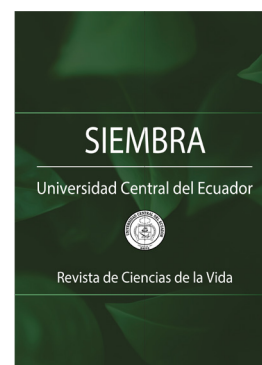


Physiological acclimatization strategies to water deficit in *Solanum phureja* Juz. et. Buk

Estrategias fisiológicas de aclimatación al déficit hídrico en *Solanum phureja* Juz. et. Buk

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Abstract

Potatoes are an important crop for global food security. *Solanum phureja* is a highly diverse group of cultivars that are economically and culturally significant. Climate change has affected potato yields, and water deficits are a determining factor. This study aimed to identify the physiological strategies of *S. phureja* for acclimatizing to water deficit stress. Tubers from two *S. phureja* cultivars (Criolla Colombia and Mambera) were planted in a greenhouse and exposed to a water deficit by maintaining soil volumetric moisture levels between 10% and 15% during periods of stress, according to the crop's phenological stage. Water potential, gas exchange, water use efficiency, chlorophyll content, dry mass accumulation, and yield were evaluated. Results showed decreases in leaf water potential (-1.28Ψ), stomatal conductance ($0.047 \text{ mol m}^{-2} \text{ s}^{-1}$), and photosynthesis rate ($\mu\text{mol } 3.6 \text{ mol m}^{-2} \text{ s}^{-1}$), as well as decreases in leaf area. There were also increases in chlorophyll concentration (566.77 mg m^{-2}) and water use efficiency ($119 \mu\text{mol CO}_2/\text{mmol H}_2\text{O}$) in treatments under hydric stress. Higher levels of stress were reported during the filling stage, as well as high recovery and adaptation to stress during tuberization. Additionally, we found differences between the cultivars related to their phenology, yield, and dry matter distribution. These results highlight a chain of physiological responses beginning with a reduction in water potential and gas exchange and ending with changes in organ growth. These results contribute to identifying tolerant cultivars, improving agronomic management, optimizing irrigation, and crop zoning.

Keywords: potato, water deficit, phenology, adaptation.

Resumen

La papa es un cultivo de importancia para la seguridad alimentaria mundial. *Solanum phureja* es un grupo con alta diversidad de interés económico y cultural. El cambio climático ha afectado los rendimientos de papa siendo el déficit hídrico una condición determinante. El objetivo de esta investigación fue identificar estrategias fisiológicas de aclimatación de *S. phureja* al estrés por déficit hídrico. Se sembraron tubérculos de dos cultivares de *S. phureja* (Criolla Colombia y Mambera) bajo condiciones de invernadero, se sometieron a déficit hídrico sosteniendo la humedad

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volumétrica del suelo entre el 15 y 10% durante periodos de estrés según la etapa fenológica del cultivo. Se evaluó potencial hídrico, intercambio gaseoso, uso eficiente del agua, clorofila, acumulación de masa seca y rendimiento. Los resultados evidenciaron la disminución del potencial hídrico foliar ($-1,28 \Psi$), la conductancia estomática ($0,047 \text{ mol m}^{-2} \text{ s}^{-1}$), tasa de fotosíntesis ($\mu\text{mol } 3,6 \text{ mol m}^{-2} \text{ s}^{-1}$), área foliar y aumento en la concentración de clorofila ($566,77 \text{ mg m}^{-2}$) y uso eficiente del agua ($119 \mu\text{mol CO}_2/\text{mmol H}_2\text{O}$) en tratamientos bajo estrés hídrico. Se identificaron mayores niveles de estrés en la etapa de llenado, una alta recuperación y adaptación en estrés en tuberización y diferencias entre los cultivares ligados a su fenología, componentes de rendimiento y distribución de la materia seca. Según los resultados se evidencia cadena de respuestas fisiológicas, iniciando con la reducción del potencial hídrico e intercambio gaseoso hasta cambios en el crecimiento entre órganos. Estos resultados contribuyen a la definición de cultivares tolerantes, manejo agronómico, riegos eficientes y zonificación del cultivo.

Palabras clave: papa, déficit hídrico, fenología, adaptación.

1. Introduction

According to data from the Food and Agriculture Organization of the United Nations [FAO], in 2023 total global potato production was approximately 383 million tons (FAO, 2025). In Colombia, it represents one of the most significant cold climate production systems, adapting to an altitude range comprised between 2,600 and 3,000 meters above sea level, although in some areas it is grown above 3,000 meters above sea level (Abaunza González et al., 2022). The national potato yield in Colombia was 22.8 t ha^{-1} in an area of 112,975 ha for 2023 (Federación Colombiana de productores de papa [FEDEPAPA], 2024); and, specifically, for *Solanum phureja* it was 16,379 ha, with a yield of 14.72 t ha^{-1} for 2023 (Red de información y comunicación del sector Agropecuario Colombiano [Agronet], 2024).

The main centers of diversity for native potato species belonging to the *Solanum phureja* group are to be found in southern Colombia and northern Ecuador. In Colombia, this crop is widely distributed throughout the three Andean mountain ranges, mainly in areas above 2,000 m a.s.l., from the south to the north of the country. The department of Nariño stands out as one of the leading areas of production and commercialization, where various diploid varieties are grown, such as Tornilla, Mambra, and Ratona, having significant cultural and agronomic value for local communities (Ñústez López & Rodríguez Molano, 2024).

In recent years, there has been growing interest in promoting the cultivation of this diploid species in Andean countries due to the acceptance among consumers both for its good flavor, nutritional quality (including vitamins A, B, and C, niacin, and thiamine), agro-industrial suitability, lower costs, and production cycles (Molina Cita et al., 2015). Also, some wild potato species possess desirable agronomic genetic characteristics, such as resistance to disease and abiotic stress, among others (Gómez et al., 2012).

Potato crops are highly susceptible to the effects of climate change, as documented by various authors (Marmolejo and Ruiz, 2018; Wang et al., 2021), being particularly sensitive to extreme conditions such as periods of heat or cold, water shortages, and flooding (Singh et al., 2020). The occurrence of extreme events has a negative impact on yields, as well as on the quality of the tuber harvested (Sierra Herrera, 2019). Therefore, the associated risks are decisive for the sustainability of small producers, growing mostly *Solanum phureja* species (Abaunza González et al., 2022), as water deficit disrupts the plant's fundamental physiological functions, such as respiration, photosynthesis, nutrient absorption, transport through xylem and phloem, interactions between organs, and yield. (Rudack et al., 2017).

