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Gnotobiotic system for selecting microorganisms with biocontrol potential against *Fusarium oxysporum* f. sp. *physali*

Sistema gnotobiótico para seleccionar microorganismos con potencial de biocontrol contra *Fusarium oxysporum* f. sp. *physali*

Gnotobiotic model.

Photo: D. García

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ABSTRACT

The cape gooseberry (*Physalis peruviana*) is a Solanaceae species with enormous economic importance in Colombia; it is the second most exported fruit, after bananas. Vascular wilt caused by *Fusarium oxysporum* f. sp. *physali* (*Fox*) is the most limiting factor of this crop, with losses of up to 80% of production. Biological control is a promising alternative for controlling this pathogen. Bacteria and fungi, originally isolated from potentially suppressive soils of cape gooseberry crops in Nariño, Colombia with different management (organic and conventional), were evaluated as biocontrol agents of *Fox* using a gnotobiotic model (seedlings cultured under axenic conditions with defined microbial strains). Of the 64 isolated microorganisms, 37.5% (15 bacteria and 9 fungi) were discarded because of toxicological risks and an unknow potential biological control. The remaining 62.5% of the microorganisms, 14 bacteria and 26 fungi, were evaluated to assess their potential as biological control agents against *Fox.* The gnotobiotic model system evaluated the protection and plant growth promotion characteristics. Response variables were used to group the microorganism using a principal component analysis (PCA), and five clusters were obtained. Cluster number four concentrated the 10 microorganisms (three bacteria and seven fungi) with the highest protection values against *Fox,* with a positive effect on growth. The isolates were identified as two *Bacillus subtilis* strains, *Rhodococcus* sp., *Podospora setosa*, *Debaryomyces vindobonensis*, *Plectosphaerella plurivora*, *Acinetobacter rhizosphaerae*, *Umbelopsis* sp. and two strains of *Trichoderma koningiopsis*. The gnobiotic system offered clear advantages for evaluating and selecting microorganisms with a biological control potential against *Fusarium oxysporum* f. sp. *physalis.*

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Additional key words: biological control; *in vitro*; vascular wilt; rhizosphere; suppressive soils; cape gooseberry; *Fusarium oxysporum*.

RESUMEN

La uchuva (*Physalis peruviana*) es Solanaceae de enorme importancia económica en Colombia ya que es la segunda fruta más exportada después del banano. La marchitez vascular causada por *Fusarium oxysporum* f. sp. *physali* (*Fox*) es el factor más limitante de este cultivo, que ocasiona pérdidas de hasta el 80% de su producción. El control biológico se ha convertido en una alternativa prometedora para controlar este patógeno. Bacterias y hongos, originalmente aislados de suelos potencialmente supresores de cultivos de uchuva de Nariño, Colombia con diferente manejo (orgánico y convencional) fueron evaluados como agentes de control de *Fox* utilizando un modelo gnotobiótico (plántulas cultivadas en condiciones axiológicas con cepas microbianas definidas). A partir de los 64 microorganismos aislados, 37.5% (15 bacterias y nueve hongos) fueron descartados debido a su riesgo toxicológico y a un control biológico potencial desconocido, el 62.5% restante de microorganismos, 14 bacterias y 26 hongos, se evaluaron para evaluar su potencial como agentes de control biológico contra *Fox*. El sistema de modelos gnotobióticos nos permitió evaluar las características de protección y promoción del crecimiento vegetal, estas variables de respuesta se utilizaron para agrupar el microorganismo utilizando un análisis de componentes principales (PCA) y se obtuvieron cinco clústeres. El clúster número cuatro concentró 10 microorganismos (tres bacterias y siete hongos) con los valores de protección más altos contra *Fox* y con un efecto positivo en la promoción del crecimiento. Los aislados fueron identificados como dos cepas de *Bacillus subtilis, Rhodococcus* sp., *Podospora setosa*, *Debaryomyces vindobonensis*, *Plectosphaerella plurivora*, *Acinetobacter rhizosphaerae, Umbelopsis* sp. y dos cepas de *Trichoderma koningiopsis*. El sistema gnobiótico presentado ofrece claras ventajas para evaluar y seleccionar microorganismos con un potencial de control biológico contra *Fusarium oxysporum* f. sp. *fisalis*.

Palabras clave adicionales: control biológico; *in vitro*; marchitamiento vascular; rizósfera; suelos supresores; uchuva; *Fusarium oxysporum*.

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INTRODUCTION

The cape gooseberry or golden berry (*Physalis peruviana* L.) is an herbaceous plant of the Solanaceae family (NRCS, 2020), with 1,311.8 ha planted in Colombia, mainly in the Boyaca, Cundinamarca and Nariño departments (Agronet, 2018), where it is grown commercially at altitudes between 1,800 and 2,800 m a.s.l., with medium temperatures between 13 and 16°C, 1,500-2,000 h year^{-1} of direct sunshine, and 1,000-1,800 mm year^{-1} of rainfall (Fischer and Melgarejo, 2020). Its fruit is a sugary berry preferred in countries such as Germany, Canada, Brazil, the Netherlands and Belgium, which are the main consumers (Hassanien *et al*., 2011). However, this crop is severely affected by vascular wilt, caused by *Fusarium oxysporum*, Schltdl., throughout Colombia (Galindo and Pardo, 2010; Enciso-Rodríguez *et al*., 2013; Villareal-Navarrete *et al*., 2017; Rodríguez, 2013; Giraldo-Betancourt *et al*., 2020), generating losses of up to 100% (Smith, 2012; Mayorga-Cubillos *et al*., 2019) and forcing the movement of crops to other producing areas (González and Barrero, 2011).

Controlling this fungus is difficult because of the presence of inoculum in the soil, crop residues, infected plant debris and contaminated soils (McGovern, 2015). Plants can be infected by mycelium, conidia and chlamydospores (dormant propagules), which germinate when they come into contact with plant root exudates (Haglund and Kraft, 2001; Michielse and Rep, 2009; Zacky and Ting, 2013). In Colombia, the principal management strategy for this disease is treatment with flutriafol, propineb, iprodione and

chlorothalonil, among other chemicals (ICA, 2020). However, their efficacy is less than 30% (Bennett *et al*., 2011). Therefore, these methods for controlling this pathogen and cultural practices have not been enough (McGovern, 2015).

