

Original Article

Response of Chinese potato (*Colocasia esculenta*, Araceae) to abiotic and biotic stress, and the effectiveness of treatment with the fungus *Trichoderma harzianum*

Resposta da batata chinesa (*Colocasia esculenta*, Araceae) aos estresses abiótico e biótico, e a eficácia do tratamento com o fungo *Trichoderma harzianum*

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Abstract

Climate change intensifies drought, which increases susceptibility to phytopathogens in several crops such as the Chinese potato (*Colocasia esculenta*). This species is cultivated in tropical areas mainly for the production of corms, which are affected by *Fusarium oxysporum* dry rot. Phytopathology treated with toxic chemicals, which highlights the biocontroller *Trichoderma harzianum*, which also helps reduce the effects related to drought in other crops. Therefore, the objective was to characterize the response of *C. esculenta* to drought and infection by *F. oxysporum*, and the effectiveness of treatment with *T. harzianum*. Greenhouse tests were carried out with three factors (*F. oxysporum*, *T. harzianum* and drought), each with two levels (presence and absence) (N=48). Plant growth was evaluated for 30 days, in addition to the relative chlorophyll content, maximum efficiency of photosystem II, water content (WC%), incidence and severity. It was obtained that abiotic and biotic stress decreases growth. Drought lowered photosynthetic efficiency, and both stressors reduced chlorophyll in plants not treated with *T. harzianum*. Stress decreased leaf and corm WC%, but this effect was reduced by the biocontroller. This fungus reduced the incidence of *F. oxysporum*, and the severity of foliar symptoms for both types of stress. In conclusion, abiotic and biotic stress differentially impacts *C. esculenta*, and *T. harzianum* tends to improve growth under stress. However, more studies are required to evaluate its benefit on productivity. This work is one of the first to describe the stress response of this crop, and highlights its importance for future technification plans.

Keywords: biocontrol, drought, *Fusarium oxysporum*, water stress.

Resumo

As mudanças climáticas intensificam a seca, o que aumenta a suscetibilidade a fitopatógenos em várias culturas, como a batata chinesa (*Colocasia esculenta*). Essa espécie é cultivada em áreas tropicais principalmente para a produção de cormos, que são afetados pela podridão seca causada por *Fusarium oxysporum*. Essa fitopatologia é tratada com produtos químicos tóxicos e biologicamente, em que se destaca o biocontrolador *Trichoderma harzianum*, que também ajuda a reduzir os efeitos relacionados à seca em outras culturas. Portanto, o objetivo foi caracterizar a resposta da *C. esculenta* à seca e à infecção por *F. oxysporum*, e a efetividade do tratamento com *T. harzianum*. Foram realizados testes em estufa com três fatores (*F. oxysporum*, *T. harzianum* e seca), cada um com dois níveis (presença e ausência) (N=48). O crescimento da planta foi avaliado por 30 dias, além do conteúdo relativo de clorofila, da eficiência máxima do fotossistema II, do conteúdo de água (WC%) e da incidência e da severidade da referida fitopatologia. Foram obtidos os seguintes resultados: os estresses abiótico e biótico diminuíram o crescimento; a seca reduziu a eficiência fotossintética, e ambos os estressores reduziram a clorofila nas plantas não tratadas com *T. harzianum*; o estresse diminuiu a WC% das folhas e dos cormos, mas esse efeito foi reduzido pelo biocontrolador. Esse fungo reduziu a incidência de *F. oxysporum* e a gravidade dos sintomas foliares em ambos os tipos de estresse. Em conclusão, os estresses abiótico e biótico afetam diferentemente a *C. esculenta*, e o *T. harzianum* tende a melhorar o crescimento sob estresse. No entanto, são necessários mais estudos para avaliar seu benefício sobre a produtividade. Este trabalho é um dos primeiros a descrever a resposta ao estresse dessa cultura e destaca sua importância para futuros planos de tecnificação.

Palavras-chave: biocontrole, secas, *Fusarium oxysporum*, estresse hídrico.

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1. Introduction

Climate change generates different types of stress on crops and weakens plant defense mechanisms, which increases colonization by phytopathogens and affects food security (Ramegowda and Senthil-Kumar, 2015; Singh et al., 2023a). In addition, anthropogenic alteration of seasonal patterns has resulted in decreased rainfall in tropical and subtropical regions, causing water deficit that affects agricultural production (Seleiman et al., 2021; Vashi et al., 2020). Water stress resulting from drought leads to a detriment in plant development, as it limits photosynthesis (Mansoor et al., 2022; Sun et al., 2020). In addition, drought increases the colonization, proliferation, and propagation of phytopathogens (Irulappan et al., 2022; Pandey et al., 2017).

On the other hand, globalization has relegated tropical crops such as the Chinese potato (*Colocasia esculenta* (L.) Schott, family Araceae) from the market (Aditika et al., 2022). This species is cultivated mainly in the humid zones of the Pacific region for the production of corms, but it lacks technification (Ararat Orozco et al., 2014; Lasso Rivas, 2020). Despite this, this crop is of great importance for the food security of the communities that plant it, since it cushions food gaps due to the lack of other crops (Kaushal et al., 2015; Mulualem et al., 2013). However, the production of this species is affected by dry rot of the corm, which causes losses of up to 80% of the harvested product (Folgueras Montiel et al., 2015; Widodo and Supramana, 2011; Ye et al., 2023). This phytopathology arises as a result of infection by soil-borne fungi such as *Fusarium oxysporum* Schltdl (Bora et al., 2020; Folgueras Montiel et al., 2015; Sireli et al., 2023). This fungus enters the plant through roots or wounds in the corm, where it colonizes the xylem and blocks the vascular system (Houterman et al., 2007; Palmero et al., 2014; Visser et al., 2004).