According to local producers, over the last decade potato crops have been highly exposed to adverse weather events. Thirty-two percent of farmers reported damage from droughts, 30% from frost, 16% from heavy rains, 7% from floods, another 7% from landslides, 4% from waterlogging, and 3% from other climatic phenomena (Zapata Murillo et al., 2023).

Under conditions of water stress, plants develop acclimatization and adaptation responses associated with a set of biochemical, molecular, physiological, and morphological strategies, which differ between cultivars of the same species and between species (Graça et al., 2010). These strategies minimize the potential negative impacts of extreme weather conditions, conferring resistance or tolerance to a particular cultivar or species.

Most potato producers in Colombia have low technological capabilities and depend on climate conditions to grow their crops. This increases their vulnerability to the negative effects of climate change. Although farmers cannot change or manage climatic conditions, some factors such as soil, water, crop type, and agricultural practices can be managed to reduce the adverse effects of climate change (Moradi et al., 2013).

Given the importance of potato cultivation, *Solanum phureja* in particular, this study was conducted with the aim of identifying the integrated physiological acclimation strategies recorded in two *Solanum phureja* cultivars in response to water deficit under controlled conditions.

2. Materials and Methods

2.1. Location

The experiment was carried out in 2021, in a greenhouse located at the Centro de investigación Obonuco of the Corporación Colombiana de Investigación Agropecuaria - AGROSAVIA, in the municipality of Pasto, Nariño, with coordinates 1°11'54.2"N 77°18'15.3"W and an altitude of 2.756 m a.s.l.

2.2. Setting up the experiment

Homogeneous tubers were selected from two potato cultivars, *Solanum phureja*, Criolla Colombia, and Mambera, which exhibit differential behaviors identified in previous studies (López-Rendón et al., 2024). They were planted in pots with a capacity of 12 kg of dry soil.

2.3. Experimental design

A randomized block design was applied in split plots with four replicates, randomly distributed throughout the experimental area, with 15 plants per experimental unit, to reduce the effect caused by differential temperature and humidity conditions within the greenhouse and the time of evaluation. The experiment consisted of three evaluation factors (phenological phase, water stress treatments, and cultivars) distributed throughout the plots and subplots that made up the design. The phenological phase of the crop formed the large plot, the division of this plot corresponded to the stress treatments, and the subdivision referred to the cultivars (Table 1).

Table 1. Study factors in the drought stress experiment on *Solanum phureja* under greenhouse conditions.

Phenological stage of the crop	Crop	Treatments
Tuberization (Tub)	Criolla Colombia	Field capacity irrigation (Ctrl+)
Tuber filling (Fill)	Mambera	Drought during tuberization (-Tub)
Senescence (Sen)		Drought during filling until harvest (-Fill)
		Drought from tuberization to harvest (Ctrl-)

2.4. Soil moisture and climatic conditions

Irrigation was managed using pressure-compensating drippers. Moisture control was performed through time-domain reflectometry (TDR), and the use of the HH2 Moisture Meter (Delta-T Devices®).

Starting from sowing onwards, moisture was maintained at field capacity throughout the experiment until the beginning of each water deficit treatment (start of tuberization, and start of tuber filling) (Table 1). Then, the volumetric moisture content [θ] of the soil was reduced from field capacity to 10% (at which point the plant loses turgidity and the stomata close). Subsequently, these plants were irrigated to a maximum of 20% [θ], keeping continuous depletion cycles between 10 and 20% until total rehydration, when they were brought to constant field capacity moisture until harvest in treatments (-Tub), unlike treatments (-Fill) and (Ctrl-), which, after being subjected to water deficit treatment, were maintained under that condition until harvest, and treatments (Ctrl+), which were at field capacity throughout the experiment.

Weather conditions were monitored using a Davis Vantage Pro2 Wireless FAN automated weather station, 6153 (Davis Instruments®, USA), which recorded an average temperature of 17.4 °C, a maximum of 36.9 °C, and a minimum of 8.8 °C during the evaluation cycle, with an average relative humidity of 69.1% and an average cumulative solar radiation of 1,689.6 (Wm⁻²) per day, as shown in the (Table 2).

Table 2. Environmental conditions during the evaluation period of the experiment under greenhouse conditions.

Growth stage	Temperature			Relative humidity			Solar radiation		
	°C			%			Wm ⁻²		
	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max
Vegetative	19.0	9.9	35.9	67.0	32	94	1,530.5	972	2,526
Tuberization	18.0	9.3	36.5	69.4	29	93	1,700.9	745	2,597
Filling	16.8	8.2	37.4	70.0	31	94	1,745.7	923	2,345
Senescence	15.9	7.9	34.6	69.8	26	95	1,781.3	465	6,991
Mean	17.4	8.8	36.1	69.1	29.5	94.0	1,689.6	776.3	3,614.8

Agronomic management, in terms of nutrition and phytosanitary control, was carried out uniformly. Fertilization was carried out at a rate of 80 kg N ha⁻¹ 150 kg P₂O₅ ha⁻¹, and 60 kg K₂O ha⁻¹, divided between the time of sowing and 15 days later.

2.5. Variables assessed

The methodology used for each variable in this research was:

- *Leaf water potential*: measured using a Scholander pressure chamber on five plants per treatment, every three days, on the third leaflet of the plant, with two evaluation times during the day, at dawn between 5:30 a.m. and 6:00 a.m. and at midday between 12 p.m. and 1 p.m. (Ariza et al., 2020; Pino et al., 2016).
- *Stem water potential*: At the first evaluation time early morning, five leaflets were selected, on the third functional leaflet per treatment, which were covered with aluminum foil until noon, when they were then uncovered for evaluation, in the same way as leaf potential (Pino et al., 2016).
- *Gas exchange*: evaluated at the same frequency as water potential, on the third leaflet of the plant between 9 and 12 a.m., using IRGA equipment (LCpro-SD, ®ADC BioScientific) simulating light at 1,200 PAR, $\mu\text{mol m}^{-2} \text{s}^{-1}$. This evaluation yielded parameters such as photosynthetic rate [A] $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, stomatal conductance [gs] $\text{mol H}_2\text{O m}^{-2} \text{ s}^{-1}$, transpiration [E] $\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$, and leaf temperature [Tfoliar] in °C. (Ariza et al., 2020; Díaz Valencia, 2016; Pino et al., 2016).
- *Water use efficiency at the leaf level*: it was calculated at two levels. First, transpiration efficiency, i.e., CO_2 assimilation/transpiration (W/E, $\mu\text{mol CO}_2 \text{ mol}^{-1} \text{ H}_2\text{O}$) and, second, intrinsic water use efficiency: CO_2 assimilation/stomatal conductance (A/gs, $\mu\text{mol CO}_2 \text{ mol}^{-1} \text{ H}_2\text{O}$) (Medrano et al., 2007).
- *Chlorophyll concentration [Chl] in mg m⁻²*: evaluated using the CCM-300 chlorophyll content meter (®ADC BioScientific) on the third functional leaflet of each plant with the same frequency and number of plants as the gas exchanger (Ariza et al., 2020; Pino et al., 2016).
- *Dry matter*: a destructive assessment by organs (root, tuber, stem, and leaves) of two plants per assessment plot was used at frequent time intervals in the pre-tuberization, tuberization [Tub], onset of tuber filling [Fill], onset of senescence [Sen], and harvest [Harv] stages. The plants were processed in the laboratory by organ, and drying was carried out in a forced-air oven at a temperature of 72 °C until a constant dry matter weight was reached (Ariza et al., 2020; Pino et al., 2016). Once the dry weights per organ were obtained, other parameters were estimated by using calculations such as the sink-source ratio, and above-ground and below-ground parts of the plant.
- *Leaf area*: this was obtained using the disc method, by extracting 20 discs of different leaflets with a punch, and drying them as mentioned above. The leaf area was then obtained using the dry leaf matter and the ratio of dry matter to disc area.
- *Yield*: evaluated by taking five plants per plot, which were harvested and, then, the number of tubers [NTu] per plant, yield per plant, and average tuber weight were counted. Additionally, the harvest index [HI], corresponding to the percentage of economic yield (tubers) in relation to biological yield (whole plant) was evaluated (Ariza et al., 2020; Díaz Valencia, 2016; Pino et al., 2016).

2.6. Statistical analysis

The information obtained was analyzed using R V.4.3.3 software, with the Agricolae, ggplot2, and ggpubur packages. Assumptions were verified where the presence of extreme outliers, normal distribution of data, was

identified using the Shapiro-Wilk statistic ($p > 0.05$), normal QQ plots, and homogeneity of variances using Levene's statistic (R Core Team, 2020). Quantitative variables were analyzed using ANDEVA for a randomized block design in subdivided plots using generalized linear models, accompanied by Tukey's mean comparison test ($p < 0.05$). Instead, for those variables that did not show statistical differences between the interactions of three and two factors, the effect of the main factors was analyzed separately.

3. Results

3.1. Water potential

Significant differences were observed both in leaf and xylem water potential [Ψ] due to irrigation treatments and the phenological stage of the crop ($\text{Pr}(>F) < 2e^{-16}$). The lowest Ψ values were recorded during the tuberization phase, at midday, and in treatments under stress, with an average of -1.28 MPa (Figure 1). During the filling and senescence stages, in plants under water stress, the values of the three potentials evaluated were similar, ranging from -0.86 MPa to -1.14 MPa. The lowest leaf Ψ at dawn was recorded at the tuber filling stage in the (-Fill) treatment, with -1.03 MPa.

The treatments that suffered early stress (-Tub), after being rehydrated, showed higher leaf Ψ values at noon in the filling phase (-0.66 MPa) compared to the control (Ctrl+) (-0.79 MPa), and in the senescence phase, with values of -0.70 MPa for -Tub and -0.83 MPa for Ctrl+ (Figure 1).

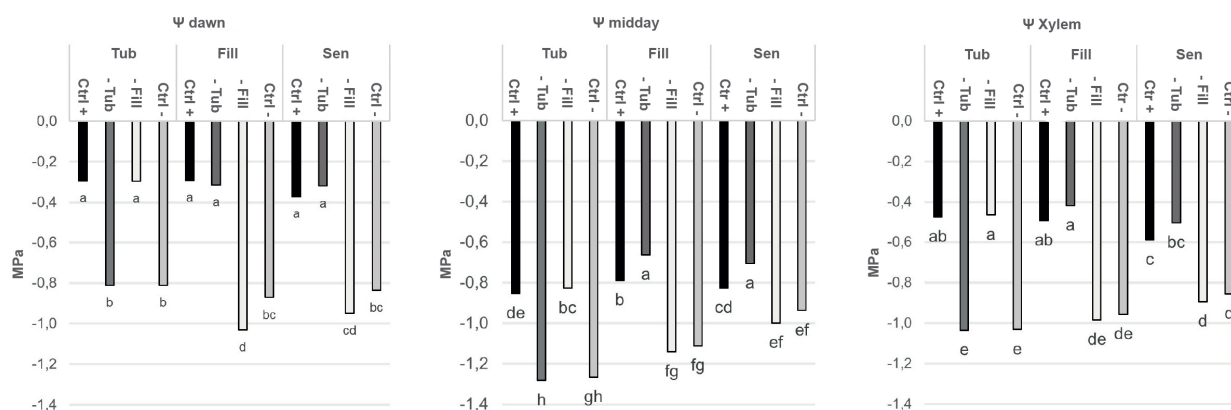


Figure 1. Leaf water potential at dawn and midday, and water potential by effect of crop phenological stage and soil moisture treatment in *Solanum phureja* plants under greenhouse conditions.*

* Means with the same letter were not significantly different ($p < 0.05$) Tukey.

3.2. Gas Exchange

Stomatal conductance [g_s] showed significant differences between the three factors: phenology, soil moisture treatments, and cultivar, with a $\text{Pr}(>F)$ value of 0.00982 (Figure 2). The Criolla Colombia variety had the highest g_s values when the plants were not stressed, in the Ctrl+ treatment during tuberization ($0.407 \text{ mol m}^{-2} \text{ s}^{-1}$) and in senescence in the -Tub treatment ($0.364 \text{ mol m}^{-2} \text{ s}^{-1}$). During stress, no statistical differences were found between cultivars. The lowest g_s values were recorded during the tuber filling stage, in -Fill with $0.050 \text{ mol m}^{-2} \text{ s}^{-1}$ for Criolla Colombia and $0.047 \text{ mol m}^{-2} \text{ s}^{-1}$ for Mambera.

Statistical differences were found for photosynthesis rate [A] and transpiration [E] with respect to the phenological phase and irrigation treatments applied, with values of $\text{Pr}(>F) < 2e^{-16}$. During the study, A values were higher in the irrigated treatments. In the tuber filling and senescence phases within the irrigation treatments, -Tub was higher than Ctrl+, reaching $14.72 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$ and $13.2 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$, and the A values in these treatments were lower than those in other phases in senescence. Likewise, the Ctrl- treatment was higher than -Fill starting from tuber filling onwards. In the case of E , the highest values were recorded in the tuberization phase, with $3.45 \text{ m}^{-2} \text{ s}^{-1}$ in Ctrl+ plants. Finally, the Ctrl- treatment showed higher values in the filling and senescence phases than -Fill, for E , a behavior similar to that described for A in the same treatments and phases of the study (Table 3).

