusarium y resistencia a nematodos mediante ensayos controlados de inoculación. El diseño experimental utilizado fue completamente al azar en arreglo factorial con tres factores. Las variables fueron: tiempo de incubación del hongo, incidencia y tamaño de la lesión, aumento de la población de nematodos, aumento de la altura de la planta y peso fresco de la planta. Los resultados más prometedores para una evaluación de campo abierto extendida fueron *N. glauca* (sin incidencias de Fusarium y un aumento bajo de 0,36 veces en la población de nematodos), seguido de *S. auriculatum*. Se evaluó el contenido de chaconina y solanina del fruto de estas plantas. Los resultados indicaron que los dos portainjertos no inducen sustancias tóxicas en los frutos, son aptos para zonas de producción comercial, mejoran el rendimiento del cultivo, aumentan la vida productiva de las plantas y utilizan menos químicos para controlar patógenos del suelo.

Palabras clave: *Meloidogyne*; *Fusarium*; rootstock; tomato; grafted plant.

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INTRODUCTION

Tree tomato, also called tamarillo (*Solanum betaceum* Cav.), is a native Andean plant (Correia and Canhoto, 2012) and its peculiar flavor as well as its nutritional facts (Gannasin *et al*., 2012) have made it popular in Ecuador and worldwide, therefore increasing its production. Recent studies carried by do Nascimento *et al*. (2013; 2015) found evidence regarding its biological activity. Tree tomato is a promising crop all over the world and it has been researched to increase its postharvest time (Pinzón-Gómez *et al*., 2014).

Nonetheless, as a member of the Solanaceae family, its root system is affected by fungi of the Fusarium genus (Souza *et al*., 2010). In addition to this, one of the members of this genus (*Fusarium solani*) not only affects tree tomato rootneck, causing plants to rot, but also affects several other plants that are important to production (Benítez *et al*., 2020). Solanaceae species' root systems are not only attacked by fungi, but are also affected by nematodes, in which *Meloidogyne incognita* is the most harmful biotic affectation (Benítez *et al*., 2020). The affected plants experience a decrease of both nutrients and water absorption, causing wilting, chlorosis, dwarfism and abortion of both flowers and fruits. Nematodes have a major impact on worldwide tree tomato crops, similar to the impact presented on melon plants (Ito *et al*., 2014). Solanaceae plants are known to produce secondary metabolites, such as solanine and chaconine, both of which are toxic to humans and animals (Sucha and Tomsik, 2016). Therefore, fruits from Solanaceae plants ought to comply with the generally maximum standard of 200 mg kg^{-1} (Korpman *et al*., 2004).

Tree tomatoes possess a scarce genetic variability; as a consequence, rootstocks can be used to continue the production of this and other fruits to minimize crops being affected by the damage caused by nematodes and fungi, while producing fruits with the lowest level of glycoakaloids possible. Most Ecuadorian tree tomato production is in hands of small producers and has a direct impact on the producers' family income. Well-chosen rootstocks could have an important impact on crop susceptibility towards nematodes (López-Pérez *et al*., 2006) and stress resistance (Martínez-Ballesta *et al*., 2010). Hence, it is necessary to improve fruit production and the economy of the producers and use fewer chemicals through friendly technologies (Viera *et al*., 2017). Rootstocks do not only provide support to the scion of the grafted plant and export nutrients to create biomass, they also compose a strategy to produce fruits in production areas infested with nematodes and *Fusarium* species. The objective of this study was to identify suitable native Solanaceae rootstocks for tree tomato, conferring pathogen resistance/tolerance towards *M. incognita* and *F. solani* present in production fields, which is a key element in higher crop performance and in producing fruits with low levels of solanine and chaconine.

MATERIAL AND MHETODS

The identification of *Meloidogyne* and *Fusarium*, was performed by the Plant Protection Department at the INIAP Santa Catalina Research Station (Quito, Ecuador), while the experiment was conducted under greenhouse conditions at the INIAP Tumbaco Research Station (latitude 00°13'00''S; longitude 78°24'00''W, an average temperature of 18 °C and average relative humidity of 47%).

The experiment was carried out using a Completely Randomized Design in factorial arrangement (5x2x2) with 6 replicates. Three factors were studied. The first factor was rootstock: *S. arboreum* (P1), *S. asperolanatum* (P2), *S. auriculatum* (P3), *N. glauca* (P4), and the control *S. betaceum* tree tomato (P5, without grafting). The second factor was nematode (*M. incognita*) presence due to infestation: 0 larvae and eggs in 1000 g of soil (N0), and 5000 larvae and eggs per 1000 g of soil (N1). The third study factor was *F. solani* fungus inoculation throughout injury infection: 0 conidia ml^{-1} (F0), and $5x10^6$ conidia ml^{-1} (F1). The plants were infected by injuries at stem base. The number of treatments was the combination of the levels of three factors i.e. 20 treatments. The identity of the fungus was confirmed by the Plant Protection Department at the Ecuadorian National Research Institute (INIAP, for its Spanish acronym) following the protocol published by Nelson *et al*. (1983).