Moreover, chemical control has traditionally been used to treat *F. oxysporum* infection, which is toxic, irritant, teratogenic, carcinogenic and generates resistance (Chacón et al., 2021; Hu and Chen, 2021). This has boosted biocontrol, being sustainable, environmentally safe, economically viable and highly specific (Pandit et al., 2022; He et al., 2021; Houterman et al., 2007; Lahlali et al., 2022; Visser et al., 2004). As an effective biological control of *F. oxysporum* for certain

crops, several fungal species of the genus *Trichoderma* have been reported, such as *T. harzianum* Rifai (Chen et al., 2019, 2021). In addition, studies indicate that this biocontroller improves plant response to drought (Chepsergon et al., 2018; Shukla et al., 2014; Singh et al., 2023b).

The lack of commercial interest in the cultivation of *C. esculenta* has generated a low level of technification and a scarcity of studies on the response of this species to extreme conditions and phytopathogens (abiotic and biotic stresses). Similarly, there is a lack of research addressing the effectiveness of *T. harzianum* in the stress response of this crop. This gap in information negatively impacts the productivity of the Chinese potato crop, which puts at risk the food security of the indigenous and Afro-descendant rural communities of the Colombian Pacific, who depend on this crop as their main source of food. Therefore, the objective of this study was to characterize the response of *C. esculenta* to abiotic stress due to drought and biotic stress due to infection by *F. oxysporum*, and the effectiveness of treatment with *T. harzianum* as a protector against water stress and biocontroller of *F. oxysporum*.

2. Material and Methods

2.1. Cultivation

48 corms of *C. esculenta* were planted in 1 kg bags with solarized substrate for 15 days. The plants were grown under greenhouse conditions at an average relative humidity of 87% and at a temperature between 25 and 34 °C. Three weeks before the beginning of the experiment, pruning was carried out to homogenize their growth.

2.2. Mounting of the experiment

An experimental design with three factors, *F. oxysporum*, *T. harzianum* and drought, was used. A total of eight treatments were established (see Table 1), each with six plants (repetitions). Inoculation of *F. oxysporum* was carried out from two phytopathogenic strains for *C. esculenta*, OCATI and Uchuva, provided by the Microbiological Research Laboratory of the Universidad del Valle. Adapted from the

Table 1. Experimental conditions for three factors, *F. oxysporum*, *T. harzianum* and drought, each with two levels, presence or absence. Irrigations were every three days with 500 mL of water and treatments that did not include *F. oxysporum* were inoculated with sterile distilled water.

Treatment	Experimental condition	Abbreviation
T1	Inoculation with <i>F. oxysporum</i> and irrigation	F
T2	Inoculation with <i>F. oxysporum</i> and drought (water stress)	FW
T3	Substrate inoculation with <i>T. harzianum</i> and irrigation	T
T4	Substrate inoculation with <i>T. harzianum</i> and drought (water stress)	TW
T5	Inoculation with <i>F. oxysporum</i> , substrate inoculation with <i>T. harzianum</i> and irrigation	FT
T6	Inoculation with <i>F. oxysporum</i> , substrate inoculation with <i>T. harzianum</i> and drought (water stress)	FTW
T7	Drought (water stress)	W
Control (T8)	Irrigation	C

methodology presented by Jarek et al. (2018), the corm of each plant was perforated 2 cm and 3 mL of conidia suspension of each strain (10^7 conidia mL⁻¹) were added. Plants that were not infected were inoculated with sterile distilled water. For inoculation with *T. harzianum*, 500 mL of a commercial spore suspension (2×10^5 conidia mL⁻¹) was added directly to the soil. Plants under irrigation were watered with 500 mL of water every two days, while plants in drought were only irrigated at time zero.

2.3. Data collection

Seven samples were taken at 0, 3, 7, 11, 18, 25 and 30 days after inoculation (dai). The greenhouse experiment had a duration of 30 days. For morphological characterization, the differential with respect to time zero of height, corm diameter and leaf area of the largest leaf (using ImageJ 1.53a) was evaluated. To measure the diameter of the stem (from the widest part), the corm was carefully dug out without altering the position of the plant. After the measurement, the corm was covered again with the same substrate. For physiological parameters, the relative amount of chlorophyll was monitored using a SPAD-502 Minolta chlorophyll meter (with three technical replicates), and the maximum photosystem II (PSII) efficiency (Fv/Fm) with an OS30p+ Opti-Sciences fluorometer (with 30 min prior darkening and saturation at 3000 μmols for one second). Both measurements were carried out on a non-wilted part of a fully extended leaf within the time window from 12m to 2pm.

On the other hand, the incidence and severity of *F. oxysporum* infection was quantified during the seven experimental times using a foliar symptomatology scale (see Table 2). The corm symptomatology was evaluated only at the end of the experiment, three corms per treatment were cut longitudinally and the severity of *F. oxysporum* was cataloged (see Table 2). In addition, the presence of drought-related leaf wilt symptoms was also quantified (see Table 2).

2.4. Post-harvest decomposition test

At the end of the greenhouse evaluations (30 dai), three corms per treatment were stored for two weeks under

traditional storage conditions. The corms were stored in open bags in a dark place with substrate residues. Subsequently, longitudinal cuts were made from each of these and the symptomatology of *F. oxysporum* was quantified (see Table 2).

2.5. Water content (WC%)

At 30 dai, each plant was separated by organs (root, stem, and leaves), which were weighed on a WTC 200 Radweg precision balance to obtain fresh weight (Wf) and dried in a DiEs TH720 oven at 65 °C to constant weight to obtain dry weight (Wd). Water content in percentage was calculated using the ratio (Equation 1; Jin et al., 2017):

$$WC\% = [(Wf - Wd) / (Wf)] \times 100 \tag{1}$$

2.6. Confirmation of the presence of *F. oxysporum* in the corms

At 30 dai, samples of 1 cm³ were taken from each corm per treatment, focusing on the parts with abnormal morphologies (diseased). Each sample was washed with 96% ethanol and 5% sodium hypochlorite for 5 min and seeded on acidified PDA medium (pH ~3.5). They were incubated for 5 days at 28 ± 0.5 °C and the fungi present were identified until genus by colony morphology, staining with lactophenol blue and microscopy.

