Mitigation of the Impact of Vascular Wilt and Soil Hypoxia on Cape Gooseberry Plants by Foliar Application of Synthetic Elicitors

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Abstract. *Physalis peruviana* L. crops are exposed to different stress conditions that limit their productivity. Within these conditions, abiotic stress caused by water and biotic stress by *Fusarium oxysporum* f. sp. *physali* (Foph) are frequent at commercial levels. The foliar application of synthetic elicitors can be a tool to mitigate the negative impacts of these stresses. The objective of this study was to evaluate the interaction between Foph inoculation and three foliar applications of brassinosteroids (BR), salicylic acid (SA), and a commercial elicitor based on botanical extracts (BE) of *Echinacea purpurea*, *Potentilla erecta*, and *Aloe vera* on the physiological [stomatal conductance (g_s), leaf water potential (Ψ_{wf}), chlorophyll fluorescence, and growth] and biochemical [photosynthetic pigments, malondialdehyde (MDA) production, and proline content] responses of cape gooseberry plants subjected to a 6-day waterlogging period. The established treatments were as follows: 1) waterlogged plants without Foph; 2) waterlogged plants with Foph; 3) waterlogged, noninoculated (Foph⁻) plants treated foliarly with BR, SA, or BE; and 4) waterlogged, inoculated (Foph⁺) plants treated foliarly with BR, SA, or BE. The results showed that the foliar application of BR or SA reduced vascular wilt development in plants subjected to a hypoxia period. In addition, three applications of BR, SA, or BE favored g_s , Ψ_{wf} , growth, and chlorophyll fluorescence parameters in cape gooseberry plants under the interaction between Foph and oxygen deficit in the soil. Also, higher photosynthetic pigment and proline contents were observed in plants treated with elicitors under stress combination, whereas a lower MDA production was evidenced in this group of plants. In conclusion, BR, SA, or BE can help mitigate the negative effects of the simultaneous occurrence of Foph and a waterlogging condition for 6 days in cape gooseberry plants.

Cape gooseberry (*P. peruviana* L.) is an herbaceous plant from the South American Andes that belongs to the Solanaceae family. *P. peruviana* is the second exported fruit species in Colombia with an export value of US\$27.8 million during 2017 (Álvarez-Flórez et al., 2017; Olivares-Tenorio et al., 2017). Also, this crop occupied 1023 ha with a production of $\approx 15,586$ t in 2017 (Agronet, 2019; Procolombia, 2019).

P. peruviana crop productivity has decreased in Colombia during recent years because of factors such as vascular wilt (Foph), abiotic stresses (waterlogging), and/or the interaction between these factors (Aldana et al., 2014; Moreno-Velandia et al., 2019; Villarreal-Navarrete et al.,

2017). Vascular wilt is the most limiting crop disease that has been reported in more than 50% of growing areas in the country, generating yield reductions or total crop loss (Osorio-Guarín et al., 2016; Simbaqueba et al., 2018). Disease symptoms include marginal leaf chlorosis, vascular tissue browning, plant wilting, atrophy, and eventual death (Abdallah et al., 2016). Pathogen infection occurs by direct penetration and intracellular growth of hyphae through the root tip into the xylem vessels, causing plant wilting (Król et al., 2015). Disease management has been hampered by the resistance of the pathogen to commercial fungicides. In addition, the presence of chlamydospores allows the prolonged survival of the pathogen, which can infect roots of new plants (Król et al., 2015; Osorio-Guarín et al., 2016).

Crops are currently facing waterlogging conditions (hypoxia) because of high rainfall, inefficient irrigation practices, and/or inadequate soil drainage, generating growth and yield limitations (Herzog et al., 2016). Waterlogging stress can cause several types of physiological responses in plants and also can favor the incidence of diseases (Rao and Li, 2003). Short

or moderate waterlogging periods can cause low root growth and dry matter accumulation, leaf senescence, plant wilting, and crop death (Wu et al., 2015). Leaf gas exchange properties (g_s , transpiration, and photosynthesis) and photosynthetic pigment content also are associated with the type of plant acclimation responses (Zhu et al., 2016). In addition, MDA and proline production have been used as biochemical markers to characterize plant responses to abiotic and biotic stresses (Dar et al., 2016; Irulappan and Senthil-Kumar, 2018).

Chlorophyll fluorescence parameters also are affected by hypoxia conditions, and these parameters can be effective in detecting changes in the mechanisms involved in plant acclimation (He et al., 2018; Shao et al., 2013). A low electron transport rate (ETR), photochemical efficiency of photosystem II (PSII) (F_v/F_m), photochemical quenching (qP), and a high nonphotochemical quenching (NPQ) have been reported under waterlogging conditions (Liu et al., 2014; Wu et al., 2015). Moderate periods of hypoxia (6–8 d) also have caused a reduction in plant height, leaf area (LA), plant dry weight, and high plant wilting in cape gooseberry plants (Aldana et al., 2014).

Waterlogging also can increase plant diseases associated with soil pathogens, such as vascular wilt caused by *F. oxysporum* f. sp. *cubense* in banana (*Musa* spp.) (Aguilar et al., 2000; Shivas et al., 1995), crown and root rot caused by *Phytophthora* spp. in apple (*Malus domestica* Borkh.) and raspberry (*Rubus idaeus* L.) (Duncan and Kennedy, 1989; Wilcox, 1993), and damping-off caused by *Pythium irregulare* in beans (*Phaseolus vulgaris* L.) (Li et al., 2015b). This greater plant susceptibility to soilborne pathogens under waterlogging conditions is associated with the ability of microorganisms to grow in anaerobic conditions (Rao and Li, 2003). Regarding the combined stress effect (waterlogging and plant pathogen), Moslemi et al. (2018) observed greater basal leaf chlorosis, wilting, and necrosis in pyrethrum plants [*Tanacetum cinerariifolium* (Trev.) Schultz. Bip.] infected with *Paraphoma vinacea*, *F. oxysporum*, and *Fusarium avenaceum* exposed to waterlogging for 7 d. Also, these authors reported that hypoxia conditions generated a lower plant biomass, and lower stem and flower number in pathogen-infected plants.