The use of antagonistic microorganisms for biological control is a promising alternative that has been incorporated into disease management (Köhl *et al*., 2019).

Studies on tomatoes and bananas under greenhouse conditions have shown that non-pathogenic strains of *F. oxysporum* reduce the severity of this disease (Shishido *et al*., 2005). A similar effect has been reported with the addition of the mycorrhizal fungus *Glomus intraradices* (Akköprü and Demir, 2005). Cape gooseberry crops have used strains of *Pseudomonas fluorescens* for biocontrols, decreasing the incidence of this disease in plants (Urrea *et al*., 2011; Toloza-Moreno *et al*., 2020). Additionally, the biocontrol agents (BCAs) *Brevibacillus brevis* and *Trichoderma harzianum* have reduced the severity of the disease caused by *F. oxysporum* f. sp. *lycopersici* and *F. oxysporum* f. sp. *cubense* in tomatoes and bananas by 30 and 55%, respectively, and by 45% against *F. oxysporum* f. sp. *phaseoli* when was applied to bean seeds at greenhouse conditions (Carvalho *et al*., 2014; Bubici *et al*., 2019).

Another interesting approach that has been studied around the world for the control of *Fusarium* sp. uses suppressive soils, where the microbial community in the soil controls this pathogen and reduces the incidence of the disease. Siegel-Hertz *et al*. (2018) reported that *Adhaeribacter, Massilia, Microvirga, Rhizobium, Rhizobacter, Arthrobacter, Amycolatopsis, Rubrobacter, Paenibacillus, Stenotrophomonas* and *Geobacter* generated suppressive soils against *F. oxysporum* f. sp. *lini* in *Linum usitatissimum.* Likewise, it has been suggested that microorganisms isolated from the rhizosphere of a specific pathosystem provide better control of this disease in the same crop since they are already adapted to the host, as opposed to introducing organisms from other pathosystems (Lucy *et al*., 2004). The use of microorganisms in consortia from potentially suppressive soils reduced this disease more efficiently than the use of individual agents in tomato and radish crops (Bubici *et al*., 2019). The microbiome of soils can limit the presence of phytopathogens, so this study focused on selecting microorganisms that have been isolated from the cape gooseberry rhizosphere of potentially suppressive soils with a biocontrol potential against *F. oxysporum* f. sp. *physali* using a gnotobiotic system.

MATERIALS AND METHODS

Biological material

Commercial cape gooseberry (*Physalis peruviana*) Colombia ecotype seeds were used for the assays. The seedlings were disinfected by immersing them in 70% ethanol (2 min) and 3% sodium hypochlorite (20 min), followed by three washings with sterile distilled water. Afterwards, they were left to dry and germinate in a humid and dark chamber for 12 d at 25°C. During this disinfection procedure, no seeds showed symptoms of pathogen development.

The *F. oxysporum* f. sp. *physali* Map5 (*Fox*) strain was selected because of its high virulence in cape gooseberries (Rodríguez, 2010). Three small disks (0.5 cm) were taken from Potato Dextrose Agar cultures (PDA) that were incubated at 25°C for 8 d, inoculated in 300 mL of Potato Dextrose Broth (PDB), and grown at 25°C with constant agitation at 125 rpm for 7 d to obtain the microconidia. Subsequently, they were filtered through sterile muslin, and the inoculum was adjusted to a final concentration of $5{\cdot}10^5$ UFC/mL using a Neubauer chamber.

Evaluation of the biocontrol activity of the microorganisms

The microorganisms used in this study were provided by the Microbial Culture Collection, maintained by Agrosavia. The isolates were originally obtained from rhizospheric soils from two cape gooseberry farms, one with organic management and the other with conventional management, located in the Gualmatan and Puerres municipalities, respectively, in the Department of Nariño (Colombia). These zones have a historical absence of *Fusarium* wilt and have been pointed out as possible sources for suppressive soils. The filamentous fungi were recovered in PDA (Potato Dextrose agar) at 25°C, the bacteria were recovered with LB (Luria-Bertani) at 28°C for 24 h, and yeast was recovered on YM (Yeast Malt agar) at 25°C for 72 h.

The taxonomic identification of these isolates was done by sequencing with molecular marker genes. For the fungi and yeasts, DNA was extracted using a ZR Fungal/Bacterial DNA MiniPrep Kit™, and, for the bacteria, an Invitrogen™ PureLink™ Genomic DNA Mini Kit was used according to the manufacturer's

instructions. Once the nucleic acids were obtained, the ITS region of the fungi and yeasts was amplified with a PCR using the primers R_ITS4_KY03 and ITS3_KY02 (Toju, 2012), and, for bacteria, the primers 515F and 806R were used to amplify variable region V3-V4 of ribosomal gene 16S rRNA (Caporaso *et al*., 2011). Subsequently, the products of this PCR were purified using magnetic beads (AgencourtAMPure XP beads) and were amplified with a second PCR with different combinations of barcode type primers for each sample to obtain a code for each one with simultaneous sequencing with pyrosequencing using the Illumina MiSeq® system.

For the 16S rRNA gene library preparation, the first PCR was performed in a final volume of 25 μL, containing 0.1 μL of Taq Platinum (Invitrogen), 0.75 μL of $MgS0_4$ 50mM, 2.5 μL of Buffer-Mg 10X, 0.5 μL of dNTPs 10mM, 0.5 μL (10μM) of each forward and reverse primers with adaptor sequences, 2 μL of DNA and 18.15 μL of Ultrapure Distilled Water (Invitrogen). The PCR was performed in a T100™ Thermal Cycler, BioRad, with the following conditions: initial denaturation at 94°C for 3 min, 35 cycles of denaturation at 94°C for 45 s, annealing at 50°C for 60 s and extension at 72°C for 90 s, with a final extension of 72°C for 10 min (Caporaso *et al*., 2011). Amplicons were visualized in agarose gels (1.5% p/v) in 1X TAE at 100 V, 30 min. All PCR products were purified following the protocol of Agentcourt® AMPure® XP.