2.7. Statistical analysis

For the physio-morphological variables, factorial analysis of variance for repeated measures were carried out using linear mixed factorial models, where the interaction between the presence of *F. oxysporum*, *T. harzianum*, drought and time (F*T*W*Time) was taken as a fixed factor, and the experimental individuals over time as a random factor. On the other hand, for the analysis of leaf and petiole symptoms, generalized mixed factorial models were based on a Poisson distribution and the same factors were used. Similarly, for the corm symptomatological data, generalized linear factorial models based on the

Table 2. Scale for scoring symptomatological severity (Ss) caused by *F. oxysporum* (F) and drought (H) on *C. esculenta*, family Araceae.

Ss	Leaf symptoms		Petiole symptoms		Corm symptoms
	F	H	F	H	F
1	Healthy plant	Healthy plant	Healthy plant	Healthy plant	Not injured
2	Yellowing of < 1/3 of the leaves	Dry parts on < 1/3 of the leaves	Withering of < 1/3 of petioles	< 1/3 of dry petioles	Brown lesions in ≤ 25%
3	Yellowing between 1/3 and 2/3 of the leaves	Dry parts between 1/3 and 2/3 of the leaves	Withering between 1/3 and 2/3 of petioles	Between 1/3 and 2/3 of the dry petioles	Brown lesions between > 25% and ≤ 50%
4	Yellowing of > 2/3 of the leaves	Dry parts on > 2/3 of the leaves	Withering of > 2/3 of the petioles	> 2/3 of the dry petioles	Brown lesions between > 50% and ≤ 75%
5	Withered plant	Withered plant	Withered plant	Withered plant	Brown lesions in > 75%

Adapted from Arinaitwe et al. (2019), Jankowicz-Cieslak and Ingelbrecht (2022), Sireli et al. (2023) and Widodo and Supramana (2011).

same distribution were used, where the interaction F*T*W and post-harvest time were taken as fixed factors. Given these models, factorial deviance analyses were performed using Chi-square tests. In addition, factorial ANOVAs were performed on the WC% data using linear factorial models, where the F*T*W interaction was taken as a fixed factor. An additional model was used to evaluate the effect of post-harvest time for the WC% of the corm. For all analyses, the respective suppositions of each model were validated, and Tukey's multiple comparisons tests were performed with the factors that showed significant differences. All statistical tests were interpreted at a significance level of 5% and were executed, as were the graphs, in the RStudio program (2023.06.1+524).

3. Results

3.1. Evaluation of morphological descriptors

The change in height over time was affected by *F. oxysporum*-drought interaction, *F. oxysporum*-*T. harzianum* interaction and drought (see Table 3; $p < 0.05$). Differences in height between treatments were significant from day 18, where the effect of abiotic and/or biotic stress generated a decrease in this variable compared to the control (see Figure 1A; $p < 0.05$). In addition, the increase in corm diameter varied as a consequence of the *F. oxysporum*-*T. harzianum* interaction and drought (see Table 3; $p < 0.05$). Among the treatments under biotic stress only, better

Table 3. Results of factorial analysis of variance of morphological and physiological changes in relation to time in *C. esculenta* (Araceae).

Factors	df		Height		Corm diameter		Leaf area		SPAD		Fv/Fm	
	Num	Den	F	P	F	P	F	P	F	P	F	P
F*T*W	5	200	0.348	0.883	0.373	0.866	1.254	0.285	0.664	0.651	0.500	0.783
T*W	5	200	0.428	0.829	2.203	0.055	1.756	0.123	0.203	0.961	1.400	0.237
F*W	5	200	4.881	<0.001	0.505	0.772	1.996	0.081	0.349	0.882	1.000	0.394
F*T	5	200	2.681	0.023	3.112	0.010	0.911	0.474	3.130	0.009	1.100	0.357
W	5	200	5.357	<0.001	13.111	<0.001	4.535	<0.001	11.785	<0.001	6.500	<0.001
T	5	200	0.799	0.551	0.730	0.601	0.329	0.895	0.592	0.706	0.400	0.830
F	5	200	1.043	0.393	0.643	0.667	3.037	0.011	8.822	<0.001	0.600	0.687

F denotes plants infected by *F. oxysporum*; T indicates the presence of *T. harzianum* in the substrate; and W water stress caused by drought. Significant effects on the response variable ($P \leq 0.05$) are highlighted in bold. In the degrees of freedom (df); Num represents those in the numerator; and Den those in the denominator.