The use of synthetic elicitors can be considered an effective tool to mitigate the negative effects generated by abiotic and biotic stresses in plants (Llorens et al., 2017; Naik and Al-Khayri, 2016). Elicitors are chemical compounds that can be sprayed on leaves, causing a stimulus on plant defense mechanisms and secondary metabolite synthesis under abiotic and biotic stress conditions (Llorens et al., 2017; Ramírez-Godoy et al., 2018; Thakur and Sohal, 2013). SA, BR, and plant BEs have been studied and characterized as compounds that activate plant defense mechanisms against stress conditions (abiotic and biotic) (Bektas and Eulgem, 2015; Singh et al., 2017; Vardhini

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and Anjum, 2015; Xue et al., 2013; Zhang et al., 2015).

SA acts as a signaling molecule modulating tolerance to stress through the activation or regulation of physiological, biochemical, and molecular processes (Bernal-Vicente et al., 2017; Khan et al., 2015). Foliar SA application decreased the size of the lesion generated by *Phytophthora cinnamomi* in lupin (*Lupinus angustifolius*) roots (Groves et al., 2015) and enhanced growth and physiological and biochemical behavior of tomato plants (*Solanum lycopersicum* L.) with waterlogging for 45 d (Singh et al., 2017).

BRs are polyhydroxylated steroidal plant hormones that also can help the tolerance to different abiotic and biotic stresses in plants (Anwar et al., 2018; Fariduddin et al., 2014). BR application decreased the negative effects generated by *Verticillium dahliae* in cotton plants (*Gossypium hirsutum* L.) (Bibi et al., 2014) and improved protein content, dry matter yield, nitrogen uptake, and harvest index in maize plants (*Zea mays* L.) with waterlogging for 10 d (Otie et al., 2019).

BEs also have been considered as an effective alternative for plant pathogen control and stress mitigation in recent years (Joseph et al., 2017; Van Oosten et al., 2017). Rongai et al. (2017) observed that BE from pomegranate (*Punica granatum*) peels showed antifungal activity on *F. oxysporum* f. sp. *lycopersici* in tomato plants (*S. lycopersicum* L.) under in vitro conditions. Elansary et al. (2017) also observed a positive effect of seaweed BE sprays on the physiological and biochemical traits of seashore paspalum (*Paspalum vaginatum*) plants subjected to water stress.

Foph management practices in cape gooseberry crops have been mainly based on the use of synthetic fungicides (Moreno-Velandia et al., 2019); however, synthetic elicitors have been used as alternatives for soilborne pathogen management in recent years (McGovern, 2015). Studies about synthetic elicitors have been focused separately on disease control (Ding et al., 2009a; Mandal et al., 2009; Mostafa et al., 2018) or their effect on abiotic stress mitigation (Csiszár et al., 2018; Mansori et al., 2015; Rao and Dixon, 2017); however, the available literature on the use of these compounds to reduce the negative impact generated by combined stresses (pathogens and abiotic stresses) in Andean fruit trees, such as cape gooseberry, is still scarce. The present research hypothesizes that foliar BR, SA, or BE sprays can help to mitigate the negative effects caused by these two stresses (Foph and waterlogging) by enhancing physiological (g_s , Ψ_{wf} , chlorophyll fluorescence parameters, and growth) and biochemical (proline, MDA, and photosynthetic pigments) responses in cape gooseberry plants.

Materials and Methods

Growth conditions and pathogen inoculation.

An experiment was carried out from Sept. 2018 to Jan. 2019 under greenhouse condi-

Fig. 1. Leaf wilting and vascular browning of cape gooseberry plants with and without *Fusarium oxysporum* f. sp. *physali* (Foph) inoculation under waterlogging conditions. Control plants (A), inoculated plants with waterlogging (B), inoculated plants without waterlogging (C), inoculated plants with waterlogging and botanicals extracts application (D), inoculated plants with waterlogging and salicylic acid application (E), and inoculated plants with waterlogging and brassinosteroids application (F).

Table 1. Area under the disease progress curve (AUDPC) and severity index of vascular wilt caused by *Fusarium oxysporum* f. sp. *physali* (Foph) in cape gooseberry plants under conditions of hypoxia in the soil and sprayed with synthetic elicitors [brassinosteroids (BR), salicylic acid (SA), or botanical extracts (BE) of *Echinacea purpurea*, *Potentilla erecta*, and *Aloe vera*] at 51 d after inoculation.

Treatment	AUDPC	Severity index of vascular wilt
No waterlogging + Foph	76.36 a ²	3.71 ab
Waterlogging + Foph	80.13 a	4.21 a
BR ³	45.73 c	2.82 d
SA	52.93 bc	3.02 cd
BE	68.15 ab	3.49 bc
Significance	***	***
cv (%)	12.68	8.71

²Values within a column followed by different letters are significantly different at $P \leq 0.05$ according to the Tukey test.

³Foph-inoculated cape gooseberry plants under waterlogging conditions and sprayed with three different synthetic elicitors (BR, SA, and BE of *E. purpurea*, *P. erecta*, and *A. vera*).

cv = coefficient of variation.

***Significant at $P \leq 0.001$.

tions at the Faculty of Agricultural Sciences of the Universidad Nacional de Colombia, Bogotá (lat. 4°35'56"N, long. 74°04'51"W, altitude 2557 m above sea level). The general environmental conditions during the experiment were as follows: natural photoperiod of 12 h (photosynthetically active radiation of 1500 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ at noon), $\approx 65\%$ relative humidity, 28.4/12.5 °C day/night temperature, and 20.5 °C average temperature. Two-month-old ecotype 'Colombia' (*P. peruviana* L.) seedlings purchased from a local nursery were used. To rule out *F. oxysporum* infection, the plants were previously indexed using the methodology described by Leslie and Summerell (2006). Then, seedlings were subjected to an acclimation period for 15 d. When plants developed between three and four true leaves, they were transplanted into 2-L plastic pots, containing a soil-based substrate (clay loam) and rice husk (3:1 v/v) with and without Foph inoculum. Before substrate inoculation, the methodology described by Park (1961) was used to confirm Foph absence in the soil used for the substrate mixture.