Seeds from the selected native Solanaceae species were collected in non-cultivated conditions where nematode and Fusarium had polluted the soils. These seeds were grown in the greenhouse to obtain rootstocks. The soil used as a substrate to fill up the 3.5 L bags to grow the plants was composed of black paramo and clay-loam soil in a 5:1 ratio with an exposure of 45 min to steam as a disinfection agent. An additional 1 kg m^{-3} 15-15-15 of fertilizer was added for plant nutrition and a drip irrigation system was provided for the plants. Rootstocks were transplanted into the bags and were kept in the greenhouse for shoot tip grafting and a follow up.

The description of the environmental conditions where each native Solanaceae species was collected, is presented below.

Tabaquillo, or tree tobacco (*N. glauca*), was collected in the western part of Tungurahua province at 2000 masl, where the average temperature is 15 °C and the average annual rainfall is 500 mm. The plants were growing in arid, sandy soils with an alkaline pH and poor nutrient availability. Palo blanco (*S. auriculatum*) was collected in the southern part of the country (Azuay province) at 2400 masl, where the average temperature is 17 °C, the average annual rainfall is 800 mm, soil is clay-loam and the pH is 7.5, thus corresponding to a subtropical zone. Turpag (*S. asperolanatum*) was collected on the south-eastern Ecuadorian highlands in Azuay province above 2800 masl, with an average temperature of 10 °C, average annual rainfall of 1000 mm and a pH of 6.2, corresponding to a high montane forest. Apumpo (*S. arboreum*) was collected at north eastern Amazon region, growing at 800 masl, with an average temperature of 21 °C, average annual precipitation of 2000 mm, clay-acidic soils and poor nutrient availability, corresponding to a low montane rainforest zone.

Nematodes were isolated according to the methodology described by Siddiqui (2004) from the root systems of tree tomato plants in open field conditions. The nematode *M. incognita* (root knot) was multiplied on tree tomato seedlings planted in pots under greenhouse conditions. The obtained nematodes were used as an inoculum according to the treatments.

The analyzed variables were: 1) incubation period of the fungus (days by first appearance of stem neck symptoms; 2) incidence of the fungus (%); 3) size of injury (mm^2); 4) increase in nematode population (roots and soil); 5) plant height increase (cm); and 6) plant fresh weight (g). While variables 1 and 2 were assessed daily until symptoms were visible, variables 3-6 were registered 90 days after the inoculation. The last two variables were accessed in order to apply the criteria proposed by Cook (2004). Depending on the increase in nematode population (rates higher or lower than 1 were assigned) and depending on whether the plant growth was affected by the pathogen, the plants were classified as resistant or susceptible.

The analysis of variance (ANOVA) was carried out using InfoStat-Statistical software. For the functional statistical analysis, means were compared by Tukey's multiple range test ($p \leq 0.05$). The plants were kept until the first fruit production was harvested in order to establish if the grafting was considered compatible or not. With the promising grafted plants, the fruits' levels of glycoalkaloids (solanine and chaconine) were assessed (Romanucci *et al*., 2018).

RESULTS AND DISCUSSION

The analysis of variance (Table 1) showed statistical differences for the main effect on rootstock for all variables assessed. The nematode analysis presented differences in incubation time (days) and increase in nematode population, while the *Fusarium* fungi analysis showed strong statistical differences in incubation time (days), incidence (%) and lesion size (mm2). The interaction between rootstock and nematode (PxN) presented statistical differences both in terms of nematode increase (Fc/Ic) and plant height increase (cm). Moreover, first and second levels of interaction (PxNxF) showed statistical differences for incubation time (days), while the interaction between rootstock and *Fusarium* (PxF) presented an effect in percentage of incidence and lesion size (Table 1). The interaction between nematode and *Fusarium* (NxF) presented a statistical difference for the variable of incubation time (days).

The rootstocks responded to the inoculation of the fungi and nematodes differently. Depending on the analyzed variable, the rootstocks were ranked in groups according to Tukey (95% Confidence Interval). Results corresponding to variables incubation days, incidence of the pathogen and lesion size at the level of the stem neck are shown in Table 2.