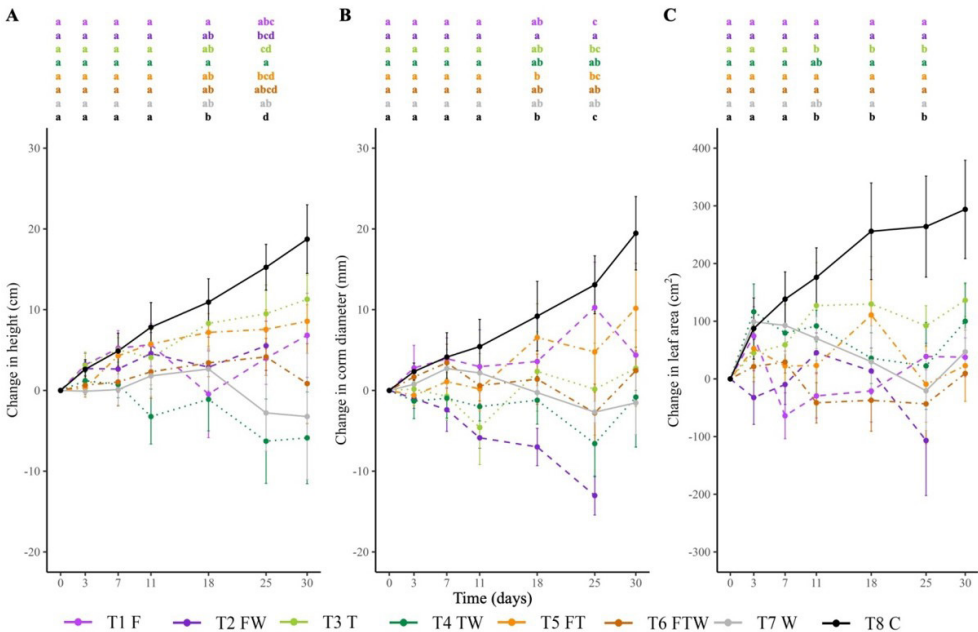


Figure 1. Morphological changes of *C. esculenta*, family Araceae, subjected to eight treatments (T) for 30 days. Change in height (A), change in corm diameter (change in stem diameter) (B), and change in leaf area (C). "F" denotes plants infected by *F. oxysporum*, "T" indicates the presence of *T. harzianum* in the substrate, "W" water stress caused by drought and "C" the control. Different letters on the graphs show significant differences resulting from the treatment-time interaction ($p < 0.05$; $N=48$). The error bars indicate the standard error. Day 30 after inoculation does not show statistical indicators due to the death of most of the individuals in some treatments.

growth was observed in plants treated with *T. harzianum*. On the other hand, drought generated a greater reduction in corm diameter than infection by *F. oxysporum*, which was noticeable from day 25, and the use of the biocontroller did not present a clear beneficial effect on the thickness of this organ (see Figure 1B; $p < 0.05$). Moreover, the change in leaf area was influenced by drought and the presence of *F. oxysporum* (see Table 3; $p < 0.05$), and from day 11 all treatments under stress showed less growth in leaf area compared to the control and the plants treated only with *T. harzianum* (see Figure 1C; $p < 0.05$).

3.2. Evaluation of photosynthetic parameters

Relative chlorophyll content (measured in SPAD units) varied over time as a result of *F. oxysporum*-*T. harzianum* interaction, drought and the presence of *F. oxysporum* (see Table 3; $p < 0.05$). From day 25, plants under abiotic or biotic stress presented low chlorophyll levels compared

to control individuals or those treated with *T. harzianum* (see Figure 2A; $p < 0.05$). Moreover, all plants under abiotic-biotic stress were the ones that presented lower SPAD values, even though the substrate of treatment 6 (T6) was inoculated with *T. harzianum*. On the other hand, the maximum efficiency of PSII (Fv/Fm) was only affected by drought (see Table 3; $p < 0.001$). This was evident from the third day, all water-stressed treatments maintained low Fv/Fm values compared to irrigated plants (see Figure 2B; $p < 0.05$).

3.3. Incidence and symptomatological severity

F. oxysporum infection for treatments T1, T2 and T6 presented an incidence of 100%, and for treatment T5 83.33%. On the other hand, symptoms of *F. oxysporum* infection on leaf and petiole derived only from biotic stress, and drought wilt was only a product of water stress (see Table 4; $p < 0.05$). In addition, symptomatological severity

Table 4. Results of factorial deviance analysis of foliar symptomatology over time and corm symptomatology after *F. oxysporum* infection and drought in *C. esculenta* (Araceae).

Factors	dff	Symptoms of <i>F. oxysporum</i>				Symptoms of drought				dfc	Corm symptomatology			
		Leaf		Petiole		Leaf		Petiole			Harvest		Postharvest	
		Chq	P	Chq	P	Chq	P	Chq	P		Chq	P	Chq	P
F*T*W	6	0.629	0.996	1.348	0.969	0.819	0.991	0.131	0.999	22	0.537	0.694	1.584	0.694
T*W	6	1.287	0.972	2.486	0.871	0.296	0.999	0.209	0.999	21	0.537	0.694	1.738	0.536
F*W	6	2.849	0.827	2.388	0.881	6.048	0.418	4.159	0.655	20	1.075	1.000	2.121	0.845
F*T	6	0.696	0.994	1.424	0.964	0.246	0.999	0.259	0.999	19	1.074	0.845	2.159	1.000
W	6	5.150	0.525	3.451	0.751	20.10	0.003	21.09	0.002	18	1.113	1.000	2.159	1.000
T	6	1.101	0.981	2.181	0.902	2.036	0.916	0.461	0.998	17	1.112	0.757	2.255	1.000
F	6	17.86	0.006	20.16	0.002	12.51	0.051	8.696	0.191	16	1.208	0.004	2.255	0.004

F denotes plants infected by *F. oxysporum*; T indicates the presence of *T. harzianum* in the substrate; and W water stress caused by drought. Significant effects on the response variable ($P \leq 0.05$) are highlighted in bold. dff represents the degrees of freedom for foliar symptoms; dfc the degrees of freedom for corm symptoms; and Chq the Chi-square test statistic. Postharvest time was two weeks.