Substrate inoculation was performed by adding 100 mL of a liquid Foph suspension at a concentration of 1×10^6 microconidia/mL per 0.9 kg of substrate (soil + rice husk), guaranteeing a final concentration of 1×10^4 microconidia/g of substrate (Osorio-Guarín et al., 2016). Finally, two inoculation conditions were obtained (with and without Foph presence). The Foph-Map5 strain supplied by the Biological Control Laboratory of the Corporación Colombiana de Investigación Agropecuaria (Agrosavia, Mosquera, Colombia) was used as a source of pathogen inoculum in the present experiment. Young mycelium segments of the supplied strain were cultured in 50 mL potato dextrose broth (Difco, Becton Dickinson, Sparks, MD) in 250-mL Erlenmeyer flasks and incubated for 7 d with constant agitation in an orbital shaker (Laboratory-Line, Melrose Park, IL) at 125 rpm and 28 °C under dark conditions (Moreno-Velandia et al., 2019).

Seedlings were irrigated daily with 50 mL of a nutrient solution prepared from a complete liquid fertilizer (Nutriponic; Walco SA, Bogotá, Colombia) at a dose of 5 mL·L⁻¹ H₂O

Fig. 2. Effect of synthetic elicitor [brassinosteroids (BR), salicylic acid (SA), or botanical extracts (BE) of *Echinacea purpurea*, *Potentilla erecta*, and *Aloe vera*] sprays on the stomatal conductance (g_s) and water potential (Ψ_{wt}) of cape gooseberry plants at 11 (A, C) and 51 (B, D) days after inoculation (DAI) with (gray bars) and without (white bars) *Fusarium oxysporum* f. sp. *physali* (Foph) subjected to a short waterlogging period (6 d). Data represent the average of five plants $\pm$ SE per treatment (n = 5). Bars followed by different letters indicate statistically significant differences according to the Tukey test ($P \leq 0.05$).

from transplanting to the beginning of the waterlogging periods, and later from the end of the natural drainage to the end of the experiment. The concentration of the nutrient solution was as follows: 2.08 mM Ca (NO₃)₂·4 H₂O, 1.99 mM MgSO₄·7 H₂O, 2.00 mM NH₄H₂PO₄, 10.09 mM KNO₃, 46.26 mM H₃BO₃, 0.45 mM Na₂MoO₄·2 H₂O, 0.32 mM CuSO₄·5 H₂O, 9.19 mM MnCl₂·4 H₂O, 0.76 mM ZnSO₄·7 H₂O, and 19.75 mM FeSO₄·H₂O. The water volume used was obtained by daily quantification of the evapotranspiration needs of the plants by means of the gravimetric technique described by Hainaut et al. (2016).

Waterlogging and synthetic elicitor treatments. At the time of transplantation, two groups of 40 plants each were obtained: the first group consisted of seedlings planted in substrate with Foph (inoculated), and the second corresponded to seedlings planted in substrate without Foph (noninoculated). Then, the two groups were subjected to a waterlogging period of 6 consecutive d. The stress condition due to waterlogging was imposed by placing the seedlings inside 120-L plastic boxes, to which 60 L tap water was added to guarantee a 5-cm level on the base of the stem 5 d after inoculation (DAI). At the end of the

waterlogging period (11 DAI), the seedlings were removed from this condition and natural drainage was allowed until reaching the field capacity in the substrate (18 DAI). Afterward, the seedlings were maintained under normal irrigation conditions until the end of the experiment (51 DAI).

A group of 10 plants was selected to be sprayed with SA, BR, or BE (a commercial product based on *E. purpurea*, *P. erecta*, and *A. vera* extracts). The doses of each synthetic elicitor were 100 ppm, 1 ppm, and 2.5 mL of the commercial product per liter of H₂O, respectively. Eight different groups of treatments were obtained depending on Foph inoculation, waterlogging condition, and synthetic elicitor spray, which are summarized as follows: 1) waterlogged plants without Foph; 2) waterlogged plants with Foph; 3) waterlogged, noninoculated (Foph⁻) plants sprayed with BR, SA, or BE; and 4) waterlogged, inoculated (Foph⁺) plants sprayed with BR, SA, or BE. Likewise, two additional groups with and without Foph inoculation, without waterlogging, and without synthetic elicitors sprays were established as absolute control (Foph⁻) and pathogen control (Foph⁺). The general characteristics of the synthetic elicitors are presented as follows: SA (2-

Hydroxybenzoic acid; Panreac Applichem, Barcelona, Spain); Biomex DI-31 [(25 R) 3β,5α-dihydroxy-spirostan-6-one; Minerales exclusivos SA, Bogotá, Colombia]; Loker (*E. purpurea*, *P. erecta*, and *A. vera* extracts, K and Mg salts; Biolchim S. p. A., Medicina, Bologna, Italy).

Foliar synthetic elicitor applications were performed at three different times during the experiment: 1) foliar application 8 d before inoculation, 2) foliar application at the time of inoculation, and 3) foliar application 8 DAI. In general, each synthetic elicitor spray was carried out between 0700 and 0900 HR, using a 1.8-L manual spray pump (Royal Condor Garden, Soacha, Colombia) with an application volume of 20 mL H₂O per plant, wetting the upper and lower leaf surfaces. A coadjuvant [Tween 20 (Merck, Darmstadt, Germany)] was used at a rate of 0.02% (v/v) in all foliar applications. Control plants were sprayed with distilled water and the adjuvant at the same concentration. The length of the waterlogging period, number of foliar applications, and doses used for each elicitor were determined from previous studies (Chávez-Arias et al., 2019). A total of 10 treatment groups were obtained and

Fig. 3. Effect of synthetic elicitor [brassinosteroids (BR), salicylic acid (SA), or botanical extracts (BE) of *Echinacea purpurea*, *Potentilla erecta*, and *Aloe vera*] sprays on leaf area (LA) (A), total dry weight (TDW) (B), and stem diameter (SD) (C) of cape gooseberry plants with (gray bars) and without (white bars) *Fusarium oxysporum* f. sp. *physali* (Foph) subjected to a short waterlogging period (6 d) at 51 d after inoculation (DAI). Data represent the average of five plants $\pm$ SE per treatment (n = 5). Bars followed by different letters indicate statistically significant differences according to the Tukey test ($P \leq 0.05$).

arranged in a completely randomized design in which each treatment consisted of 10 plants (repetitions). Finally, the experiment lasted 74 d.