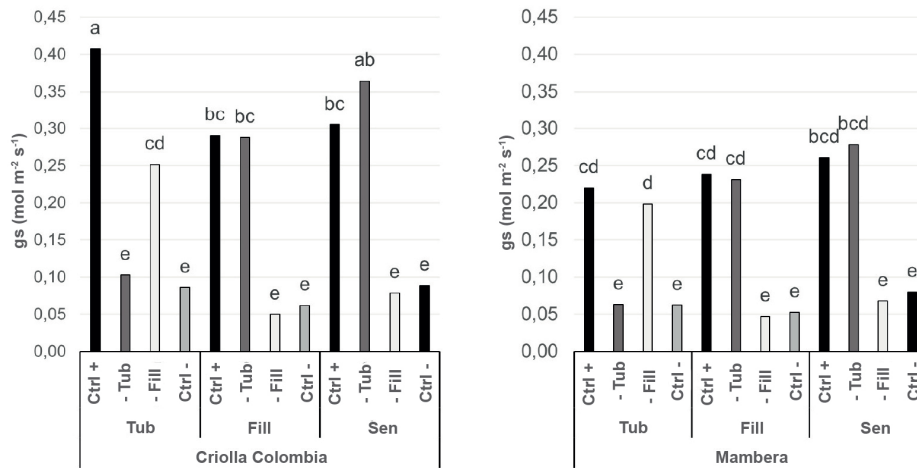


Figure 2. Stomatal conductance by effect of crop phenological stage, soil moisture treatment and cultivar in *Solanum phureja* potato plants under greenhouse conditions.*

* Means with the same letter were not significantly different ($p < 0.05$) Tukey.

Leaf temperature (T_{leaf}) was influenced by ambient temperature, and water deficit stress treatments. Stressed plants had higher temperatures than non-stressed plants. The highest temperatures were recorded during the senescence phase, reaching $30.96\text{ }^{\circ}\text{C}$ in -Fill and $30.63\text{ }^{\circ}\text{C}$ in Ctrl-. In addition, the -Tub treatments tended to have higher T_{leaf} values after rehydration compared to the control plants Ctrl+ (Table 3).

Significant statistical differences were found in Water Use Efficiency with $\text{Pr}(>F) < 2e^{-16}$ for intrinsic water use efficiency [WUEi] and $\text{Pr}(>F)$ of 0.00034 for transpiration efficiency [W/E]. The highest WUEi values were recorded during the tuber filling stage, reaching $107.35\text{ }\mu\text{mol CO}_2/\text{mmol}^{-1}\text{ H}_2\text{O}$ in (-Fill) and $119.03\text{ }\mu\text{mol CO}_2\text{ mmol}^{-1}\text{ H}_2\text{O}$ in (Ctrl-); for W/E, the maximum value was $11.41\text{ }\mu\text{mol CO}_2\text{ mol}^{-1}\text{ H}_2\text{O}$ in (-Fill). The lowest values were observed during the senescence stage, with $49.86\text{ }\mu\text{mol CO}_2\text{ mmol}^{-1}\text{ H}_2\text{O}$ for WUEi in (-Tub) and $4.31\text{ }\mu\text{mol CO}_2\text{ mmol}^{-1}\text{ H}_2\text{O}$ for W/E in (Ctrl+) (Table 3)

3.3. Chlorophyll concentration

For the interaction between the phenological stage, the water stress treatment, and the cultivar, significant differences were found with a $\text{Pr}(>F)$ value of $2.33e^{-05}$. Chlorophyll contents were higher in the tuber filling stage in Ctrl-, reaching 566.77 mg m^{-2} for Criolla Colombia and 553 mg m^{-2} for Mambra. The lowest values were recorded in the senescence stage in Ctrl+, with 471.43 mg m^{-2} for Criolla Colombia and 373 mg m^{-2} for Mambra, showing differences between the cultivars. In the senescence stage, in irrigated treatments the chlorophyll concentration was higher in -Tub compared to Ctrl+ in both cultivars. In the non-irrigated treatments, Ctrl- showed a higher chlorophyll concentration compared to -Fill (Figure 3).

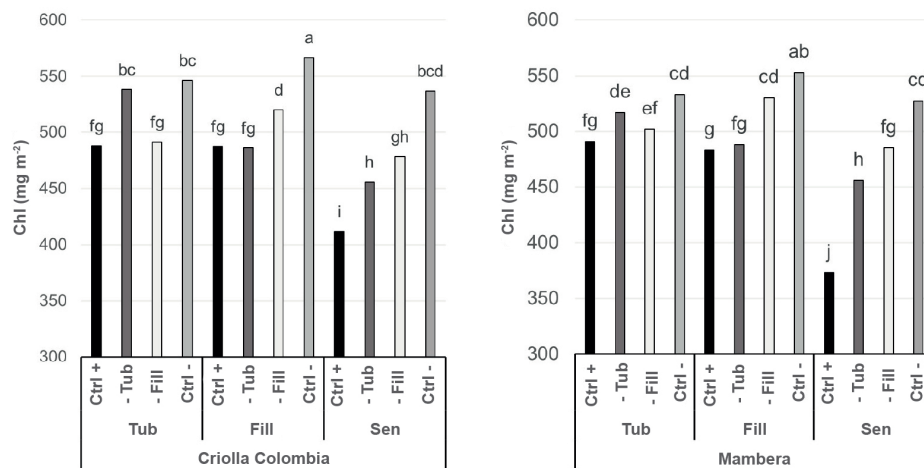


Figure 3. Chlorophyll concentration by effect of crop phenological stage, soil moisture treatment and cultivar in *Solanum phureja* plants under greenhouse conditions.*

* Means with the same letter were not significantly different ($p < 0.05$) Tukey.