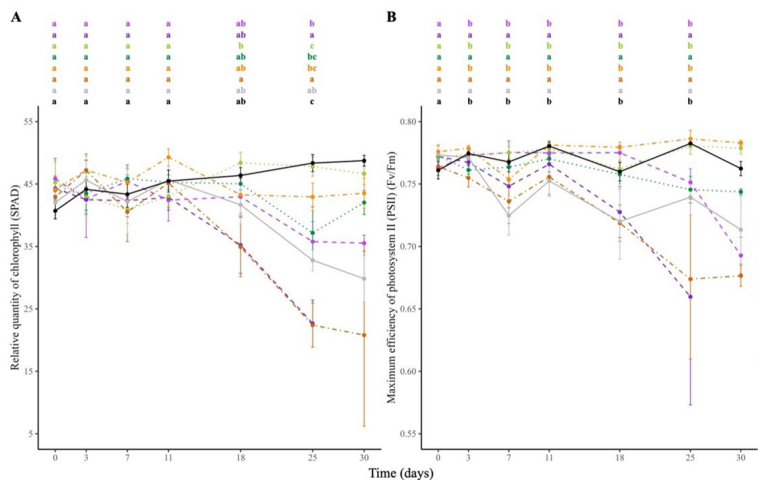


Figure 2. Physiological changes of *C. esculenta*, family Araceae, subjected to eight treatments (T) for 30 days. Relative amount of chlorophyll (A) and estimated maximum quantum yield of photosystem II (B). “F” denotes plants infected by *F. oxysporum*, “T” indicates the presence of *T. harzianum* in the substrate, “W” water stress caused by drought and “C” the control. Different letters on the graphs show significant differences resulting from the treatment-time interaction ($p < 0.05$; $N=48$). The error bars indicate the standard error. Day 30 after inoculation does not show statistical indicators due to the death of most of the individuals in some treatments.

of *F. oxysporum* infection was significant from day 11, while drought symptoms were only marked after day 25 (see Figure 3 and 4; $p < 0.05$). Treatment with *T. harzianum* attenuated the severity of symptoms of both types of stress. In addition, mortality was higher in treatments under abiotic and/or biotic stresses that were not treated

with *T. harzianum*, even reaching 100% for plants under simultaneous abiotic-biotic stress (T2).

Symptoms of corm decay in treatments T1, T2, T5 and T6 were characterized by brown areas with distinct margins between healthy parts and were derived solely from *F. oxysporum* infection (see Table 4; $p < 0.05$).

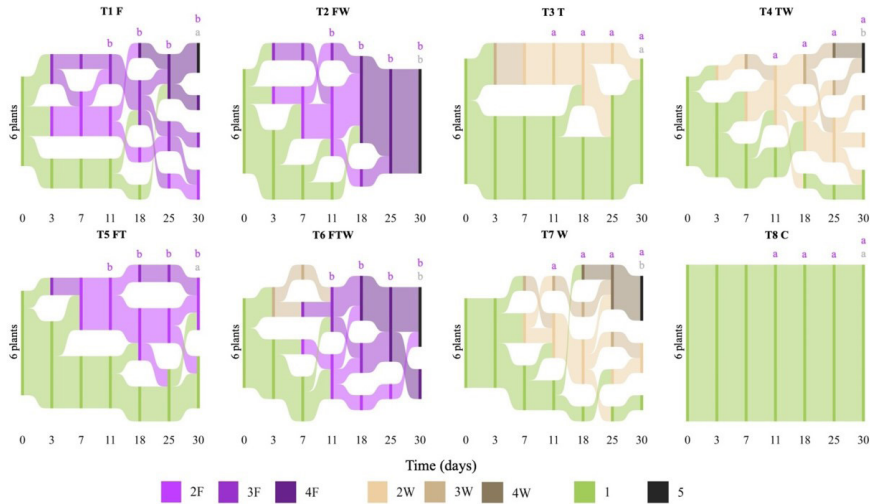


Figure 3. Sankey plot of leaf symptomatology of *C. esculenta*, family Araceae, subjected to eight treatments (T). In the title of the diagrams “F” denotes plants infected by *F. oxysporum*, “T” indicates the presence of *T. harzianum* in the substrate, “W” water stress caused by drought and “C” the control. Each treatment consists of six individuals. Healthy plants are shown in green (1) and dead plants in black (5). Purple denotes symptoms associated with *F. oxysporum* infection and brown with drought water stress. In terms of symptom severity, 2 indicates less than 1/3 of diseased leaves, 3 between 1/3 and 2/3, and 4 more than 2/3. Different letters above the nodes of each graph denote significant differences in symptomatological severity between treatments, in purple symptoms related to *F. oxysporum* infection and in gray to drought ($p < 0.05$; $N=48$).

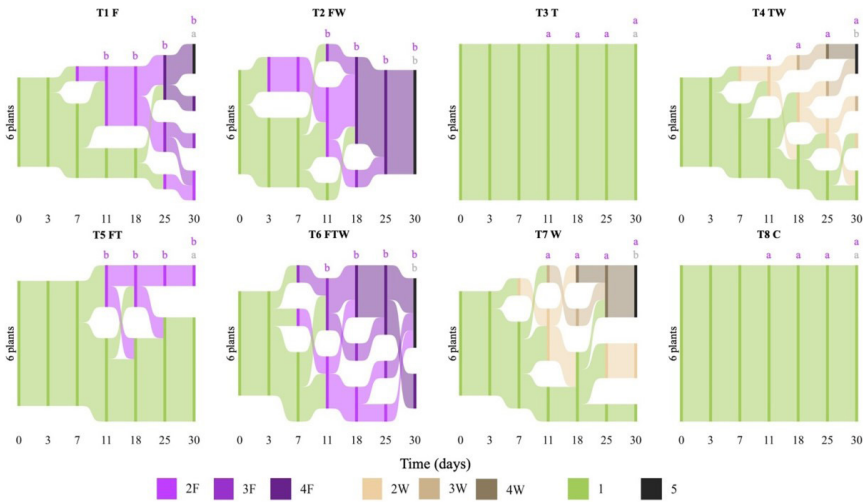


Figure 4. Sankey plot of petiole symptomatology of *C. esculenta*, family Araceae, subjected to eight treatments (T). In the title of the diagrams “F” denotes plants infected by *F. oxysporum*, “T” indicates the presence of *T. harzianum* in the substrate, “W” water stress caused by drought and “C” the control. Each treatment consists of six individuals. Healthy plants are shown in green (1) and dead plants in black (5). Purple denotes symptoms associated with *F. oxysporum* infection and brown with drought water stress. In terms of symptom severity, 2 indicates less than 1/3 of diseased petioles, 3 between 1/3 and 2/3, and 4 more than 2/3. Different letters above the nodes of each graph denote significant differences in symptomatological severity between treatments, in purple symptoms related to *F. oxysporum* infection and in gray to drought ($p < 0.05$; $N=48$).