Analysis of vascular wilt severity. Vascular wilt severity was determined from the beginning of the waterlogging period (5 DAI) to the end of the experiment (51 DAI). Severity was estimated through visual assessments of the characteristic symptoms of the disease every 3 d. To perform the evaluation, the scale described by Moreno-Velandia (2017) was followed: 0) asymptomatic plants; 1) slight epinastic response and mild chlorosis of the lower third of the plant; 2) epinastic response in 30% to 50% of the leaves and moderate chlorosis in mature leaves; 3) epinastic response in 60% to 80% of the leaves and moderate chlorosis in the middle third; 4) epinastic response in all the leaves of the plant, severe chlorosis and defoliation; and 5) wilting, severe defoliation, and/or dead plant. The disease severity index can be used to indicate plant performance to compare treatment effectiveness (in this case, synthetic elicitor application) to reduce disease. The disease severity index

was calculated using Eq. [1], described by Chiang et al. (2017).

$$\text{Disease severity index} = \left(\frac{\sum(nv)}{V} \right), \quad [1]$$

where n is the level of infection according to the scale, v is the number of plants present in each level, and V is the total number of evaluated plants.

Afterward, disease intensity was analyzed by calculating the area under the disease progress curve (AUDPC), which is a useful quantitative summary of disease intensity over time, for comparison across management tactics (in this case, foliar application of synthetic elicitors). The AUDPC was estimated in each treatment by the trapezoidal integration method shown in Eq. [2] (Alves et al., 2017; Campbell and Madden, 1990):

$$\text{AUDPC} = \left\{ \sum_{i=1}^{n-1} [(y_i + y_{i+1})/2] * (t_{i+1} - t_i) \right\}, \quad [2]$$

where n is the number of evaluations, y_i and y_{i+1} are the values of the severity scale at

evaluation time, and $(t_{i+1} - t_i)$ is the time interval between evaluations.

Finally, pathogen presence or absence in Foph-inoculated and noninoculated plants was confirmed by isolates in potato dextrose agar (PDA) medium (Oxoid, Basingstoke, UK) from explants taken from the base of the stem at each evaluation time (11 and 51 DAI) (Leslie and Summerell, 2006).

g_s and Ψ_{wf} . g_s and Ψ_{wf} were estimated on the fourth fully expanded leaf from the upper portion of the canopy. A steady-state porometer (SC-1; Decagon Devices Inc., Pullman, WA) was used to estimate g_s . Then, Ψ_{wf} was measured with a Scholander pressure chamber (Model 615; PMS, Corvallis, OR) on the same leaf used to estimate g_s on completely sunny days at 11 and 51 DAI between 0900 and 1200 HR.

Chlorophyll fluorescence parameters. The same leaves used to estimate g_s were used for the measurement of maximum quantum yield of PSII (F_v/F_m), qP , NPQ, and ETR using a modulated fluorometer (MINI-PAM; Walz, Effeltrich, Germany). Before taking the measurements, leaves were adapted to darkness using the fluorometer's clips for 10

Fig. 4. Effect of synthetic elicitor [brassinosteroids (BR), salicylic acid (SA), or botanical extracts (BE) of *Echinacea purpurea*, *Potentilla erecta*, and *Aloe vera*] sprays on maximum photochemical efficiency of PSII (F_v/F_m) (A), electron transport rate (ETR) (B), photochemical quenching (qP) (C), and nonphotochemical quenching (NPQ) (D) of cape gooseberry plants with (gray bars) and without (white bars) *Fusarium oxysporum* f. sp. *physali* (Foph) subjected to a short waterlogging period (6 d) at 51 d after inoculation (DAI). Data represent the average of five plants $\pm$ SE per treatment ($n = 5$). Bars followed by different letters indicate statistically significant differences according to the Tukey test ($P \leq 0.05$).

min. Then, leaves received a pulse of actinic light of up to $2600 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ on their surface to obtain the fluorescence parameters. These measurements were also taken at 11 and 51 DAI.

Growth parameters. Leaves, stems, and roots of each plant per treatment were collected separately at 11 and 51 DAI and dried in a compressed dry air oven (Model 27; Thelco, Chicago, IL) at 80°C for 48 h to estimate their dry weight. The stem diameter for each treatment was estimated using a caliper and LA was obtained from digital images in TIFF (Tagged Image File Format) format using a digital camera (D3300; Nikon, Bangkok, Thailand). Images were analyzed using a Java image processing program (Image J; National Institute of Mental Health, Bethesda, MD). Based on the total dry weight (TDW) of the plants from all the treatments, the relative tolerance index (RTI) was estimated according to Eq. [3] (Dutta Gupta et al., 1995; Roussos et al., 2010).

$$\text{RTI} = \left(\frac{\text{Total biomass under the interaction Foph} \times \text{waterlogging}}{\text{Total biomass of plants without stress}} \right) \times 100 \quad [3]$$

Leaf photosynthetic pigments. The equations described by Wellburn (1994) were used to estimate total chlorophyll (TChl) and carotenoid (Cx+c) contents. Leaf samples of 30 mg from the middle third of the

canopy were collected and then homogenized in 3 mL of 80% acetone. Then, the samples were centrifuged (centrifuge model 420101; Becton Dickinson Primary Care Diagnostics, Sparks, MD) at 5000 rpm for 10 min to remove particles. The supernatant was diluted to a final volume of 6 mL by adding acetone (Sims and Gamon, 2002). Chlorophyll content was determined at 663 and 646 nm, and carotenoids were measured at 470 nm using a spectrophotometer (Spectronic BioMate 3 ultraviolet-vis; Thermo, Madison, WI).