Table 3. Photosynthetic rate [A], transpiration [E] and leaf temperature (Tleaf), leaf-scale water use efficiency [WUE_l, W/E] by the effect of the interaction between phenological stage and moisture treatments in *Solanum phureja* plants under greenhouse conditions.*

Phenological stage of the crop	Treatment	A	gs	E	Tleaf	(WUE _l)	W/E
		μmol m ⁻² s ⁻¹	mol m ⁻² s ⁻¹	mmol m ⁻² s ⁻¹	°C		
Tuberization (Tub)	Ctrl+	13.9 ^{ab}	0.31 ^a	3.4 ^a	29.7 ^d	68.3 ^{cde}	4.4 ^c
		+/-0.39	+/- 0.032	+/-0.069	+/-0.146	+/-1.56	+/-0.062
	-Tub	4.8 ^d	0.08 ^c	1.2 ^c	30.3 ^{abc}	84.4 ^b	5.2 ^{bc}
		+/-0.209	+/- 0.005	+/-0.051	+/-0.131	+/-2.54	+/-0.678
	-Fill	13.8 ^{bc}	0.22 ^b	3.3 ^{ab}	30.1 ^{bcd}	77.0 ^{bcd}	4.3 ^c
		+/-0.129	+/- 0.006	+/-0.045	+/-0.134	+/-1.74	+/-0.051
Ctrl-	4.7 ^d	0.06 ^c	1.1 ^{cd}	30.1 ^{bcd}	79.3 ^{bc}	6.2 ^{bc}	
	+/-0.213	+/- 0.005	+/-0.049	+/-0.132	+/-2.49	+/-0.723	
Tuber filling (Fill)	Ctrl+	13.9 ^{ab}	0.26 ^{ab}	3.1 ^b	29.6 ^d	65.3 ^{de}	5.3 ^{bc}
		+/- 0.143	+/- 0.008	+/-0.065	+/-0.164	+/-1.55	+/-0.129
	-Tub	14.7 ^a	0.26 ^{ab}	3.1 ^b	29.8 ^{cd}	67.3 ^{cde}	6.1 ^{bc}
		+/-0.126	+/- 0.006	+/-0.078	+/-0.148	+/-1.68	+/-0.181
	-Fill	3.8 ^e	0.05 ^c	0.9 ^d	30.2 ^{bcd}	107.3 ^a	11.4 ^a
		+/- 0.180	+/- 0.004	+/-0.056	+/-0.149	+/-4.90	+/-0.764
Ctrl-	4.9 ^d	0.06 ^c	1.2 ^c	30.0 ^{bcd}	119.0 ^a	7.4 ^b	
	+/-0.204	+/- 0.004	+/-0.066	+/-0.16	+/-4.61	+/-0.657	
Senescence (Sen)	Ctrl+	12.9 ^c	0.28 ^{ab}	3.3 ^{ab}	29.7 ^{cd}	55.9 ^{ef}	4.3 ^c
		+/- 0.147	+/- 0.007	+/-0.054	+/-0.201	+/-2.11	+/-0.147
	-Tub	13.2 ^{bc}	0.32 ^a	3.2 ^{ab}	29.9 ^{bcd}	49.8 ^f	4.7 ^c
		+/- 0.131	+/- 0.008	+/-0.060	+/-0.186	+/-2.10	+/-0.19
	-Fill	3.6 ^e	0.07 ^c	0.9 ^{cd}	31.0 ^a	63.4 ^{def}	5.0 ^{bc}
		+/- 0.300	+/- 0.007	+/-0.073	+/-0.190	+/-2.94	+/-0.543
Ctrl-	5.2 ^d	0.08 ^c	1.3 ^c	30.6 ^{abc}	88.8 ^b	5.0 ^{bc}	
	+/- 0.274	+/- 0.007	+/-0.067	+/-0.202	+/-3.56	+/-0.232	

* Means with the same letter were not significantly different ($p < 0.05$) Tukey.

3.4. Leaf area

Significant differences were found ($\text{Pr}(>F) = 0.00597$). Leaf area was reduced by water deficit, with lower values in the -Tub, Ctrl-, and -Fill treatments compared to Ctrl+. The latter showed the highest values with 256.1 dm² plant⁻¹ for Mambra and 209.80 dm² plant⁻¹ for Criolla Colombia at the onset of senescence. In -Fill, leaf growth slowed in Mambra, while -Tub plants showed recovery after rehydration. Finally, Ctrl- showed slow but progressive growth until harvest, being more pronounced in Mambra (Figure 4).

3.5. Dry matter of the aerial part of the plant

The accumulation of dry matter in the leaves showed significant differences ($\text{Pr}(>F) = 0.0168$), reaching its maximum at the onset of senescence with 51.99 g plant⁻¹ in Mambra and 47.47 g in Criolla Colombia in the Ctrl+ treatment. It was observed that the -Fill treatment stopped growing after irrigation was suspended, and that there was a high recovery in -Tub, mainly in Criolla Colombia (Figure 5).

Significant differences were also found in dry matter accumulation in the stem ($\text{Pr}(>F) = 3.71 \times 10^{-10}$), with higher

values in Criolla Colombia, especially in the Ctrl+ and -Tub treatments. In the -Fill and Ctrl- treatments, the values tended to equalize (Figure 5).

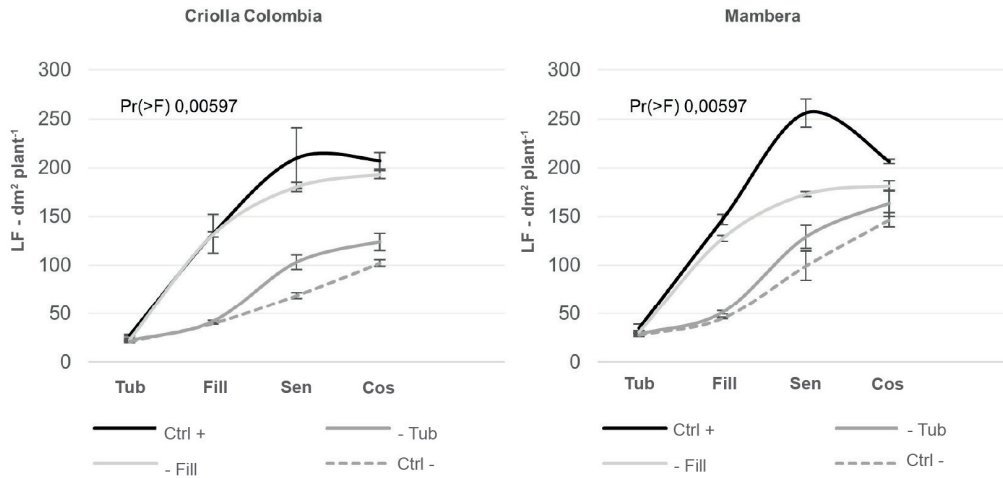


Figure 4. Leaf area by effect of phenological stage, soil moisture treatments, and cultivar on *Solanum phureja* plants under greenhouse conditions.