Table 1
Analysis of variance of the effects of the inoculation of *F. solani* (F) on five Solanaceae (P) assessed as potential rootstocks for tree tomato

Source of Variation	d.f.	Mean Square					
		Incubation (d)	Incidence (%)	Lesion size (mm^2)	Nematode increase (FC/IC)	Plant height increase (cm)	Plant fresh weight (g)
Total	119						
Rootstock (P)	4	148.20**	13261.70**	6882.80**	8.32**	41179.90**	85589.80**
Nematode (N)	1	0.08*	53.30^{ns}	34.90^{ns}	104.80**	61.30^{ns}	367.15^{ns}
P x N	4	0.04^{ns}	45.00^{ns}	6.96^{ns}	8.32**	69.23*	1650.80*
Fungi (F)	1	854.10**	79053.30**	40978.70**	0.00^{ns}	0.40^{ns}	8.48^{ns}
P x F	4	148.20**	13261.70**	6882.80**	0.00^{ns}	2.62^{ns}	623.99^{ns}
N x F	1	0.08*	53.30^{ns}	34.90^{ns}	0.00^{ns}	4.87^{ns}	317.20^{ns}
P x N x F	4	0.05*	45.00^{ns}	6.90^{ns}	0.00^{ns}	2.98^{ns}	131.90^{ns}
EE	100	0.02	69.30	43.10	0.40	22.25	656.49
CV (%)		5.30	32.40	35.50	21.50	6.99	8.22

ns: not significant, ** and *: significant by F test ($p < 0.05$). P = rootstocks; N = nematode; F = Fusarium; FC/IC = Final count/Initial count; EE = experimental error, CV = coefficient of variance.

Even though the F1 plants were inoculated with *F. solani*, only 3 species presented signs of root-system infection, as reported by Souza *et al*. (2010), while 2 species showed a higher resistance: *S. asperolanatum* with *Fusarium* and *N. glauca* with *Fusarium*. Among the susceptible species, *S. auriculatum* presented infection signs sooner than the tree tomato. Regarding incidence, S. auriculatum presented the highest score, followed by *S. betaceum* and finally *S. arboreum*. These results confirm that these Solanaceae are susceptible to *F. solani*. Moreover, the affected species showed the same degree of severity (stem neck lesion), as *S. betaceum*. According to the results, *S. asperolanatum* and *N. glauca* were resistant to the pathogen *F. solani* (Table 2).

An increase in nematode population relative to the initial nematode count was seen in all the treatments in which *Meloidogyne incognita* was inoculated. The species with the lowest increase in the soil and roots was *N. glauca*, followed by *S. arboreum*, *S. auriculatum*, tree tomato and finally *S. asperolanatum*. On the other hand, *N. glauca* presented a 0.36-fold increase in nematode infestation, suggesting that the tissue has a high resistance to nematode colonization and the potential for further performance as rootstock in field research (Table 3).

In contrast to these findings and the fact that for a set of plants from all the species was inoculated with *Meloidogyne*, not all the plants reacted the same way. In *S. asperolanatum* tissue, the nematode population count increased substantially, making it the most susceptible Solanaceae studied, yet this increase was less evident in *S. auriculatum* and *S. arboretum*. Tree tomato presented a population increase of 12.2-fold, which explains why it had the lowest increment in plant height due to damage to the root system, affecting the fruit crop (Feicán *et al*., 2016) (Table 3).

To interpret Cook's classification regarding nematode resistance, it can be stated that resistant plants (R) are considered those that presented an increase in nematode ratio < 1, whereas susceptible plants (S) presented a ratio > 1. Under this consideration, four species (*S. arboreum, S. auriculatum, S. asperolanatum* and *S. betaceum*) were categorized as Susceptible (S) to *M. incognita* infection. Meanwhile, the Solanaceae *N. glauca* stood out and was instead ranked as Resistant (R). This can be partially explained by its natural ability to grow despite adverse environmental conditions-poor soil fertility and drought. Tree tomato is cultivated under a broad range of environmental conditions (climatic and soil). Therefore, the susceptible species still have rootstock potential, since a lower incidence in relation to the control was shown (*S. betaceum*). Choosing the right rootstock will depend on the characteristics of the cultivation site (Table 3). In general, the treatments did not differentiate from the controls (no nematode or *Fusarium* inoculation = N0F0) at the end of the experiments regarding plant height increase as a response of the plants towards the pathogen infection.