Additionally, the absence of water and/or the presence of *T. harzianum* did not affect the symptomatological severity of the stem (see Figure 5; $p > 0.05$). In addition, the application of *T. harzianum* was related to the appearance of yellow lesions clearly differentiated from healthy tissue, but these were not significant ($p = 0.3446$). Also, post-harvest time had no effect on the symptomatological severity of the stem ($p = 1$).

3.4. Water content (WC%)

Leaf water content was affected by drought, the presence of *T. harzianum* and the interaction of both factors (see Table 5; $p < 0.05$). Plants under water stress that were not treated with *T. harzianum* (T2 and T7) showed significantly lower leaf water contents than the other treatments (see Figure 6A; $p < 0.05$). In contrast, root water content is affected by the presence of both abiotic and/or biotic stressors (see Table 5; $p < 0.05$), but not by the *T. harzianum*

treatment. Thus, individuals without any stress (T3 and T8) exhibited higher root water contents than the other treatments (see Figure 6B; $p < 0.05$).

Corm water content varied because of the three experimental factors (see Table 4; $p < 0.05$), but not because of post-harvest time ($p = 0.1033$). Overall, corm water percentage was higher in the *T. harzianum* treatments and the control, and significantly lower for corms of plants under abiotic-biotic stress (see Figure 7; $p < 0.05$).

3.5. Confirmation of the presence of *F. oxysporum* in the corms

In all the samples of the treatments infected with *F. oxysporum* (T1, T2, T5 and T6), the presence of *F. oxysporum* was corroborated. In addition, two species of fungi, one of the genus *Aspergillus* and the other of the genus *Penicillium*, were isolated in the diseased corms of treatments T3 and T4.

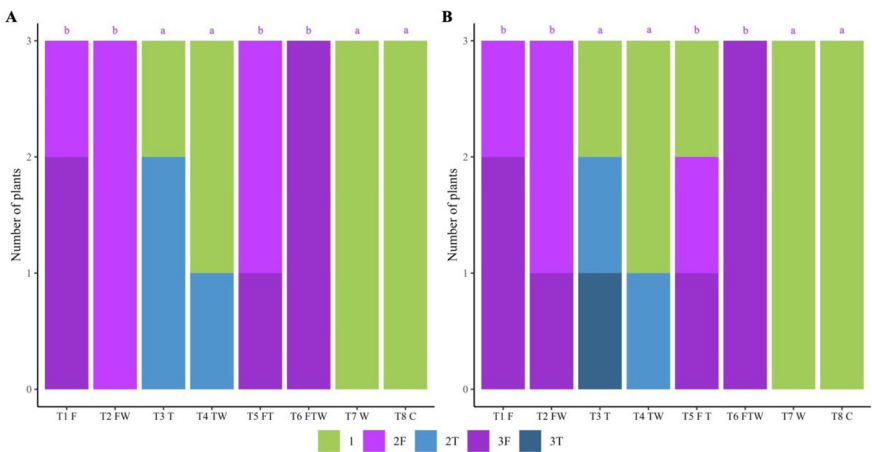


Figure 5. Stacked bar diagram of corm symptomatology of *C. esculenta*, family Araceae, at harvest (A) and after two weeks (B). Plants were subjected to eight treatments (T) for 30 days. On the horizontal axis “F” denotes plants infected by *F. oxysporum*, “T” indicates the presence of *T. harzianum* in the substrate, “W” water stress caused by drought and “C” the control. Healthy plants are shown in green (1). Purple denotes symptoms associated with *F. oxysporum* infection and blue denotes opportunistic fungi promoted by the presence of *T. harzianum* in the substrate. In terms of severity of symptomatology, 2 indicates less than 25% of the injured corm and 3 between 25% and 50%. Different letters above the bars indicate significant differences in the severity of *F. oxysporum* infection between treatments ($p < 0.05$; $N=48$). Post-harvest time and the presence of *T. harzianum* had no significant effect on corm symptoms ($p > 0.05$; $N=48$).

Table 5. Results of factorial analysis of variance of water content per organ of *C. esculenta* (Araceae).

Factors	df	Foliar water content		Root water content		Corm water content			
						Harvest		Postharvest	
		F	P	F	P	F	P	F	P
F*T*W	1	0.004	0.947	0.563	0.457	1.945	0.182	2.166	0.160
T*W	1	11.702	0.001	1.125	0.295	1.707	0.209	0.717	0.409
F*W	1	0.022	0.883	4.502	0.040	1.433	0.249	0.048	0.829
F*T	1	0.013	0.908	3.917	0.055	0.542	0.472	0.512	0.484
W	1	38.007	<0.001	29.139	<0.001	21.241	<0.001	19.875	<0.001
T	1	11.529	0.001	2.959	0.0931	12.378	0.003	6.889	0.018
F	1	0.848	0.362	24.313	<0.001	18.918	<0.001	16.309	<0.001

F denotes plants infected by *F. oxysporum*; T indicates the presence of *T. harzianum* in the substrate; and W water stress caused by drought. Postharvest is two weeks after harvest. Significant effects on the response variable ($P \leq 0.05$) are highlighted in bold, and df represents the degrees of freedom.