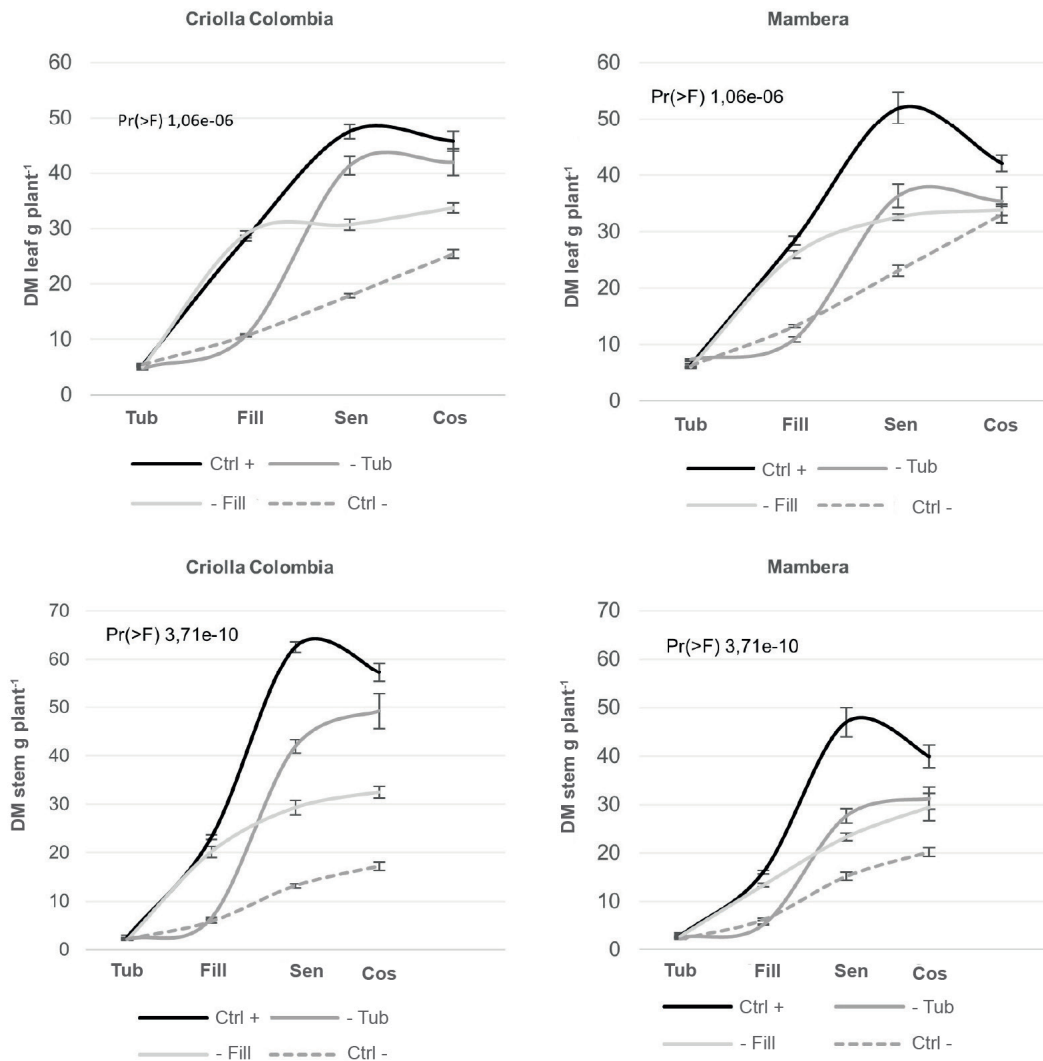


Figure 5. Dry matter accumulation in aerial part of the plant by effect of phenological stage, soil moisture treatment, and cultivar in *Solanum phureja* plants under greenhouse conditions.

3.6. Dry matter of the belowground part of the plant

The dry matter of the root, stolon, and tuber showed significant differences with $\text{Pr}(> F)$ 0.000129, 7.35×10^{-5} , and 0.00597, respectively. For the root, differential growth patterns were identified between cultivars according to the stage of stress influence, with the highest values occurring at the onset of senescence with 5.48 and 5.35 g plant^{-1} for Criolla Colombia in -Fill and for Mambera in Ctrl+, respectively (Figure 6). In addition, it was observed that from the start of filling, Criolla Colombia-Fill continued to grow above the other treatments until harvest. In contrast, Mambera-Fill stopped growing.

As for stolons, the peak accumulation for all treatments occurred at the onset of senescence, with Criolla Colombia-Fill showing the highest values at $1.77 \text{ g plant}^{-1}$. In terms of tuber dry matter accumulation, Mambera was highest in the Ctrl+ treatments with $213.77 \text{ g plant}^{-1}$, -Tub with $107.13 \text{ g plant}^{-1}$, and -Fill with $80.99 \text{ g plant}^{-1}$ compared to Criolla Colombia.

