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The Combined Impact of Higher Temperatures and Water Deficit During Tuber Bulking Induces Contrasting Photosynthetic Performance

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Abstract

In Chile, most potato crops are cultivated under rainfed systems, frequently facing temperature increases and water deficits during the growing season. This field study aimed to evaluate the physiological responses and genotypic variations between the Chilean native potato variety Chona Negra and commercial varieties (Karú INIA and Desiree) when exposed to moderately high temperatures (+5.0 to+5.9 °C) for 40 days during the tuber bulking phase under different hydro- (or water availability) conditions. Four treatments were applied: (i) ambient temperature with rainfed conditions (T0H0), (ii) high temperature with rainfed conditions (T1H0), (iii) ambient temperature with irrigation (T0H1), and (iv) high temperature with irrigation (T1H1). The results showed that lower water availability and a moderate temperature increase (+5 °C) affected the leaf pigment content, photosynthetic performance and, chlorophyll fluorescence in both commercial and native potato genotypes. While moderately high temperatures and water deficits generally did not have stronger combined effects than each condition alone, our findings highlight the critical role of water availability in environments like southern Chile. Notably, the native potato, Chona Negra, exhibited enhanced photosynthetic performance under higher temperatures with irrigation, associated with increases in specific leaf area, stomatal conductance, photochemical quenching, and chlorophyll content. These findings suggest that Chona Negra may possess adaptive traits that improve its tolerance to heat stress when adequate water is available. In contrast, commercial varieties appeared more susceptible to limitations in photosynthetic activity under higher or prolonged periods of elevated temperatures.

Keywords Chlorophyll fluorescence · Climate change · Field experiment · Photosynthesis · *Solanum tuberosum* spp. *tuberosum*

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Introduction

In high-yielding environments for potato cultivation, such as southern Chile, current climatic scenarios include an increase in mean temperatures, particularly during the spring–summer season, and a decrease in rainfall of up to 50%. Previous findings suggest that in these environments a moderate increase in temperature (+ 2.3–5.3 °C) may positively affect potato yields, including for Chilean native varieties (Lizana et al. 2017). However, the physiological responses associated with these changes have not yet been extensively studied.

High temperatures and low water availability are major abiotic factors that limit plant photosynthesis, biomass production, and crop productivity in many agricultural regions worldwide, and they frequently have additional deleterious effects on plants (Monneveux et al. 2014; Birch et al. 2012; Dreesen et al. 2012). In potatoes, critical yield-determining processes such as tuberization, biomass partitioning, and tuber bulking are affected by heat stress and water deficit (Vos and Haverkort 2007; Monneveux et al. 2014), leading to significant losses in tuber yield and quality.

Supra-optimal temperatures induce a severe inhibition of CO_2 fixation and increased carbohydrate loss through a respiration increase (i.e., photo- and mitochondrial respiration) in sensitive cultivars, resulting in reduced carbohydrate translocation to the tubers (Bushnell 1925; Reynolds et al. 1990; Hasanuzzaman et al. 2013; Levy and Veilleux 2007; Fleisher et al. 2006). Conversely, temperature increases in areas with sub-optimal growing temperatures could potentially benefit physiological processes such as photosynthesis.

In drought-sensitive potato cultivars, water deficit triggers stomatal closure, inhibiting photosynthesis and limiting gas exchange (Fleisher et al. 2008; Schapendonk et al. 1989; Salazar et al. 2016). Additionally, prolonged water deficit has been shown to reduce leaf area index (LAI) and leaf area duration (LAD), leading to decreased net CO_2 assimilation and reduced interception of photosynthetically active radiation (PAR) (Fleisher et al. 2008; Deblonde and Ledent 2001).

Both high temperatures and low water availability conditions also affect Rubisco activity and content, the quantum efficiency of photosystem II (ΦPSII), and photosynthetic pigments. A sharp drop in photosynthetic carbon fixation at 25 °C in potatoes (Ku et al. 1977; Dwelle et al. 1981) has been associated with reduced ΦPSII, considered one of the most thermolabile components of the photosynthetic apparatus (Prange et al. 1990). Water deficit and temperatures above 30 °C accelerate chlorophyll degradation in potato leaves, decreasing Chl a + b content and the Chl/carotenoid ratio while increasing the Chl a/b ratio (Wahid et al. 2007). This indicates substantial degradation of the light-harvesting chlorophyll-binding proteins associated with PSII (Brestic et al. 2014).

This study aimed to assess the genotypic variation in potatoes in response to a moderate increase in air temperature (c. + 5 °C) under different water availability scenarios (i.e., with and without irrigation) during tuber bulking in field conditions within a high-yielding environment of southern Chile. We investigated differences between Chona Negra, a Chilean native genotype, and two commercial

potatoes with respect to their photosynthetic performance and chlorophyll fluorescence to identify traits associated with susceptibility or adaptation to future climate conditions.