Proline and MDA content. The method described by Bates et al. (1973) was used to estimate proline content in each evaluated treatment. Samples of 300 mg from leaves of the middle third of the canopy were homogenized in liquid nitrogen and stored for further analysis. Then, 10 mL of a 3% aqueous sulfosalicylic acid solution was added to the stored samples, which were filtered through Whatman paper (No. 2); 2 mL of this filtrate was reacted with 2 mL of ninhydrin acid and 2 mL of glacial acetic acid. The mixture was placed in a water bath at 90°C for 1 h, and the reaction was stopped by incubation in ice. The resulting solution was dissolved in 4 mL toluene, and test tubes were shaken using a vortex shaker (V-1; BOECO, Hamburg, Germany). Finally, the absorbance readings were

determined at 520 nm with the spectrophotometer. Proline content was calculated using the fresh weight of the sample with a standard calibration curve, as in Eq. [4].

$$\frac{\mu\text{mol Proline}}{\text{fresh vegetal material}} = \frac{\left(\frac{\mu\text{g Proline}}{\text{mL}} \times \text{mL Toluene} \right)}{\left[\frac{115.5 \mu\text{g}}{\mu\text{mol}} \right] \left[\frac{\text{g sample}}{5} \right]} \quad [4]$$

The thiobarbituric acid method described by Hodges et al. (1999) was used to estimate membrane lipid peroxidation (MDA). Leaf samples of 300 mg from the middle third of the canopy of plants from the different treatments were macerated and stored in liquid nitrogen. Samples were centrifuged at 5000 rpm for 10 min and their absorbances were estimated at 440, 532, and 600 nm with the spectrophotometer. Finally, an extinction coefficient ($157 \text{ M}\cdot\text{mL}^{-1}$) was used to obtain the MDA concentration. Proline and MDA were measured at 51 DAI.

Experimental design and data analysis. Data were analyzed by a factorial arrangement with inoculation with the pathogen (with and without Foph) as the first factor, and synthetic elicitors (SA, BR, or BE) as the second factor. Each treatment group consisted of 10 plants. A principal components analysis was performed using the InfoStat

Fig. 5. Effect of synthetic elicitor [brassinosteroids (BR), salicylic acid (SA), or botanical extracts (BE) of *Echinacea purpurea*, *Potentilla erecta*, and *Aloe vera*] sprays on total chlorophyll content (TChl) (A), carotenoids (Cx+c) (B), malondialdehyde production (MDA) (C), and leaf proline content (D) of cape gooseberry plants with (gray bars) and without (white bars) *Fusarium oxysporum* f. sp. *physali* (Foph) subjected to a short waterlogging period (6 d) at 51 d after inoculation (DAI). Data represent the average of five plants $\pm$ SE per treatment (n = 5). Bars followed by different letters indicate statistically significant differences according to the Tukey test ($P \leq 0.05$). FW = fresh weight.

2016 program (analytical software; Universidad Nacional de Córdoba, Córdoba, Argentina) to select the best synthetic elicitors under the interaction between waterlogging and *F. oxysporum* f. sp. *physali* (Foph) inoculation. Then, the selected treatments were compared with the absolute control (Foph⁻) and pathogen control (Foph⁺) through a completely randomized analysis. An analysis of variance was performed in all cases, and when significant differences ($P \leq 0.05$) were found, a Tukey post hoc test was used for means comparison. The percentage values were transformed using the arcsine function. Data were analyzed using the Statistix v 9.0 software (Analytical Software, Tallahassee, FL). The figures and cluster analysis were carried out using the software SigmaPlot (version 12.0; Systat Software, San Jose, CA).

Results

Vascular wilt severity expressed as AUDPC and disease index. The evaluation of the AUDPC and vascular wilt index showed differences at $P \leq 0.001$ between plants of all Foph-inoculated treatments at 51 DAI. Foph presence was confirmed by isolates in PDA from affected material (Fig. 1). The pathogen was not isolated from plants without inoculation, without any synthetic elicitor

sprays, without any stress, or from plants with only waterlogging (Fig. 1A).

The highest AUDPC values were obtained in inoculated plants with and without waterlogging, and with no synthetic elicitor sprays (80.13 and 76.36, respectively) at the end of the experiment (51 DAI), which may show a higher vascular wilt progress (Table 1; Fig. 1B and C). An intermediate development of the disease was observed in plants with Foph, under waterlogging, and sprayed with BE (68.15), whereas plants with exogenous SA (52.93) and BR (45.73) applications showed the lowest levels of the disease (Table 1; Fig. 1D–F). Trends similar to those obtained in the AUDPC were observed on the vascular wilt index (Table 1).

g_s and Ψ_{wf} . Differences were also found on g_s in the interaction between Foph inoculation and synthetic elicitors at 11 ($P = 0.0002$) and 51 DAI ($P = 0.0000$) in plants under waterlogging conditions. In general, Foph presence caused a greater g_s reduction in both sampling points. At 11 DAI, foliar sprays, mainly with BR or SA, obtained the highest g_s values (208.9 and 194.3 mmol·m⁻²·s⁻¹, respectively) under waterlogging conditions in nondiseased plants. On the other hand, it was observed that SA sprays favored a higher g_s (116.8 mmol·m⁻²·s⁻¹) only in Foph-inoculated cape gooseberry plants and subjected to hypoxia in the soil (Fig. 2A). At 51

DAI, the plants without pathogen presence continued recording the highest g_s values. In these plants, foliar BR sprays increased this variable under oxygen deficit in the soil (241.7 mmol·m⁻²·s⁻¹). A positive effect on g_s was evidenced when the inoculated plants were treated with BR, SA, or BE (≈132.9 mmol·m⁻²·s⁻¹) compared with diseased plants, with no synthetic elicitor sprays and under waterlogging conditions (79.2 mmol·m⁻²·s⁻¹) (Fig. 2B). Differences between the evaluated factors (presence of the pathogen and synthetic elicitors) were also recorded on Ψ_{wf} at 11 and 51 DAI ($P = 0.0328$ and 0.0000, respectively) in waterlogged cape gooseberry plants. Foph presence in waterlogged cape gooseberry plants generated more negative Ψ_{wf} values at both sampling moments. At 11 DAI, SA or BR sprays favored the water status of non-inoculated plants through a higher Ψ_{wf} under hypoxia conditions (≈-0.53 Mpa) (Fig. 2C).