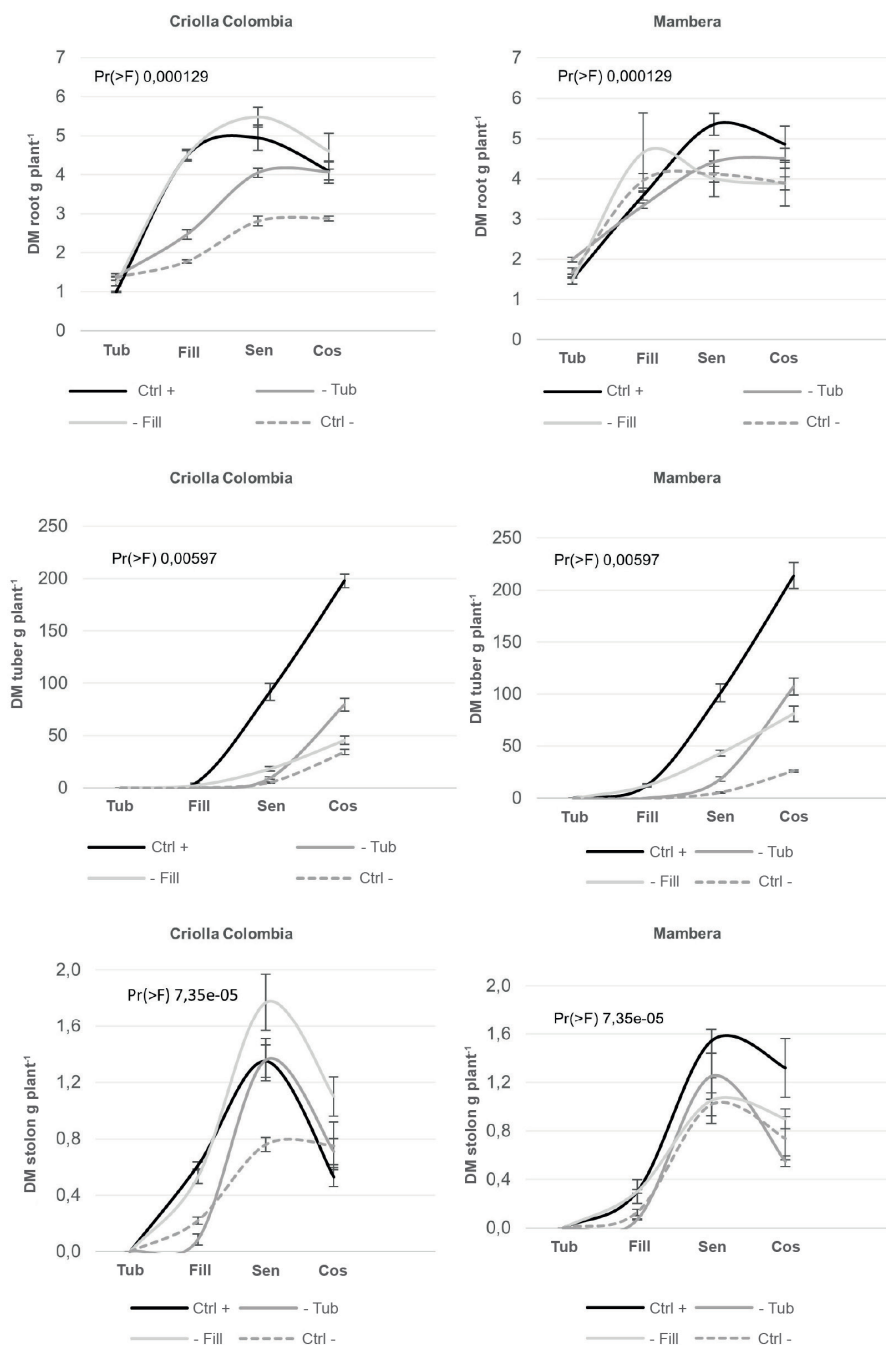


Figure 6. Belowground biomass measured from the top to the bottom of the root, tuber and stolon by the effect of phenological stage, soil moisture treatments, and cultivar in *Solanum phureja* plants under greenhouse conditions.

3.7. Yield

In terms of yield, it was observed that the cultivars exhibited different behavior in their yield components, with higher values for Mambra than for Criolla Colombia in -Tub in the variables harvest index with 59.47%, yield per plant with 468.6 g plant⁻¹, and average tuber weight with 24.1 g tuber⁻¹. As to what regards the variable number of tubers [NTu] per plant, Criolla Colombia in -Tub and -Fill was higher with 27 NTu plant⁻¹ (Table 4).

Table 4. Yield components at harvest due to the effect of cultivar and water deficit stress treatments on *Solanum phureja* plants.*

Treatment	Crops	Harvest/Crop Index (%)	Yield (g planta ⁻¹)	Number of tubers per plant ⁻¹	Average tuber weight (g tuber ⁻¹)
Ctrl+	CC	64.64 ^b +/-0.962	659.9 ^b +/-15.6	27 ^a +/-0.967	24.9 ^b +/-1.27
	MAM	70.49 ^a +/-1.73	841.3 ^a +/-32.6	19 ^b +/-0.981	47.8 ^a +/-3.08
-Tub	CC	45.230 ^d +/-3.35	302.5 ^d +/-21.0	27 ^a +/-1.46	11.4 ^c +/-0.849
	MAM	59.47 ^c +/-3.03	468.6 ^c +/-28.4	21 ^b +/-1.29	24.1 ^b +/-1.74
-Fill	CC	38.32 ^c +/-2.12	175.6 ^c +/-10.1	27 ^a +/-1.29	6.6 ^c +/-0.38
	MAM	53.60 ^d +/-2.48	369.3 ^d +/-20.8	18 ^b +/-0.778	21.0 ^b +/-1.57
Ctrl-	CC	42.19 ^c +/-2.51	144.4 ^c +/-8.93	20 ^b +/-1.03	7.4 ^c +/-0.441
	MAM	31.13 ^c +/-1.21	175.8 ^c +/-33.0	9 ^c +/-0.734	18.5 ^b +/-2.06

4. Discussion

Responses to water deficit were identified where the evaluated parameters interacted, being determined by the cultivar and the phenological phase of stress occurrence, consistent with the findings reported by Ramírez et al. (2014) in similar studies conducted on potatoes under protected and field conditions. For their part, Fang and Xiong (2015) determined categories of response to water stress adaptation, integrating the action of physiological parameters, as highlighted in this study.

The behavior of leaf and xylem water potential depended on environmental conditions during the day and the intensity of the water deficit. A greater vapor pressure deficit at midday increases transpiration, which contributes to intensifying stress at that time of day. Authors such as Pino et al. (2016) have described values for xylem water potential of 0.59 MPa with 100% irrigation and -1.15 MPa with 25% irrigation. Regarding leaf water potential, Díaz Valencia (2016) reported values ranging from -1.34 MPa to -1.56 MPa under stress conditions, similar to those resulting from this research (Figure 1).

The decrease in leaf water potential causes a loss of cell turgidity, affecting plant growth, limiting its structural and functional development (Vila, 2011). As a physiological response, the plant closed its stomata as a mechanism to reduce water loss through transpiration, although at the cost of restricting gas exchange and photosynthetic activity (Gervais et al., 2021). This process leads to a reduction in leaf area, either through a decrease in the number of leaves or through a limitation in their expansion, which constitutes an adaptation strategy to minimize water demand (Hill et al., 2021; Mahmud et al., 2015). Furthermore, under conditions of water stress, the plant increases its energy in root development translating

into an increase in the root/leaf ratio, favoring soil exploration and water uptake (Hill et al., 2015). Similarly, osmotic adjustment is activated through the accumulation of compatible solutes, which reduces osmotic potential and preserves cell turgidity, thus helping to maintain tissue moisture and essential physiological processes during drought. (Sánchez-Rodríguez et al., 2010).

The stomatal closure observed resulted in an increase in leaf temperature, a decrease in transpiration and photosynthesis, and a reduction in CO₂ uptake and, as a consequence, in carbohydrate production and yield (Ariza et al., 2020). Prolonged increases in leaf temperature under severe stress could have negative side effects on photosynthesis, respiration, membrane stability, hormone modulation, and secondary metabolites due to water deficit stress (Kim et al., 2017; Paul et al., 2016). These parameters were not evaluated within this study, but could be the subject of further research in order to understand the effect of leaf temperature as a covariate that can modulate the response, contribute to increasing the severity of stress, and, according to Gerhards et al. (2016), may be of interest for remote sensing of stress processes.