In the second PCR, 5 μL of the previous amplicon were used as the template, with 1 μL (10μM) of each of the forward and reverse barcoding primer, 0.1 μL of Taq Platinum (Invitrogen), 0.75 μL of $MgCl_2$ 50mM, 2.5 Buffer-Mg 10X, 0.5 μL of dNTPs 10 mM and 14.15 μL of Ultrapure Distilled Water (Invitrogen) added. The amplification conditions were the same but with 12 cycles. The final PCR products were purified, and the quality was observed in agarose gels (1.5% p/v).

For the ITS gene library, the first PCR was performed in a final volume of 25 μL, containing 0.1 μL of Taq Platinum (Invitrogen), 1.5 μL of $MgS0_4$ 50mM, 2.5 μL of Buffer-Mg 10X, 0.5 μL of dNTPs 10 mM, 0.5 μL (10 μM) of each forward and reverse primers with adaptor sequences, 2 μL of ADN and 17.4 μL of Ultrapure Distilled Water (Invitrogen). The following conditions were used: initial denaturation at 95°C for 2 min, 35 cycles of denaturation at 95°C for 30 s, annealing at 55°C for 30 s and extension at 72°C for 60 s, with a final extension of 72°C for 5 min. The amplicons were visualized in agarose gels (1.5% p/v) in 1X TAE at 100 V, 30 min. The procedure for the second step PCR and product purification were as described above, adding 5 μL of the amplicon to the mixture and decreasing the cycles to 12 in the thermocycler program.

The purified DNA amplicons were quantified in a NanoDrop™ 1000 Spectrophotometer, pooled and adjusted to the same concentration for the sequencing in the Illumina MiSeq System at the Microbial genomics laboratory of the Molecular Genetics and Antimicrobial Resistance Unit at the Universidad El Bosque (Bogota, Colombia).

The quality of the high throughput sequencing data was analyzed with Fastqc (Blankenberg *et al*., 2010) and compared to the GenBank database using the Blastn algorithm. Once the microorganisms were identified, a decision matrix was designed to eliminate those species that, according to scientific literature, had ecotoxicological or toxicological risks, keeping those that did not present any risks and that had been reported as having biocontrol activity.

Gnotobiotic system for the selection of potential biocontrol microorganisms

The biocontrol activity was evaluated following the methodology described by Moreno *et al*. (2014). Two 13 d-old cape gooseberry seedlings grown from disinfected seeds were placed in a plastic Petri dish (138.9 by 21.1 cm) with Gelified Nutrient Medium Agar – agar enriched with microelements (KI, H_3BO_3, $MnSO_4$, $ZnSO_4$, Na_2MoO_4 and $CuSO_4$). The seedlings were placed 2 cm away from the periphery towards the center of the Petri dish (Fig. 1A).

The Biological Control Agent inoculum (BCA) was obtained with cell washing by scraping the surface of culture plates for the bacteria and yeasts (bacterial colonies grown on LB at 28°C for 24 h and yeast colonies on YM at 25°C for 72 h), adjusting the concentration to $1{\cdot}10^8$ UFC/mL and $1{\cdot}10^7$ UFC/mL, respectively. For the inoculum of the sporulating filamentous fungi, colonies grown in PDA at 25°C for 8 d were scraped with a 0.1% Tween 80 solution, and the spore suspension was filtered through 2 layers of sterile muslin to remove mycelial fragments and adjusted to a final concentration of $1{\cdot}10^6$ UFC/mL. The inoculum concentration was determined according to previous reports (Bleve *et al*., 2006; Sahebani and Hadavi, 2008; Arrebola *et al*., 2010). The suspensions of non-sporulated fungi were obtained by

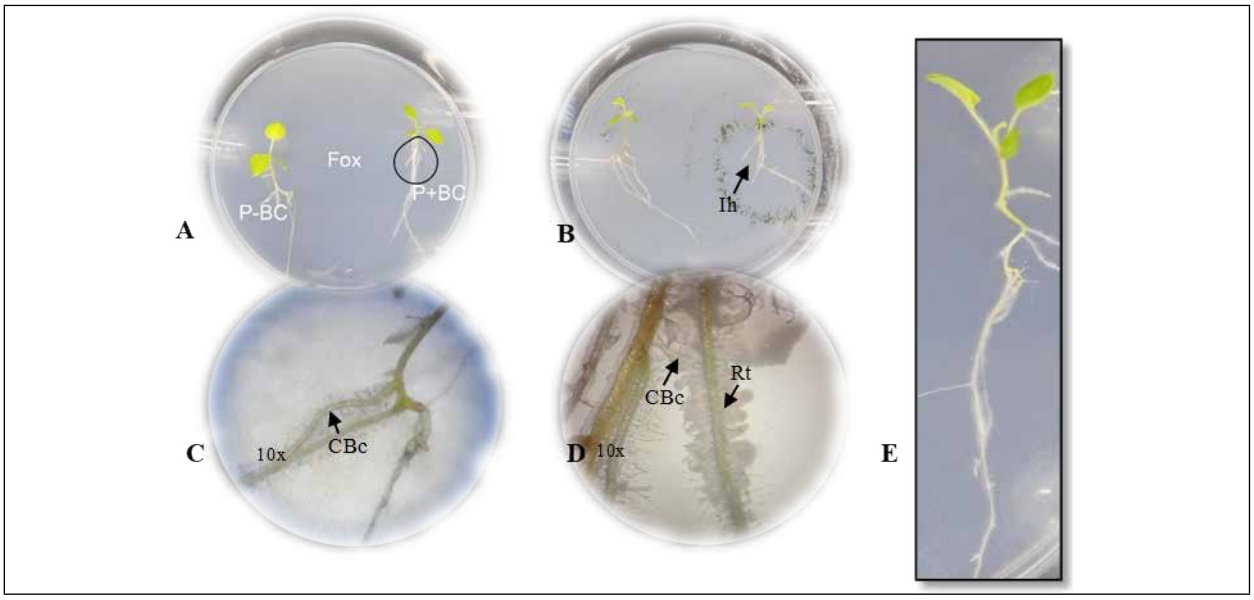


Figure 1. Gnotobiotic model and parameters evaluated in microorganisms with biocontrol potential. A. plant (P) - biocontrol (BC) interaction - *Fox* in the gnotobiotic model; P-BC: seedling without the biocontrol microorganisms, P + BC: seedling with the biocontrol microorganism, (*Fox*) *Fusarium oxysporum*. B. formation of inhibition halo of the pathogen (Ih). C. and D. colonization of the biocontrol microorganisms (CBc) in the radicle (Rt) with 10X magnifications. C., D. biofilm formation with 10X magnifications. E. plant growth.