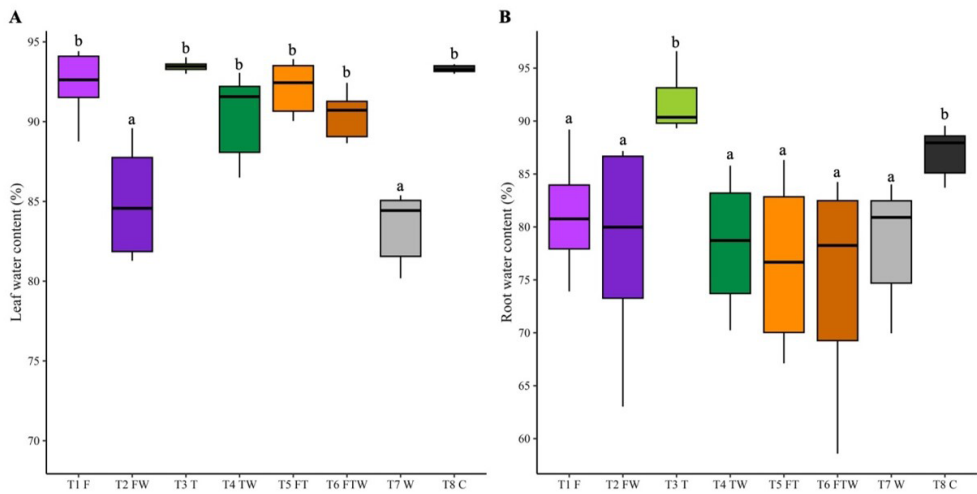


Figure 6. Box plot of leaf (A) and root (B) water content of *C. esculenta*, family Araceae, subjected to eight treatments (T) for 30 days. “F” denotes plants infected by *F. oxysporum*, “T” indicates the presence of *T. harzianum* in the substrate, “W” water stress caused by drought and “C” the control. Different letters above the boxes show significant differences between treatments ($p < 0.05$; $N=48$).

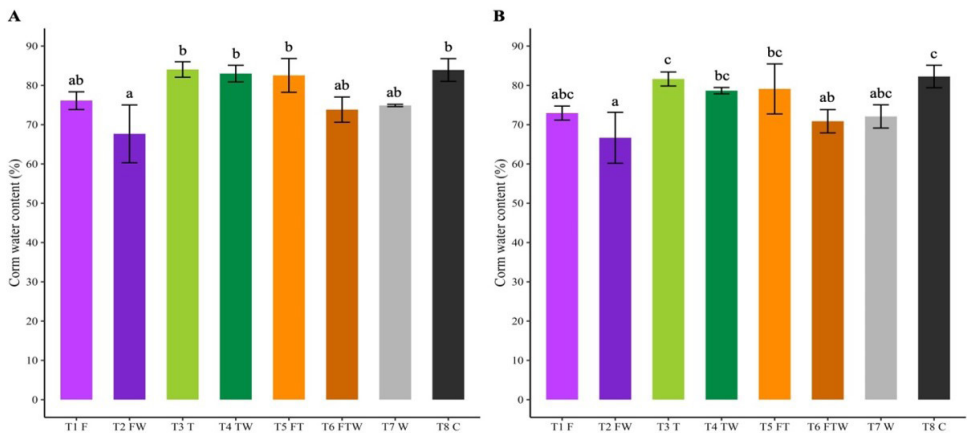


Figure 7. Bar chart of water content of the corm of *C. esculenta*, family Araceae, subjected to eight treatments (T) for 30 days. (A) at the end of the experiment and (B) 15 days after harvest. Storage of corms after harvest was in open bags in a dark place, following traditional cultivation methods. “F” denotes plants infected by *F. oxysporum*, “T” indicates the presence of *T. harzianum* in the substrate, “W” water stress caused by drought and “C” the control. Different letters above the bars show significant differences between treatments ($p < 0.05$; $N=24$). There are no significant differences in corm water content resulting from post-harvest ($p = 0.1033$; $N=48$). Error bars indicate standard error.

4. Discussion

Drought reduced the growth of *C. esculenta* plants. This detriment is attributed to changes caused by water stress, which generate a reduction in turgor pressure, nutrient uptake, cell expansion, protein biosynthesis, stomatal aperture and growth (Jaleel et al., 2009; Nieves-Cordones et al., 2019; Pimentel, 2022). Water deficit also increases ROS formation, causes oxidative stress, generates cell damage, and decreases productivity (Moustakas et al., 2022; Sperdoui et al., 2021). In addition, drought also decreased the maximum efficiency of PSII. Water stress reduces photosynthetic rate by stomatal closure, this mechanism prevents water loss by transpiration, but decreases internal CO_2 concentration and limits

carboxylation (Chaves et al., 2002; Liu et al., 2016; Maxwell and Johnson, 2000; Moustakas et al., 2022). In addition, this type of stress reduces the Fv/Fm ratio due to the lack of the electron donor, resulting in low electron transport and damage to PSII (Hura et al., 2007; Maxwell and Johnson, 2000).

Infection by *F. oxysporum* also decreased the growth of Chinese potato. This phytopathogen, being necrotrophic, blocks and decomposes vascular tissues, which impedes the translocation of water and nutrients (Boba et al., 2020; Michielse and Rep, 2009). In addition, *F. oxysporum* has been reported to produce mycotoxins such as fusaric acid (FA), which in advanced stages of infection elevates ROS levels, decreases the efficacy of antioxidant enzymes, and induces cell death (Perincherry et al., 2019). On the

other hand, *C. esculenta* plants were susceptible to both stressors, and the sum of these generated an abiotic-biotic stress that drastically decreased growth and resulted in 100% mortality. Plants under water stress are more susceptible to fungal infection, since stress weakens host defenses (Irulappan et al., 2022; Muhammad et al., 2023). In addition, phytopathogens and drought reduce water potential, which triggers stomatal closure as a common response and leads to further deterioration in development (Pandey et al., 2015; Sawinski et al., 2013). In addition, during prolonged periods of drought, cells release nutrients to the apoplast, which increases colonization by phytopathogens (Ahluwalia et al., 2021).