Table 2

The effect inoculating five Solanaceae species with *F. solani* on incubation time, incidence and lesion size

Fusarium	Rootstock				
	S. arboreum	*S. asperolanatum*	*S. auriculatum*	*N. glauca*	*S. betaceum* (control)
			Incubation (days)		
Without	0.00 ± 0.00 A	0.00 ± 0.00 A	0.00 ± 0.00 A	0.00 ± 0.00 A	0.00 ± 0.00 A
With	10.50 ± 0.38 D	0.00 ± 0.00 A	7.97 ± 0.08 B	0.00 ± 0.00 A	8.21 ± 0.27 C
			Incidence (%)		
Without	0.00 ± 0.00 A	0.00 ± 0.00 A	0.00 ± 0.00 A	0.00 ± 0.00 A	0.00 ± 0.00 A
With	81.67 ±10.30 B	0.00 ± 0.00 A	91.67 ± 10.30 C	0.00 ± 0.00 A	85.00 ± 12.43 BC
			Lesion size (mm^2)		
Without	0.00 ± 0.00 A	0.00 ± 0.00 A	0.00 ± 0.00 A	0.00 ± 0.00 A	0.00 ± 0.00 A
With	56.75 ± 8.45 B	0.00 ± 0.00 A	63.77 ± 10.52 B	0.00 ± 0.00 A	64.28 ± 14.88 B

Means in each analyzed variable followed by the same letter belong to the same Tukey statistical group (p ≤ 0.05). n= 6.

Table 3

The effect inoculating five Solanaceae species with *F. solani* on nematode increase and susceptibility, according to Cook's classification (90 days after inoculation)

Nematode	Rootstock				
	S. arboreum	*S. asperolanatum*	*S. auriculatum*	*N. glauca*	*S. betaceum* (control)
			Plant height (cm)		
Without	60.84 ± 3.41 B	48.11 ± 5.01 C	52.73 ± 2.24 C	139.39 ± 7.22 A	40.03 ± 3.21 D
With	61.47 ± 3.02 B	41.82 ± 6.15 D	53.82 ± 4.16 C	140.55 ± 4.88 A	36.30 ± 3.56 D
			Fresh weight (g)		
Without	323.73 ± 21.63 B	224.00 ± 36.40 C	307.93 ± 29.92 B	330.11± 23.82 B	380.61 ± 27.10 A
With	329.33 ± 14.40 B	200.90 ± 8.14 C	327.69 ± 41.12 B	322.58 ± 8.14 B	368.38 ± 15.87 A
			Nematode increased (FC/IC)		
Without	0.00 ± 0.00 A	0.00 ± 0.00 A	0.00 ± 0.00 A	0.00 ± 0.00 A	0.00 ± 0.00 A
With	2.29 ± 0.37 C	29.73 ± 13.62 F	6.38 ± 2.04 D	0.36 ± 0.15 B	12.17 ± 2.16 E
Classification	S	S	S	R	S

S= Susceptible; R=Resistant. FC=final nematode count; IC= initial nematode count. Means in each analyzed variable followed by the same letter belong to the same Tukey statistical group (p ≤ 0.05). n= 6.

The Solanaceae species that grew the most was *N. glauca* (140.55 cm) despite being inoculated with M. incognita. Meanwhile, *S. betaceum* experienced the lowest height increase (36.30 cm), therefore confirming its susceptibility towards nematode infection (Table 3). This data is supported by the findings of Schütz (2014) who stated that one of this crop's problems is nematode infection.

Moreover, fresh weights were analyzed, showing that all the native Solanaceae species, including tree tomato, presented no statistical differences between pathogen-free and inoculated plants. This finding is important because it highlights the Solanaceae species' importance as potential rootstocks for providing nutrient availability and supporting a tree tomato grafted scion despite the infection of both pathogens. *S. betaceum* remained the species that yielded the highest fresh weight in a non-infected plant. This fact could be attributed to the crop's growth at early stages due to a high root emission witnessed during the first growth stage, allowing it to cope with the pressure of nematode infection. The control treatment (without nematodes) used in this research was planted in steam-treated soil as a disinfection agent; therefore, it is assumed that there were no viable nematodes present in the soil. Nevertheless, it is important to remark that under tree tomato production field conditions, it becomes impossible to obtain more than 2 years of fruit production in a non-grafted plant.

The decrease in fresh weight when a tree tomato plant was inoculated shows that it had begun to be affected by the pathogen. This fact reveals what is happening in affected crops: lower biomass with an eventual lower production in terms of yield and a diminished lifespan. It is worth stressing that the data shown depict the results after 90 days of the initial contact between plants and pathogen.

Another finding is also important: *S. asperolanatum* was the species with the lowest fresh weight at the end of the experiments, exhibiting the impact of *Meloidogyne* infestation (Table 3).