fragmenting mycelium into an approximate size of 2 mm^2 and scraping colonies with a 0.1% Tween 80 solution and diluting them 100-fold. A volume of 4 μL of each microorganism was applied to inoculate the seedlings on one plant, on the neck of the stem, which was incubated at 25°C for 4 d (Fig. 1A). The center of the Petri dish was inoculated with 4 μL of a *Fox* suspension adjusted at $5{\cdot}10^5$ UFC/mL, and the dish was incubated at 25°C in a vertical position. Three repetitions (Petri dishes) were used for each microorganism with biocontrol potential. Two biological replicates were done.

Three different controls were considered in the experiment: the absolute control that consisted of seedlings without a biocontrol microorganism for *Fox*; the pathogen control with only seedlings inoculated with *Fox*; and the relative control consisting of seedlings treated with the biocontrol agent.

Ten days after incubation of the gnotobiotic dishes, the following parameters were evaluated to select microorganisms with biocontrol potential against *Fox*: (i) symptoms in the seedlings expressed as the presence of chlorotic and roller leaves, (ii) radicle colonization by *Fox*, (iii) *Fox* radial growth, (iv) formation of inhibition halo from biocontrol agent against *Fox,* (v) radicle colonization by fungi or bacteria biofilm formation and growth promotion expressed by total plant length (Fig. 1). A score was assigned to each of the parameters as shown in table 1.

In order to select biocontrol microorganisms, the evaluated parameters were compiled (Tab. 1, Fig. 1). A decision matrix analysis was used that weighed the different factors accordingly to the relative importance assigned to protection characteristics against *Fox* and plant growth promotion. This selection was based on the following criteria: review of toxicology risks and effects on non-target organisms, results of preliminary tests performed on mass production, results of their biocontrol activity against the pathogen and plant-growth promotion effect (Tab. 1).

Statistical analysis

A principal component analysis (PCA) was performed to determine the correlations between the data groups corresponding to microorganisms in growth promotion and protection against the pathogen, using R-Studio version 3.3 to detect differences and/or similarities between the microorganisms with potential biocontrol activity.

Table 1. Parameters evaluated and the percent contribution to selection of microorganism with biocontrol potential in a gnotobiotic system.

Features	Parameters	Score	Meaning	Contribution of the parameter to the feature (%)*
Protection against Fox	Symptoms development	0	Chlorotic and roller leaves	0
		1	Extended leaves	40
	Radicle colonization by *Fox*	0	*Fox* growth on the radicle	0
		1	Any growth of *Fox* on the radicle	25
	Fox radial growth	0	Less growth of *Fox* in the presence of biocontrol agent than in its absence	15
		1	Greater growth of *Fox* in the presence of biocontrol agent than in its absence	0
	Formation of inhibition halo from biocontrol agent against *Fox*	0	Not inhibition halo. Radicle colonization by *Fox*	0
		1	Halo produced by the biocontrol agent towards the pathogen. Not radicle colonization by *Fox*	15
	Radicle colonization by fungi or biofilm formation by bacteria	0	Any growth of biocontrol agent on the radicle	0
		1	Growth of biocontrol agent on the radicle	5
Plant growth promotion	Total length plant	0	Less or same growth of plant length without biocontrol agent	0
		1	Higher plant length growth in presence of biocontrol agent	100

* Multicriteria analysis for the qualification both characteristics: protection against *Fox* and growth promotion according to the evaluated parameters.

RESULTS AND DISCUSSION

Identification and selection of microorganisms with biocontrol potential

The AGROSAVIA National Microbial Culture Collection for Food and Agriculture provided 64 microorganisms isolated from the rhizosphere of potentially suppressive cape gooseberry soils in Nariño (Tab. 2), 29 were bacteria, and 35 were fungi. Nevertheless, 24 strains (15 bacteria and nine fungi) were discarded because they represented a risk for the environment (E) and for human and animal health (T) and/or they have not been reported as successful biological control agents (CB) (Tab. 2). As a result, 40 microorganisms, of which 14 were bacteria (five from a farm with conventional management and nine from an organic farm). i.e. 35%, and 26 were fungi (13 from each farm), i.e. 65%, which were evaluated in the gnotobiotic model against *Fox* (Tab. 2).