On the other hand, foliar BR, SA, or BE sprays had a positive effect on Ψ_{wf} (≈-0.74 Mpa) in Foph-inoculated cape gooseberry plants and subjected to hypoxia conditions in the soil (Fig. 2C). At 51 DAI, noninoculated plants and with BR sprays showed a slight increase in Ψ_{wf} values (-0.22 Mpa) under waterlogging conditions. Likewise, foliar BR, SA, or BE sprays under oxygen deficiency in the soil caused an increase of Ψ_{wf} in Foph-inoculated plants (≈-0.48 Mpa)

Fig. 6. Effect of the interaction between *Fusarium oxysporum* f. sp. *physali* (Foph) inoculation and synthetic elicitor [brassinosteroids (BR), salicylic acid (SA), or botanical extracts (BE) of *Echinacea purpurea*, *Potentilla erecta*, and *Aloe vera*] sprays on the biplot analysis (A) and dendrogram using Euclidean distance (B) of cape gooseberry plants subjected to a short waterlogging period (6 d) at 51 d after inoculation (DAI). TA = noninoculated plants without any synthetic elicitor spray; TP = Foph-inoculated plants without any synthetic elicitor spray; An = plants subjected to a short waterlogging period (6 d); BR = plants with three foliar brassinosteroid applications; SA = plants with three foliar salicylic acid applications; BE = plants with three foliar botanical extract applications; DWT = dry weight total; LA = leaf area; SD = stem diameter; Pr = proline; TChl = total chlorophyll; Cx = carotenoids; MDA = malondialdehyde; qP = photochemical quenching; NPQ = nonphotochemical quenching; F_v/F_m = photochemical efficiency of PSII; ETR = electron transport rate; g_s = stomatal conductance; Ψ_{wf} = leaf water potential; PC = principal component.

compared with diseased and untreated plants (-0.71 Mpa) (Fig. 2D).

Plant growth variables. Growth parameters (LA, TDW, and stem diameter) of cape gooseberry plants subjected to hypoxia showed differences ($P = 0.0002$, 0.0000 , and 0.0164 , respectively) in the interaction between Foph presence and synthetic elicitors at 51 DAI. In general, the group of plants without Foph showed the highest growth parameters compared with inoculated plants under waterlogging conditions (Fig. 3). Foliar BR, SA, or BE sprays favored LA in Foph-inoculated plants (BR 260.1 cm², SA 238.8 cm², and BE 204.4 cm²) under waterlogging conditions. In addition, foliar BR and SA sprays enhanced the same variable in noninoculated (BR 413.2 cm² and SA 373.3 cm²) plants under soil oxygen deficiency (Fig. 3A). The TDW of cape gooseberry

plants subjected to hypoxia in the soil was mainly favored in the treatment with BR sprays in both situations of pathogen inoculation (with and without Foph) (4.93 and 6.52 g, respectively). However, SA and BE favored this variable in inoculated cape gooseberry plants under hypoxia (Fig. 3B). Finally, foliar BR, SA, or BE sprays also produced an increase in stem diameter values in plants with and without Foph presence under the condition of oxygen deficit in the soil (Fig. 3C).

Chlorophyll *a* fluorescence parameters. Significant differences were observed between Foph inoculation and synthetic elicitor sprays on the chlorophyll *a* fluorescence parameters (F_v/F_m , ETR, qP, and NPQ) of cape gooseberry plants under waterlogging conditions at 51 DAI. Foph inoculation caused lower values of the F_v/F_m ratio,

ETR, and qP of cape gooseberry plants under waterlogging conditions; however, an opposite trend was obtained with NPQ for these same plants (Fig. 4). BR, SA, or BE sprays showed two effects on the fluorescence parameters in cape gooseberry plants with waterlogging and without Foph. In the first case, the use of synthetic elicitors did not cause any differences on F_v/F_m and qP (Fig. 4A and C); in the second case, the application of these elicitors generated higher ETR (≈ 10.9) and lower NPQ (≈ 1.38) values (Fig. 4B and D). On the other hand, Foph-inoculated plants under waterlogging showed an increase in the parameters F_v/F_m (≈ 0.62), ETR (≈ 7.71), and qP (≈ 0.47) after the foliar treatment with BR, SA, or BE compared with inoculated plants subjected to waterlogging and without any elicitor application (0.37 , 5.87 , and 0.27 for F_v/F_m , ETR, and qP,

Table 2. Comparative analysis of vascular wilt and hypoxia in the soil mitigation in cape gooseberry plants by synthetic elicitor [brassinosteroids (BR), salicylic acid (SA), or botanical extracts (BE) of *Echinacea purpurea*, *Potentilla erecta*, and *Aloe vera*] sprays on stomatal conductance (g_s), leaf water potential (Ψ_{wf}), total dry weight (TDW), leaf area (LA), stem diameter (SD), total chlorophyll (TChl), carotenoids (Cx+c), maximum PSII efficiency (F_v/F_m), electron transport rate (ETR), MDA production, and leaf proline content at 51 d after inoculation (DAI).

Treatment	g_s (mmol·m ⁻² ·s ⁻¹)	Ψ_{wf} (Mpa)	TDW (g)	LA (cm ²)	SD (mm)	TChl (µg·mg ⁻¹ FW)	Cx+c (µg·mg ⁻¹ FW)	F_v/F_m	ETR	MDA (µmol·g ⁻¹ FW)	Proline (µmol·g ⁻¹ FW)
Plants + BR + Foph + W	135.5 c ^z	0.48 c	4.93 c	260.1 c	88.7 b	1275.5 b	353.3 b	0.64 b	8.31 c	12.6 d	13.6 c
Plants + SA + Foph + W	129.3 c	0.49 c	4.59 d	238.9 cd	85.1 b	1142.9 c	324.4 bc	0.62 b	7.92 cd	13.1 cd	13.2 c
Plants + BE + Foph + W	133.7 c	0.47 c	4.23 e	204.4 e	86.8 b	1174.5 c	329.7 bc	0.61 b	7.02 d	13.9 bc	13.8 c
Plants + Foph + W	79.27 e	0.71 e	3.55 f	151.8 f	60.1 d	626.2 e	160.1 e	0.37 c	5.86 e	18.5 a	9.62 d
Plants + W	105.9 d	0.61 d	4.44 de	211.1 de	71.2 c	727.6 d	301.9 cd	0.43 c	7.17 d	14.4 b	7.12 e
Plants without stress	198.6 b	0.31 b	6.14 b	310.3 b	115 a	1368.9 b	566.4 a	0.78 a	10.1 b	12.7 cd	18.45 a
Significance (P)	320.3 a	0.19 a	6.82 a	508.4 a	86.2 b	1944.1 a	0.0000	0.0000	14.6 a	7.71 e	15.82 b
CV (%)	0.0000	8.86	2.62	5.31	4.98	3.46	3.89	5.5	0.0000	0.0000	0.0000
	3.66								4.7	3.85	4.25

^zValues within a column followed by different letters are significantly different at $P \leq 0.05$ according to the Tukey test.