The pathogen inoculation effect on *F. solani* incubation time is displayed in Table 4, where interaction with nematodes is evident: when nematodes were present (N1), *F. solani* affected the rootstocks and its absence (N0) yielded no infection at all.

Average incubation time per treatment (PxNxF) is shown in Table 5, where there is no interaction between rootstock and pathogen infection for N. glauca and *S. asperolanatum*, as there were no infection signs at the time of evaluation (90 days after inoculation). *S. auriculatum* presented the shortest time in showing infection signs out of all the Solanaceae species, therefore stressing its susceptibility towards pathogen infection.

These results, together with the fact that plant's grafting has proven to be an effective technique for controlling not only fungi but also nematodes (Vargas *et al*., 2018; McAvoy *et al*., 2012; Rivard *et al*., 2010), constitute a very promising technique that can be adopted for the Ecuadorian tree tomato industry.

Table 4
Effect of the inoculation of *M. incognita* and *F. solani* on incubation time

Levels	Incubation time (days)
Without *Fusarium*, without *Meloidogyne*	0.00± 0.00 C
With *Fusarium*, without *Meloidogyne*	0.00± 0.00 C
Without *Fusarium*, with *Meloidogyne*	5.39± 4.58 A
With *Fusarium*, with *Meloidogyne*	5.28± 4.47 B

Means in each analyzed variable followed by the same letter belong to the same Tukey statistical group ($p \leq 0.05$). n= 6; sd= standard deviation.

Table 5
Effect of the incubation time on the rootstock (P), nematode (N) and Fusarium (F) interaction

Treatments	Incubation time (days)
P1N0F1	10.70 ± 0.42 A
P1N1F1	10.30 ± 0.26 B
P5N0F1	8.28 ± 0.31 C
P5N1F1	8.15 ± 0.23 CD
P3N0F1	7.97 ± 0.08 D
P3N1F1	7.97 ± 0.08 D
P1N1F0	0.00 ± 0.00 E
P1N0F0	0.00 ± 0.00 E
P2N0F0	0.00 ± 0.00 E
P4N0F0	0.00 ± 0.00 E
P4N1F0	0.00 ± 0.00 E
P3N0F0	0.00 ± 0.00 E
P2N1F0	0.00 ± 0.00 E
P3N1F0	0.00 ± 0.00 E
P5N0F0	0.00 ± 0.00 E
P5N1F0	0.00 ± 0.00 E
P2N0F1	0.00 ± 0.00 E
P2N1F1	0.00 ± 0.00 E
P4N1F1	0.00 ± 0.00 E
P4N0F1	0.00 ± 0.00 E

P1 = *S. arboreum*, P2 = *S. asperolanatum*, P3 = S. auriculatum, P4 = N. glauca, P5 = S. betaceum. N1 = with Meloidogyne, N0 = without Meloidogyne. F1 = with Fusarium, F0 = without Fusarium. Means followed by the same letter are not significant different measured by Tukey ($p \leq 0.05$). n = 6; sd = standard deviation.

After the first fruit harvest, the grafting of plants was declared as successful or not depending on the plants' ability (compatibility and affinity) to bear fruits. *N. glauca* and *S. auriculatum* resulted in a successful rootstock as both allowed the scion to grow and develop. Therefore, Solanaceae's toxin levels (chaconine and solanine) were assessed to determine contents in the fruits. The results of the analysis are presented in Table 6.

Both promising rootstocks (*N. glauca* and *S. auriculatum*) have relatively low levels of chaconine and solanine, which, according to the internationally accepted levels of toxicity (Navarrete *et al*., 2018) may be considered as suitable rootstocks for *S. betaceum.*

Table 6
Solanine and chaconine content in the fruits of tree tomato grafted plants (mg/100g)

Species	Chaconine	Solanine
N. glauca	1.10 ± 0,545 ^{ns}	3.46 ± 0.011 a
S. auriculatum	1.10 ± 0.046 ^{ns}	2.89 ± 0.064 b
S. betaceum	0.69 ± 0.022 ^{ns}	2.73 ±0.022 b

Means followed by the same letter are not significant different measured by Tukey ($p \leq 0.05$). n = 3; sd = standard deviation.

CONCLUSIONS

This study suggests that *N. glauca* is the best potential rootstock for tree tomato, based on the climate present in the Ecuadorian Andean valleys. This species did not present any signs of *F. solani* infection and was the rootstock that experience the lowest increase in *M. incognita*. It therefore presents new possibilities for increasing nontoxic fruit harvesting and is suitable for mass production.

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