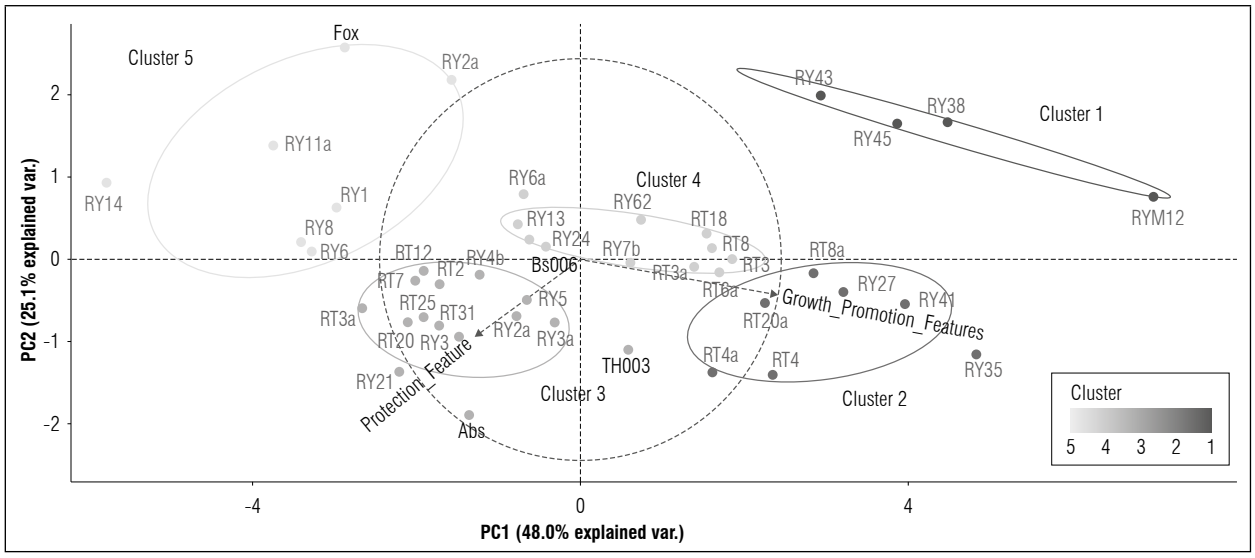
Evaluation of biocontrol activity of microorganisms

According to the principal component analysis (PCA), the plant growth promotion, expressed as total plant length (Tab. 1), presented 73.1% of the variability explained by the two characteristics total plant length and growth promotion (Fig. 2).

The microorganisms with biocontrol potential against *Fox* were grouped into five different clusters. Cluster 1 grouped 9.10% of the strains that, albeit with the lowest values for seedling protection (25%) in all evaluated parameters (formation of inhibition halo against *Fox*, symptom development, radicle colonization by fungi or biofilm formation by bacteria, radicle colonization by *Fox* and *Fox* radial growth), had the greatest effect on promoting growth in the seedlings with an average length of 11.2 cm (Fig. 2; Tab. 3). This cluster contained microorganisms (RY12-*Paenibacillus peoriae*, RY38-*Serratia liquefaciens*,

RY45-*Bacillus simplex*, and RY43-*Pseudomonas chlororaphis*) that have strains that have been reported in many studies as plant growth promoting rhizobacteria (PGPR) (Kloepper *et al*., 1986; Raaijmakers and Weller, 1998; Pieterse *et al*., 2014; Bubici *et al*., 2019). Chin-A-Woeng *et al*. (2003) found that *Pseudomonas* spp. produces antifungal metabolites, such as phenazine, that favor growth promotion in *Cucumis sativus* and *Solanum lycopersicum* plants. Likewise, other bacterial rhizosphere isolates from a potato crop, such as *B. simplex*, induced growth promotion in seedlings (Rete, 2011). *S. liquefaciens* has been reported as a plant growth-promoting rhizobacteria in cucumber (Kloepper *et al*., 1986), and *P. peoriae* has been reported as an antimicrobial agent that counteracts both fungi and phytopathogenic bacteria (Von der Weid *et al*., 2003). However, in this study, *P. peoria* had a growth promotion effect but no protection against *Fox*.

Cluster 2 grouped 15.9% of the microorganisms that generated a less protective effect on the seedlings (score of 25%) than the positive effect in terms of growth promotion (an average length of 12.2 cm) (Tab. 1; Fig. 2; Tab. 3). This cluster contained the microorganisms RY35-*Lysinibacillus* sp., RY41-*Bacillus*



Figures 2. Principal component analysis (PCA) for the grouping of microorganisms with suppressive potential against *F. oxysporum* according to their similarity in the characteristics of biocontrol and growth promotion, obtained from the multicriteria table. The ellipses indicate the 95% confidence intervals for each cluster.

Table 2. Criteria for microorganism selection with biocontrol potential to be evaluated in a gnotobiotic model.

Identity of the strain	Code[1]	Toxicological risks			Biological control reports		Selected isolates (+,-)
		E2	T3	Reference	CB4	Reference	
Acinetobacter rhizosphaerae	RTM3	-	-	Chastre (2003)	+	Indiragandhi *et al*. (2008)	+
Alcaligenes faecalis	RTM40	+	+	Tena *et al*. (2015)	-	Dorman and Deans, (2000) and Shoda (2000)	-
Bacillus anthracis	RTM1	+	+	Spencer (2003)	-		-
Bacillus anthracis	RTM10	+	+	Spencer (2003)	-		-
Bacillus anthracis	RTM30	+	+	Spencer (2003)	-		-
Bacillus anthracis	RYM36	+	+	Spencer (2003)	-		-
Bacillus anthracis	RYM65	+	+	Spencer (2003)	-		-

Table 2 continuation.