Plants subjected to stress showed higher WUE_i during the tuber filling phase. WUE (W/E, WUE_i) refers to the ability to achieve photosynthesis rates with less water loss. The difference between W/E and WUE_i is that W/E depends on the plant and environmental conditions, so that the same stomatal opening can result in different levels of transpiration depending on variations in temperature and humidity. WUE_i, on the other hand, measures the leaf's ability to regulate A and g_s independently of atmospheric conditions. Therefore, the latter parameter may be more related to the plant's tolerance or adaptability to drought conditions (Medrano et al., 2007).

WUE_i and reduced leaf area are characteristics that improve yield in situations of severe stress (Tardieu, 2013). However, this approach is not suitable in conditions of moderate drought, where cultivars with low WUE_i may be more efficient (Blum, 2009). According to the results obtained, it can be observed that during the tuberization phase, there was lower WUE_i, and the smaller leaf area during this phase resulted in low total transpiration, thus allowing photosynthetic processes to remain active through the use of small pulses of water generated internally by the plant due to low transpiration rates.

Similar to what was observed in this study, the reduction in leaf area not only decreases water losses, but also causes an increase in chlorophyll concentration and delays senescence (Ramírez et al., 2014; Rolando et al., 2015). This phenomenon has been linked to drought-tolerant cultivars, as it indicates lower photooxidation, chlorophyll degradation, and the maintenance of certain physiological activities due to the activation of genes related to stress response (Alhoshan et al., 2019; Ariza et al., 2020; Zhang et al., 2014). Tolerance mechanisms include damage mitigation through protective enzymes, osmotic adjustment, and chlorophyll increase (Fang & Xiong, 2015).

The increase in greenness during the senescence phase extends photosynthesis by lengthening the life cycle. This behavior is a strategy for escaping drought, which is associated with adjustments in the duration of the crop's phenological phases (Araus et al., 2002). Studies by Hörtensteiner (2009) and Thomas and Howarth (2000) report prolonged functional and non-functional greenness. The former involves an increase in chlorophyll and photosynthetic capacity, while the latter does not involve an increase in this capacity. In the present study, it was observed that photosynthesis and chlorophyll concentration during senescence were higher in the Ctrl- and -Tub treatments than in the treatments under the same water conditions. Likewise, a progressive increase in leaf area and leaf dry matter was observed in Ctrl- for this phase, which could indicate prolonged functional greenness. However, this must be validated in subsequent studies, with a focus on detailed evaluations of crop phenology under water deficit conditions.

Regarding the greenness of non-functional leaves, also known as cosmetic greenness, authors such as Rolando et al. (2015) reported that the genotypes with the highest susceptibility to drought identified in their studies were those that increased chlorophyll concentration the most after water restriction. In turn, Ramírez et al. (2014) mention that the increase in chlorophyll concentration can have possible negative consequences on yield due to extra energy costs and physiological imbalance between growth and investment in secondary metabolism. Therefore, chlorophyll behavior is a variable that needs to be analyzed comprehensively in order to define tolerance, or susceptibility.

The response per action of the cultivars was decisive in this study, coinciding with the results obtained by Rodríguez-Pérez et al. (2017), who compared four cultivars of *Solanum tuberosum* and found differences in their physiological response under stress. The earlier tuberization, low stomatal conductance, and smaller number and larger size of tubers contributed to improving the response of Mambera compared to Criolla Colombia (Ariza et al., 2020). According to Deblonde and Ledent (2001), it is necessary to further study the

phenology of cultivars and their response to water deficit, suggesting that shorter-cycle cultivars would escape late periods of drought.

Finally, when stress occurred early, there was greater recovery and control of moisture loss. According to Fang and Xiong (2015), resilience is the ability to resume growth and increase yield after exposure to drought stress. In addition, authors such as Rowland et al. (2012) have emphasized that mild stress in the early stages can lead to acclimatization. In contrast, the present study showed that when stress occurred later, it was more severe due to the large leaf area and growing source organs, meaning that the plant prioritized completing the consolidation of its yield components (tuber size and maturation) over the plant's aerial growth. This could even shorten the plant's life cycle, but further phenological evaluations are needed in this respect.

Beyond this research, recent studies focused on identifying molecular mechanisms associated with tolerance to this type of stress are referenced. On the one hand, Wei et al. (2025) characterized the StERF79 gene, a transcription factor of the AP2/ERF family, whose overexpression improves drought tolerance by activating genes related to the accumulation of osmoprotectants such as proline, SOD, POD, CAT, and late-early response (LEA) proteins, such as StDHN-2, while MDA content decreased under water stress conditions. On the other hand, Pieczynski et al. (2018), through large-scale transcriptomic analysis (RNA-seq), identified multiple genes expressed under drought conditions, functional candidates such as MAPKKK15 nutrient transporters, whose validation in *Arabidopsis* confirmed their conserved role in the response to water stress. These findings open up new possibilities for both marker-assisted genetic improvement and genetic engineering strategies aimed at mitigating the effects of climate change on this strategic crop.

5. Conclusions

The physiological response of *Solanum phureja* to water deficit stress depends on a combination of factors such as drought intensity, the phenological stage at which stress occurs, and the cultivar exposed to this condition. Therefore, integrated analysis of the behavior of various groups of variables according to their type allows us to understand complex responses in order to define cultivars that are tolerant or susceptible to drought. Associating these results with climate forecasts will be strategic for making agronomic management recommendations for the crop and, thus, reducing losses. For example, stress in the early stages of the crop, such as tuberization, favors the plant's water memory, acquiring efficient water use during the remaining crop cycle. This, can be beneficial for future more severe water deficits. Stress in intermediate crop stages, such as tuber filling, requires supplemental irrigation depending on its intensity. Furthermore, defining planting seasons will help establish escape windows from severe crop water deficits in the most susceptible phenological stages, define irrigation schedules, and fractionate fertilization.

The Mamberra cultivar was characterized by producing fewer tubers, but of larger size. Additionally, under water deficit conditions, it prioritized tuber growth over the aerial part of the plant, which favored its productive response under these conditions by allowing the harvest of commercial-sized tubers. Unlike the Criolla Colombia cultivar, which produced small tubers under water deficit conditions that were unsuitable for commercialization. The latter cultivar is more suitable for planting under optimal precipitation conditions for the crop.

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Contributor roles

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- Hyrcania Vanessa López Peñafiel: conceptualization, investigation, funding acquisition, resources, super-

vision, visualization, writing – original draft, writing – review & editing.

- Pedro Rodríguez Hernández: data curation, investigation, methodology, validation, visualization, supervision, writing – original draft, writing – review & editing.

Ethical implications

Ethics approval not applicable.

Conflict of interest

The authors declare that they have no affiliation with any organization with a direct or indirect financial interest that could have appeared to influence the work reported.

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