CV = coefficient of variation; FW = fresh weight; W = waterlogging.

respectively) (Fig. 4A–C). In contrast, a decrease in NPQ values was registered with the use of synthetic elicitors (≈ 1.58) compared with diseased, waterlogged, and untreated plants (2.03) (Fig. 4D).

Leaf photosynthetic pigments. Figure 5 shows the content of leaf photosynthetic pigments (TChl and Cx+c). Differences ($P = 0.0000$) were found in the photosynthetic pigment content between the evaluated factors (Foph presence $\times$ synthetic elicitors) at the end of the experiment (51 DAI). In general, the content of TChl and Cx+c was lower in Foph-inoculated plants compared with noninoculated plants under waterlogging conditions. BR, SA, or EB sprays generated an increase in the photosynthetic pigment concentration (TChl and Cx+c) in cape gooseberry plants subjected to a waterlogging period for both inoculation conditions (with and without Foph) (Fig. 5A and B).

MDA production and leaf proline content. Significant differences were observed between Foph inoculation and synthetic elicitor sprays on MDA production ($P = 0.0000$) and leaf proline content ($P = 0.0008$) of cape gooseberry plants under waterlogging conditions at 51 DAI. Regarding these biochemical variables, opposite effects were observed in waterlogged cape gooseberry plants under both inoculation conditions (with and without Foph). A reduction of lipid peroxidation (MDA) was obtained with the application of elicitors (BR, SA, or BE), whereas a higher proline production was recorded under the foliar sprays of these inducers (Fig. 5C and D).

Biplot analysis of physiological and biochemical responses to Foph management with synthetic elicitors under waterlogging conditions. The principal component analysis showed that the evaluated variables explained 96.6% of the physiological response of cape gooseberry plants infected with Foph, subjected to waterlogging, and treated with synthetic elicitors at 51 DAI. Figure 6A shows the evaluated variables represented by vectors and the plants of the different treatments identified with points. The vectors generated for the variables g_s , Ψ_{wf} , TDW, LA, stem diameter, F_v/F_m , ETR, qP, TChl, Cx+c, and proline present angles close to the origin, showing that there is a high correlation between these variables and the plant physiological behavior. It was observed that Foph-inoculated plants without the application of elicitors under waterlogging conditions (plants + Foph + W) form a single group (I). It can be inferred that this group presented the greatest effects due to the evaluated interaction of biotic and abiotic stresses. In contrast, noninoculated plants, subjected to a short waterlogging period (6 d) and with and without BR, SA, or BE sprays (group III), were located in the sector opposite to group I, observing a positive effect of the treatments on plant physiology. On the other hand, plants with Foph under waterlogging and sprayed with the synthetic elicitors (BR, SA, or BE) showed an intermediate

behavior (group II), evidencing a positive effect of the treatments with elicitors on the mitigation of the interaction between the two stresses (Foph + waterlogging). This analysis is corroborated by the cluster analysis, with the dendrogram reflecting a lower Euclidean distance between waterlogged plants with and without Foph inoculation and synthetic elicitor sprays (BR, SA, or BE). This group of plants is notably farther from the plants inoculated with the pathogen and without synthetic elicitor sprays under waterlogging conditions (Fig. 6B).

Comparative analysis of vascular wilt and waterlogging mitigation by synthetic elicitor sprays. Table 2 shows the effect of foliar BR, SA, or BE sprays on Foph-inoculated cape gooseberry plants under waterlogging conditions (plants + W + Foph), Foph-inoculated plants without the waterlogging condition (plants + Foph), plants without Foph inoculation under waterlogging conditions (plants + W), and noninoculated plants without waterlogging and without elicitor sprays (plants without stress) at 51 DAI. These results demonstrated that three foliar BR, SA, or BE sprays helped plants to cope with the combined condition of vascular wilt and waterlogging, because a positive stimulus of these elicitors was observed on physiological and biochemical variables, such as g_s , Ψ_{wf} , TDW, LA, TChl, Cx+c, F_v/F_m , ETR, MDA, and proline. In addition, the RTI based on the TDW corroborated that the foliar applications with BR, SA, or BE help to tolerate the double-stress condition in cape gooseberry plants, observing an RTI between 61.3% and 71.4% compared with the RTI of 51.3% observed in plants subjected to the two stress conditions (Foph and waterlogging) (Fig. 7).

Discussion

The results obtained in this research confirmed previous observations in which BR, SA, or BE reduces Foph severity under oxygen deficit in the soil. BR, SA, or BE caused a decrease in the development of vascular wilt caused by *F. oxysporum*, which also has been documented in cucumber, tomato, and pepper, respectively (Ding et al., 2009b; Poussio et al., 2018; Yousif, 2018). BR decreases vascular wilt severity because it can participate in several physiological processes that activate the defense system (Anwar et al., 2018; Peres et al., 2019). This synthetic elicitor can also be involved in the expression of pathogenesis-related proteins, which lead to an increase in the resistance to pathogens (Ding et al., 2009b; Filek et al., 2018; Saini et al., 2015). In addition, SA can contribute to the regulation of defense against biotrophic and hemibiotrophic pathogens; it plays a key role in the systemic acquired resistance of plants, the modulation of the hypersensitivity response associated with programmed cell death, the increase in the levels of reactive oxygen species, and the activation of lipid peroxidation (Bernsdorff et al., 2016; Dempsey and Klessig, 2017; Qi et al., 2018). Finally,

Fig. 7. Effect of synthetic elicitor [brassinosteroids (BR), salicylic acid (SA), or botanical extracts (BE) of *Echinacea purpurea*, *Potentilla erecta*, and *Aloe vera*] sprays on the relative tolerance index (RTI) of cape gooseberry plants with and without *Fusarium oxysporum* f. sp. *physali* (Foph) subjected to a short period of waterlogging (W) (6 d) at 51 d after inoculation (DAI). Data represent the average of five plants $\pm$ SE per treatment (n = 5). Bars followed by different letters indicate statistically significant differences according to the Tukey test ($P \leq 0.05$).

different BEs are constituted by aromatic hydrocarbons, such as phenylpropanoids, which are involved in various disease-resistance responses through secondary metabolite synthesis (Li et al., 2017). In this sense, commercial products based on different BEs also are rich in polysaccharides and amino acids that can induce plant defense (Jayaraman et al., 2011; Shifa et al., 2018).