Identity of the strain	Code[1]	Toxicological risks			Biological control reports		Selected isolates (+,-)
		E2	T3	Reference	CB4	Reference	
Bacillus cereus	RTM2	+	+	Spencer (2003)	-		-
Bacillus foraminis	RYM27	-	-	Lagier *et al*. (2012)	+	Kumar *et al*. (2015)	+
Bacillus simplex	RYM31	-	-	de Boer Sietske and Diderichsen (1991)	+	Gutiérrez-Luna *et al*. (2010) and Rashid *et al*. (2012)	+
Bacillus simplex	RYM41	-	-	de Boer Sietske and Diderichsen (1991)	+	Gutiérrez-Luna *et al*. (2010) and Rashid *et al*. (2012)	+
Bacillus simplex	RYM45	-	-	de Boer Sietske and Diderichsen (1991)	+	Gutiérrez-Luna *et al*. (2010) and Rashid *et al*. (2012)	+
Bacillus sp.	RTM31	-	-	de Boer Sietske and Diderichsen (1991)	+	Handelsman *et al.* (1990), He *et al*. (1994) and Osburn *et al*. (1995)	+
Bacillus sp.	RTM7	+	+	de Boer Sietske and Diderichsen (1991)	-	Handelsman *et al*. (1990), He *et al*. (1994), Osburn *et al*. (1995) and Ploper *et al*. (1992)	-
Bacillus subtilis	RTM6	-	-	de Boer Sietske and Diderichsen (1991)	+	Bais *et al*. (2004) and Asaka and Shoda (2002)	+
Bacillus subtilis	RYM21	-	-	de Boer Sietske and Diderichsen (1991)	+	Bais *et al*. (2004) and Asaka and Shoda (2002)	+
Bacillus subtilis	RYM25	-	-	de Boer Sietske and Diderichsen (1991)	+	Bais *et al*. 2004 and Asaka and Shoda (2002)	+
Bacillus thuringiensis	RTM20	-	-	Ghelardi *et al*. (2007)	+	Rodríguez *et al*. (2019)	+
Citrobacter sp.	RTM4	+	+	Deng *et al*. (2003)	-		-
Citrobacter sp.	RTM5	+	+	Deng *et al*. (2003)	+		+
Citrobacter sp.	RTM9	+	+	Deng *et al*. (2003)	-		-
Citrobacter sp.	RTM15	+	+	Deng *et al*. (2003)	-		-
Lysinibacillus sp.	RYM35	-	-		+	Martínez and Dussán (2018) and Melnick *et al.* (2011)	+
Paenibacillus peoriae	RYM12	-	-		+	Von der Weid *et al*. (2003)	+
Pseudomonas chlororaphis	RYM43	-	-		+	Gunther *et al*. (2005)	+
Pseudomonas chlororaphis	RYM50	+	+		-	López *et al*. (2012)	-
Pseudomonas corrugata	RYM39	+	+		-	Kůdela *et al*. (2010) and Catara *et al*. (2007)	-
Rahnella sp.	RTM8	-	-	Hoppe *et al.* (1993)	+	Chen *et al*. (2007), Opelt *et al*. (2007) and Felestrino *et al*. (2017)	+
Rhodococcus sp.	RYM13	-	-	Prescott (1991)	+	(Creason *et al*., 2014)	+
Serratia liquefaciens	RYM38	-	-	Grohskopf *et al*. (2001)	+	Kalbe *et al*. (1996), Kurze *et al*. (2001) and Zahid *et al*. (2015)	+
Beauveria bassiana	RY3	-	-		+	Ownley *et al*. (2008)	+
Debaryomyces vindobonensis	RY62	-	-		+	Gutiérrez (2017)	+
Doratomyces asperulus	RT14	-	-	Sandoval-Denis *et al*. (2016) and de Hoog *et al*. (2013)	+	Carmarán and Novas (2003)	+

Table 2 continuation.

Identity of the strain	Code[1]	Toxicological risks			Biological control reports		Selected isolates (+,-)
		E2	T3	Reference	CB4	Reference	
Fusarium sp.	RT8	+	+	Gally *et al*. (2006)	-		-
Fusarium sp.	RT9	+	+	Gally *et al*. (2006)	-		-
Fusarium sp.	RT10	+	+	Gally *et al*. (2006)	-		-
Fusarium sp.	RT13	+	+	Gally *et al*. (2006)	-		-
Gibellulopsis nigrescens	RT19	+	+	Korolev *et al*. (2000)	-	Verma and Allison (1970)	-
Humicola grisea	RT11	-	-	de Hoog *et al*. (2013)	+	Verma and Allison (1970)	+
Humicola grisea	RT20	-	-	de Hoog *et al*. (2013)	+	Verma and Allison (1970)	+
Humicola grisea	RT25	-	-	de Hoog *et al*. (2013)	+	Sobita and Anamika (2011) and Moreno *et al*. (2009)	+
Mucor racemosus	RT3a	-	-	Szaniszlo and Harris (1985)	+	Rai and Saxena (1975)	+
Penicillium cremeogriseum	RT2	-	-	Refai *et al*. (2015)	+	Nicoletti *et al*. (2008)	+
Penicillium janthinellum	RT7	-	-		+	Marinho *et al*. (2005)	+
Penicillium sp.	RT5	+	+		-	Moreno-Limón *et al*. (2011)	-
Penicillium sp.	RT6	+	+		-	Moreno-Limón *et al*. (2011)	-
Penicillium sp.	RT11a	+	+		-	Moreno-Limón *et al*. (2011)	-
Penicillium sp.	RT24	+	+		-	Moreno-Limón *et al*. (2011)	-
Plectosphaerella plurivora	RY7B	-	-		+	Toju *et al*. (2012)	+
Podosporasetosa sp.	RY6	-	-		+	Eshraghi *et al*. (2014)	+
Purpureocillium lilacinum	RT12	-	-	Rickerts *et al*. (2000)	+	Anastasiadis *et al*. (2008)	+
Scopulariopsis brevicaulis	RY3a	-	-		+	Zhang *et al*. (2015)	+
Trichoderma gamsii	RT4	-	-		+	Zhang *et al*. (2015)	+
Trichoderma gamsii	RY2a	-	-		+	Zhang *et al*. (2015)	+
Trichoderma gamsii	RY4B	-	-		+	Zhang *et al*. (2015)	+
Trichoderma ghanense	RY6a	-	-	Druzhinina *et al*. (2011)	+	Bayman *et al*. (2011)	+
Trichoderma koningiopsis	RT3	-	-	Kuhls *et al*. (1999)	+	Sobita and Anamika, (2011) and Moreno *et al*. (2009)	+
Trichoderma koningiopsis	RT8	-	-		+	Sobita and Anamika (2011) and Moreno *et al*. (2009)	+
Trichoderma koningiopsis	RY1	-	-	Kuhls *et al*. (1999)	+	Sobita and Anamika (2011) and Moreno *et al*. (2009)	+
Trichoderma sp.	RT4a	-	-	Kuhls *et al*. (1999)	+	Zhang *et al*. (2015)	+
Trichoderma sp.	RY2	-	-	Kuhls *et al*. (1999)	+	Zhang *et al*. (2015)	+
Trichoderma viride	RY5	-	-	Kuhls *et al*. (1999)	+	Martínez-Medina *et al*. (2014) and Banaay *et al*. (2012)	+
Trichosporon sp.	RY8	-	-	Kuhls *et al*. (1999)	+	Zhang *et al*. (2015)	+
Umbelopsis sp.	RT18	-	-	Rodríguez *et al*. (2010)	+	Korolev *et al*. (2000)	+

[1] RT, microorganisms isolated from the rhizosphere of the farm with conventional management; RY, microorganisms isolated from the rhizosphere of the farm with organic management. E^2(+), presence of ecotoxicological risk; E^2(-), absence of ecotoxicological risk. T^3(+), presence of toxicological risk; T^3(-), absence of toxicological risk. CB^4(+), successful reports of biocontrol activity; CB^4(-), absence of unsuccessful reports of biocontrol activity. The selected microorganisms are highlighted in the table and are indicated with (+) and unselected with (-).