Likewise, chlorophyll content decreased as a result of abiotic and biotic stresses. This pattern has been reported in several crops because of drought, where the decrease in chlorophyll content is related to the formation of antioxidant pigments (Farooq et al., 2009; Jaleel et al., 2009). In the same way, certain mycotoxins generate a decrease in photosynthetic pigments (Wagacha and Muthomi, 2007). Despite this, the application of *T. harzianum* helped to maintain chlorophyll levels in *C. esculenta* plants under stress. It has been found that, some species of the genus *Trichoderma*, such as *T. harzianum*, increase chlorophyll content by modulating the expression of genes that regulate its synthesis (Harman et al., 2021; Mahmoodian et al., 2022; Vukelić et al., 2021).

Furthermore, it was observed that the application of *T. harzianum* tends to decrease the effect of *F. oxysporum* infection on the height of Chinese potato plants, which is since this biocontroller improves the availability and uptake of nutrients by plants (Chen et al., 2019; Singh et al., 2014). Likewise, it has been reported that some strains of *T. harzianum* in addition to being biocontrollers of *F. oxysporum* produce indole compounds such as indole-3-acetic acid (IAA, a phytohormone of the auxin class), which also stimulates plant growth (Bader et al., 2020; Contreras-Cornejo et al., 2024; Herrera-Jiménez et al., 2018).

Despite this, corm diameter and leaf area of Chinese potato plants did not show significant improvements with the presence of *T. harzianum*. This contrasts with what has been reported in corm crops such as banana and gladiolus, where *T. harzianum* significantly increases corm diameter by producing phytohormones such as AIA and solubilize phosphates and nitrogen (Hashmi et al., 2018; Wong et al., 2021). Moreover, it has been observed that this bioinoculant, in addition to counteracting infection by *F. oxysporum*, increases leaf area in various crops by releasing growth-promoting metabolites, such as auxins, and improving the physiological and metabolic activity of plants (El-Sharkawy et al., 2021; Li et al., 2019; Zhang et al., 2020). However, further studies are needed to investigate the reasons why *T. harzianum* differentially affects morphological traits in *C. esculenta*.

On the other hand, the incidence of *F. oxysporum* infection was lower in plants treated with *T. harzianum*. This biocontroller presents a greater capacity to absorb and mobilize nutrients from the soil, which deprives plant pathogens of carbon, nitrogen, and iron sources (Dutta et al., 2023; Singh et al., 2014; Tyśkiewicz et al., 2022). Likewise, strains of the genus *Trichoderma* exhibit

mycoparasitic activity against *F. oxysporum*, produce enzymes that degrade the fungal cell wall and antifungal metabolites such as pyrones and lactones (Dutta et al., 2023; Tyśkiewicz et al., 2022). In addition, species of the genus *Trichoderma* induce elicitor-mediated defense responses in plants, which prevent the spread of phytopathogens by increasing the synthesis of defensive metabolites such as phytoalexins and enzymes peroxidase and chitinase (Chen et al., 2019; Montesano et al., 2003; Sood et al., 2020; Thakur and Sohal, 2013).

Moreover, it was observed that treatment with *T. harzianum* tends to generate a decrease in leaf and petiole symptoms of Chinese potato. This effect has been reported for other crops, where the application of *T. harzianum* improves drought tolerance and decreases the severity of *F. oxysporum* infection (Chen et al., 2019; Lian et al., 2023; Shukla et al., 2012; Sood et al., 2020; Nawu et al., 2022). This biocontroller helps maintain photosynthetic activity, reduces ROS accumulation, and prevents oxidative damage (Tyśkiewicz et al., 2022). Despite this, the effectiveness of *T. harzianum* treatment on the symptomatology of *C. esculenta* plants was low for both stressful conditions since the reduction in severity was not significant. In contrast, treatment with *T. harzianum* counteracted the effects of drought on leaf WC%. In addition, it reduced the consequences of both types of stress on corm WC%. It has been reported that the application of *T. harzianum* generates the activation of proline osmolyte biosynthesis under water deficit, which stimulates water uptake (Alwhibi et al., 2017; Cushman, 2001; Hayat et al., 2012).

Symptoms of *F. oxysporum* infection were significant earlier than drought symptoms on Chinese potato. This is related to the response of plants to water deficit. In the short term, osmotic adjustments are generated to tolerate drought, but when drought is prolonged, growth is repressed, senescence increases and symptoms appear (Ahluwalia et al., 2021). On the other hand, the symptomatology of corm resulting from *F. oxysporum* infection coincided with that reported by Sireli et al. (2023). In addition, its severity was not affected by time after harvest, although the opposite has been reported (Ye et al., 2023). The application of *T. harzianum* did not improve corm dry rot, which differs with the results found by Bora et al. (2020) for another species of the genus (*T. viride* Pers) in in vitro cultures. Moreover, the application of *T. harzianum* was associated with corm infection by opportunistic fungi of the genus *Aspergillus* and *Penicillium*. A somewhat similar phenomenon has been reported in plants of the Brassicaceae family, where the application of this biocontroller favors root colonization by arbuscular mycorrhizae (Poveda et al., 2019).

5. Conclusions

The present study reveals that abiotic and/or biotic stresses differentially impact the physio-morphological traits of *C. esculenta*. This species has low tolerance to drought and is highly susceptible to *F. oxysporum* infection, where abiotic-biotic stress combinations increase the detrimental effects. In photosynthetic terms,

drought has a greater impact than *F. oxysporum* infection; however, the latter shows severe symptoms in a shorter period of time. On the other hand, the application of *T. harzianum* on Chinese potato tends to increase plant height under *F. oxysporum* infection and to improve leaf water content under water deficit conditions. Nevertheless, its effectiveness as a biocontroller of the phytopathogen and as a protector against water stress is low or null for the other response variables. Further research is needed to evaluate the effect of *T. harzianum* on crop productivity and its relationship with corm colonization by opportunistic phytopathogens. In addition, this study is one of the first to demonstrate the stress response of Chinese potato, which is of great utility for future plans for the technification of the crop.

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