Foliar synthetic elicitors sprays favored physiological and biochemical parameters, especially in cape gooseberry plants affected by hypoxia conditions in the soil. In the present study, three foliar BR, SA, or BE sprays had a positive effect mainly on the variables g_s , Ψ_{wf} , growth, photosynthetic pigments, MDA, and proline. It has been reported that exogenous BR sprays at low concentrations ($1 \text{ mg} \cdot \text{L}^{-1}$) can help the osmotic adjustment and induce stomatal opening. These responses improve leaf gas exchange properties, plant water status, photosynthetic pigment contents, and photochemical activity of PSII, which favor plant growth under waterlogging stress conditions (Kang et al., 2017; Li et al., 2015a; Lima and Lobato, 2017; Xia et al., 2014). Likewise, the positive effects of SA on the physiological behavior of plants under waterlogging stress conditions may be because this hormone plays an important role in the leaf's stomatal opening and closing, the synthesis of photosynthetic pigments, the stability of membrane

integrity, and the increase in the activity of antioxidant enzymes (Bai et al., 2009; Hara et al., 2012; Singh et al., 2017). Finally, BE can help to modulate the metabolism of phytohormones such as SA or jasmonic acid, and improve water and nutrient uptake, the activity of antioxidant enzymes, photosynthesis, gene expression, g_s , dry matter distribution, and water relations in plants subjected to abiotic stress (Bogatek and Gniazdowska, 2007; Farooq et al., 2017; Jabran and Farooq, 2013).

Abiotic stress can negatively or positively influence the development of a disease depending on the type of pathogen, the time of infection, and the intensity of the abiotic stress (Chojak-Koźniewska et al., 2018; Pandey et al., 2017; Suzuki et al., 2014). Similarly, the use of synthetic elicitors can help the plant to stimulate physiological responses that mitigate the negative effects of both abiotic and biotic stress conditions (Naik and Al-Khayri, 2016; Thakur and Sohal, 2013). In the present study, foliar BR, SA, or BE sprays showed interesting results on the tolerance of cape gooseberry plants to conditions of combined stresses (Foph + waterlogging). Xia et al. (2009) observed that exogenous BR applications generated tolerance to the combination of cold stress and infection of cucumber mosaic virus in cucumber (*Cucumis sativus* L.). This tolerance was achieved through the transcriptional induction of genes involved in defense,

the increase of chlorophyll fluorescence parameters (F_v/F_m and ETR) and the activity of antioxidant enzymes. Under stress conditions, BR can regulate physiological processes, such as the reduction of electrolyte leakage and MDA content. Furthermore, this synthetic elicitor also can increase proline accumulation, soluble sugars, total phenolic and glutathione contents, and antioxidant machinery activation (Anwar et al., 2018; Nawaz et al., 2017; Vardhini and Anjum, 2015). The preceding explains the positive effect of BR, which is superior at conferring tolerance to the two stress conditions (Foph and waterlogging) compared with the other elicitors evaluated in cape gooseberry plants.

SA is a plant hormone that is involved in the activation of plant defense responses against a wide range of abiotic and biotic stresses (Cekic, 2017; Fragnière et al., 2011; Hernández-Ruiz and Arnao, 2018). Studies by Mann et al. (2011) showed that foliar SA applications mitigated the negative effect of the combination of thermal stress and Huanglongbing presence in citrus fruits (*Citrus sinensis* L.). The evaluated variables (g_s , Ψ_{wf} , growth, fluorescence parameters, MDA, and proline content) were favored after SA sprays in cape gooseberry plants under the combined stress condition (Foph and waterlogging) in the present experiment. This may be because SA is related to the activation of cell division in the meristems and the improvement of the photosynthetic rate, carboxylase activity of the Rubisco enzyme, and membrane stability. In addition, this synthetic elicitor also increases phenols, chlorophyll, carbohydrates, and proline contents, and promotes the activity of antioxidant enzymes (Asgharei, 2015; Hayat et al., 2010; Khoshbakht and Su et al., 2018).

The use of BE can be considered a promising strategy to help the plant under conditions of abiotic and biotic stress (Ben Salah et al., 2018; Santaniello et al., 2017; Shukla et al., 2017). Maymoune et al. (2015) observed that the application of BE of green algae (*Ulva* sp.) decreased the necrosis diameter, inhibited spore germination, and increased protection efficacy in tomato plants (*Solanum lycopersicum* L.) infected with *Botrytis cinerea* under water stress conditions. Although BR and SA sprays showed better results than those obtained with BE from plants of *E. purpurea*, *P. erecta*, and *A. vera*, these extracts also favored the physiological response of Foph-inoculated cape gooseberry plants under hypoxia conditions in the soil. This positive effect of BE can be because these compounds stimulate plant growth and development, improve water and nutrient uptake efficiency, regulate stomatal dynamics, and increase the ascorbate content and the antioxidant enzyme activity (Carvalho et al., 2018; Guinan et al., 2012; Howladar, 2014; Shukla et al., 2017).

Conclusion

This study showed that sprays of synthetic elicitors, such as BR, SA, or BE,

reduced vascular wilt severity by improving the physiological and biochemical response of Foph-infected cape gooseberry plants under hypoxia conditions in the soil. Likewise, it was observed that the use of these elicitors has positive effects on plant physiology, favoring g_s , Ψ_{wf} growth (expressed as dry matter accumulation and LA), photochemical efficiency of PSII, ETR, qP, TChl, and proline content. Synthetic elicitor sprays also showed a significant reduction of NPQ and lipid peroxidation of membranes under a combination of stress conditions (Foph + waterlogging); however, additional research is needed on topics such as gene expression as a product of these synthetic elicitor sprays. In addition, field trials are suggested to evaluate the effect of BR, SA, or BE on crop yield and fruit quality parameters under the interaction of these two stresses (Foph and waterlogging). The obtained results suggest that BR, SA, or EB sprays in cape gooseberry plants could be considered as an alternative for the integrated management of vascular wilt in cape gooseberry-producing areas where waterlogging episodes could be expected.

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