Table 3. Values of contribution to the selection of microorganism with and without a biocontrol potential agent in a gnotobiotic system.

Code	Strain	Cluster	Protection against *Fox* + BC (%)	Growth promotion *Fox* + BC (%)	Growth promotion *Fox* + BC (cm)
RY12	*Paenibacillus peoriae*	1	25	100	9.4
RY38	*Serratia liquefaciens*	1	25	100	9.2
RY45	*Bacillus simplex*	1	25	100	13.0
RY43	*Pseudomonas chlororaphis*	1	25	100	13.0
RY35	*Lysinibacillus* sp.	2	25	100	10.6
RY41	*Bacillus simplex*	2	25	100	12.4
RY27	*Bacillus foraminis*	2	25	100	11.6
RT8a	*Rahnella* sp.	2	25	100	11.3
RT20a	*Bacillus thuringiensis*	2	25	100	13.1
RT4a	*Trichoderma* sp.	2	25	100	11.9
RT4	*Trichoderma gamsii*	2	25	100	14.6
Abs	Absolulo	3	75	100	9.6
TH003	*Trichoderma koningiopsis*	3	60	100	8.2
RY21	*Bacillus subtilis*	3	60	100	10.9
RY3a	*Scopulariopsis brevicaulis*	3	60	100	10.1
RY5	*Trichoderma viride*	3	60	100	8.8
RY2a	*Trichoderma gamsii*	3	60	100	8.4
RY4b	*Trichoderma gamsii*	3	60	100	8.2
RY3	*Beauveria bassiana*	3	50	100	9.3
RT31	*Bacillus* sp.	3	55	100	9.7
RT3a	*Mucor racemosus*	3	55	100	8.8
RT20	*Chaetomiaceae* sp.	3	55	100	9.0
RT25	*Chaetomiaceae* sp.	3	55	100	9.1
RT2	*Penicillium cremeogriseum*	3	55	100	8.3
RT7	*Penicillium janthinellum*	3	55	100	9.7
RT12	*Purpureocillium lilacinum*	3	75	100	10.4
Bs006	*Bacillus subtilis*	4	60	100	9.3
RY25	*Bacillus subtilis*	4	60	100	12.3
RY13	*Rhodococcus* sp.	4	60	100	9.2
RY6a	*Podospora setosa*	4	40	100	9.0
RY62	*Debaryomyces vindobonensis*	4	40	100	9.6
RY7b	*Plectosphaerella plurivora*	4	60	100	8.7
RT3	*Acinetobacter rhizosphaerae*	4	45	100	11.5
RT6	*Bacillus subtilis*	4	60	100	9.0
RT3	*Trichoderma koningiopsis*	4	60	100	9.6
RT8	*Trichoderma koningiopsis*	4	75	100	11.2
RT18	*Umbelopsis* sp.	4	45	100	11.0
Fox	*Fusarium oxysporum*	5	25	0	8.2

Table 3, continuation.

Code	Strain	Cluster	Protection against *Fox* + BC (%)	Growth promotion *Fox* + BC (%)	Growth promotion *Fox* + BC (cm)
RY2	*Trichoderma* sp.	5	25	0	6.4
RY1	*Trichoderma koningiopsis*	5	25	100	8.3
RY6	*Trichoderma ghanense*	5	25	0	7.9
RY8	*Trichosporon lignicola*	5	25	0	6.5
RT11a	*Humicola grisea*	5	5	0	7.6
RT14	*Doratomyces asperulus*	5	25	0	5.5

* The contribution of protection characteristics against *Fox* and promotion of growth in seedlings without biocontrol was zero because of the absence of the microorganism.

simplex, RY27-*Bacillus foraminis*, RT8a-*Rahnell*a sp., RT20a-*Bacillus thuringiensis*, RT4a-*Trichoderma* sp. and RT4-*Trichoderma gamsii*. Previous studies have reported the presence of *B. simplex* and *R. aquatilis* in the rhizosphere of *Vitis* spp., which facilitate nitrogen fixation and promote plant growth in *Solanum tuberosum* and *Vitis* spp. (Chen *et al*., 2007; Velivelli *et al*., 2015). Singh *et al*. (2015) reported that *B. foraminis*, not only exerts a protective effect against *Fusarium* sp., but also favors the promotion of growth in *Zea mays*. Additionally, *L. fusiformis*, *Lysinibacillus* spp. and *B. thuringiensis* have been described as potential biocontrol agents of *F. oxysporum* f. sp. *ciceri* race 1 in *Cicer arietinum* (Singh *et al*., 2014). Similar results were found in the present study. Moreover, this study confirmed the biocontrol activity of *Trichoderma* sp. since *T. gamsii* and other species from this genus had a control effect against *Fox* in the cape gooseberry seedlings (Fig. 1B).

Cluster 3 included 34.1% of the microorganisms with high values in terms of seedling protection, a high score of 50% in these parameters, and a positive effect in terms of growth promotion (average length of 9.2 cm), but there were no differences between plant length (Tab. 1; Fig. 2; Tab. 3). This cluster contained microorganisms with biocontrol potential, such as TH003-*Trichoderma koningiopsis*, RY21-*Bacillus subtilis*, RY3-*Scopulariopsis brevicaulis*, RY5-*Trichoderma viride*, RY2-*T. gamsii*, RY4b-*Trichoderma gamsii*, RY3-*Beauveria bassiana*, RT31-*Bacillus* sp., RT3a-*Mucor racemosus*, RT20-*Humicola grisea*, RT25-*H. grisea*, RT2-*Penicillium cremeogriseum*, RT7-*Penicillium janthinellum* and RT12-*Purpureocillium lilacinum*. Some species of the *Trichoderma* genus are effective biocontrol agents (Schirmböck *et al*., 1994; Lorito *et al*., 1996; Howell, 2003), and *T. koningiopsis, T. viride, T. gamsii* and *S. brevicaulis* have been reported as antagonistic agents of *Fusarium culmorum* in *Zea mays* (Luongo *et al*., 2005). The Th003 strain of *T. koningiopsis* is the active ingredient of Tricotec®, a product registered in Colombia by Agrosavia for the control of *F. oxysporum* f. sp. *lycopersici* in tomato crops (Cotes *et al*., 2018). On the other hand, *B. bassiana, M. racemosus* and *Penicillium* spp. have been reported as mycoparasites on *F. oxysporum* f. sp. *radicis-lycopersici* (Palma-Guerrero *et al*., 2008). *H. grisea* and *Purpureocillium* sp. have been reported as biocontrol agents because of the production of antibiotics (Hubbard *et al*., 1982; Di Pietro *et al*., 1992) that inhibit pathogens such as *F. culmorum* and *Pythium ultimum* (Galindo-Flores *et al*., 2005). Asaka and Shoda (2002) found that *B. subtilis* produces antibiotics, such as iturin A and surfactin, that counteract pathogens such as *Rhizoctonia solani* in tomato plants.

Cluster 4 concentrated 25% of the microorganisms that generated the highest protection values against *Fox* (Score highest than 60%) and showed a positive effect in growth promotion (average length of 10 cm) (Tab. 1; Fig. 2; Tab. 3). The microorganisms in this cluster were Bs006-*Bacillus velezensis*, RY25-*Bacillus subtilis*, RY13-*Rhodococcus* sp., RY6-*Podospora setosa*, RY62-*Debaryomyces vindobonensis*, RY7b-*Plectosphaerella plurivora*, RT3-*Acinetobacter rhizosphaerae*, RT6-*Bacillus subtilis*, RT3-*Trichoderma koningiopsis*, RT8-*Trichoderma koningiopsis*, and RT18-*Umbelopsis* sp. Previous studies have shown that Bs006, a strain of *B. velezensis,* is an excellent *Fox* inhibiting microorganism because of antibiotic secretions (Moreno *et al*., 2014) and that *Rhodococcus* sp. inhibits *Pythium aphanidermatum* under *in vitro* conditions because the enzymes are capable of degrading the cell wall (El-Tarabily, 2006), which could explain the control

activity of this microorganism against *Fox*. In contrast, *Debaryomyces* sp., *Plectosphaerella* sp., *Umbelopsis* sp. and *Acinetobacter* sp. have been widely studied as growth promoters (Rokhbakhsh-Zamin *et al*., 2011; Zhao *et al*., 2014), and *Podospora* sp. has been reported as an abundant microorganism in healthy *Musa* sp. and *Pyrus* sp. soils and has been associated with the suppression of vascular wilt caused by *Fox* (Xu *et al*., 2012; Huang *et al*., 2017).

Cluster 5 represented 15.90% of the microorganisms, which did not generate a protection effect against the pathogen in the seedlings or an effect on growth promotion (average length of 7.2 cm) (Fig. 2; Tab. 3). This group had the treatment that only contained *Fox* (pathogenic control). This cluster contained the microorganisms RY2-*Trichoderma* sp., RY1-*Trichoderma koningiopsis*, RY6-*Trichoderma ghanense*, RY8-*Trichosporon lignicola*, RT11-*H. grisea* and RT14-*Doratomyces asperulus*. In contrast to cluster 4, the two strains of *Trichoderma* from this group did not have a protective effect against the pathogen. Di Pietro *et al*. (1992) reported that *H. grisea* and *D. asperulus* are biocontrol agents because of the production of antimicrobial substances that counteract *F. culmorum*. Nevertheless, the strains in this cluster did not protect against the pathogen. On the contrary, some of them favored *Fox* because they allowed abundant growth and development of vascular wilt symptoms.

CONCLUSION

The biocontrol activity and growth responses of the cape gooseberries to the treatments with the evaluated rhizospheric microorganisms varied with the isolate-type and the origin of the isolates. The majority of the bacteria obtained from the organic farm expressed a biocontrol activity and positively affected plant growth, whereas the fungal isolates with a biocontrol activity and plant growth promotion were similar for the two farms. This effect reflects the capability of different microorganism species to counteract this pathogen and promote plant growth. However, a practical application of these results should be further evaluated in field experiments. Based on our results, Bs006-*Bacillus velezensis*, RY25-*Bacillus subtilis*, RY13-*Rhodococcus* sp., RY6-*Podospora setosa*, RY62-*Debaryomyces vindobonensis*, RY7b-*Plectosphaerella plurivora*, RT3-*Acinetobacter rhizosphaerae*, RT6-*Bacillus subtilis*, RT3-*Trichoderma koningiopsis*, RT8-*Trichoderma koningiopsis*, are RT18-*Umbelopsis* sp. are promising *F. oxysporum* control treatments for cape gooseberries (more than 60%), which should be evaluated both individually and in consortia under greenhouse conditions.

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Conflict of interests: The authors declare that this research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest. A.M Cotes conceived the research idea. D.S. García carried out the experiments and drafted the manuscript under the advice of A.M. Cotes and A. Gonzalez, who contributed to the date analysis and interpretation, as well as critical revisions and approval of the final version of the manuscript. A. Caro and L.L. Dávila contributed to the molecular identification of the isolates. Each author contributed drafts of specific sections of the manuscript and repeatedly edited the manuscript.

Author's note: The microorganisms used in this study were provided by the collection of bacteria and fungi from Agrosavia, obtained in a previous sampling conducted under the guidelines indicated in resolution 1466 of December 03, 2014 of ANLA, Colombia.

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