Materials and Methods

Site, Crop Management, Treatments, and Experimental Design

The experiment was carried out under field conditions at the experimental station of the Universidad Austral de Chile in Valdivia (39° 47' LS, 73° 14' W, 19 m a.s.l.) in a Duric Hapludand soil from the Valdivia series**.** This area has a temperate rainy climate, characterized by high rainfall concentrated in the winter (c. 300 – 400 mm) (i.e., between June and September—Southern Hemisphere) (Gonzales-Reyes and Muñoz 2013). The planting date was October 10th, 2015, and the plant density was 5.3 plants m^{-2} in plots (experimental units) of 4 rows, 0.75 m apart, and 3 m long. Plots were fertilized with 80 kg N ha^{-1}, 120 kg P_2O_5 ha^{-1}, and 180 kg K_2O at planting and 50 kg N ha^{-1} and 60 kg K_2O at ridging, according to previous soil analyses. Insecticides and fungicides were used to control biotic damage per the manufacturer's instructions.

The treatments consisted of the combination of the following factors: (i) three potato genotypes: Karú INIA, Desiree, and Chona Negra (ii); two temperature conditions: ambient temperature (T0) and high temperature (T1) applied for 40 days from the beginning of the tuber bulking development stage; and (iii) two hydro- (or water availability) scenarios during the crop cycle: rainfed (H0; 297 mm) and irrigated (H1; 437 mm). The beginning of tuber bulking in both commercial genotypes (Karú INIA and Desiree) began on day 76 after planting and on day 83 after planting in the native genotype (Chona Negra). Plots were arranged in a split-plot design with three replicates (blocks), where the water treatments were assigned to the main plots, and thermal treatments and genotypes were randomly assigned to subplots.

The Desiree commercial variety has been identified as sensitive to high temperatures (Ahn et al. 2004; Levy 1986); it has also shown moderate tolerance to non-severe drought and no tolerance to severe drought (Levy 1986). Karú INIA has proven to be tolerant to drought stress (Kalazich et al. 2004; Pino and Gonzales 2016), but previous studies have also shown that it is more sensitive than Desiree to a moderate increase in temperature (Lizana et al. 2017). The native genotype Chona Negra (NG-5) from the Chilota Potato Genebank (Universidad Austral de Chile) is originally from the Chonos Archipelago. It has an erect canopy structure, a denser and deeper root system than the two commercial varieties, and tubers rich in total polyphenols and antioxidant capacity (Ah-Hen et al. 2012; Ávila-Valdés et al. 2020, 2024). The tuber yield of Chona Negra is lower, although yield stability across thermal environments is higher than in commercial varieties (Lizana et al. 2017).

The temperature increase was around 5.5 °C above the ambient temperature (Table 1) using polyethylene chambers equipped with thermostatic electric heaters. Temperature was controlled by thermal sensors placed at canopy height, which were connected to a temperature regulator to increase crop temperature, as described in

Table 1 Mean ambient temperature (T0) and temperature inside the chambers during thermal treatments (T1H0 and T1H1), during daytime (7:00-21:00 h), nighttime (21:00-7:00 h), and daily average (all day)

Temperature (°C)					
Time	T0	T1H0	T1H1	Difference T1H0 − T0	Difference T1H1 − T0
7:00-21:00	20.1 ± 0.8	25.0 ± 1.2	24.6 ± 1.1	4.9 ± 0.8	4.5 ± 0.7
21:00-7:00	13.2 ± 0.4	20.0 ± 0.7	18.5 ± 0.5	6.8 ± 0.6	5.3 ± 0.4
All day	16.5 ± 0.9	22.5 ± 1.1	21.5 ± 1.1	5.9 ± 0.7	5.0 ± 0.5

Differences correspond to treatment temperature minus ambient air temperature (T0) when thermal treatments were imposed. Treatments: *T1H0* high temperature under rainfed conditions, *T1H1* high temperature under irrigation conditions. Values are means of three replications ± standard error

Ávila-Valdés et al. (2020). Chambers of 3 m × 3 m × 1 m were built of wood and covered by transparent polyethylene (100 µm thick). The tops of the chambers were removed daily between 8:00 am and 6:00 pm to avoid extreme temperatures and prevent solar radiation interception. Thermal sensors placed at canopy height registered the air temperature during the crop cycle every 15 min.

Plant Measurement

Fully developed leaves from the upper strata of the canopy were collected one week before the beginning of the thermal treatments, at two points during the thermal treatment, and one week after the end of thermal treatments. For the determination of total chlorophyll (Chl a + Chl b) and total carotenoid contents (xanthophylls + β-carotene), frozen leaf samples (0.25 g) were ground into a fine powder in liquid N_2 before adding 80% (v/v) cold acetone and vortexing for 1 min. The extract was centrifuged at 1200 × g for 5 min at 4 °C, and the absorbance of the clarified supernatant was determined at 663 nm (Chl a), 646 nm (Chl b), and 470 nm (carotenoids). Pigment concentrations (mg g^{-1} FW) were calculated as described by Steubing et al. (2002) and Lichtenthaler and Wellbrum (1983). The total soluble protein was extracted from 100 mg of frozen leaf samples using 50 mM HEPES buffer (pH 7.4) and quantified by the Bradford method (Bradford 1976).

Gas exchange was measured with an infrared gas analyzer (IRGA) (LCpro model, ADC BioScientific Ltd. USA) equipped with a cuvette unit of 6.25 cm^2 leaf area. The maximum photosynthetic rate (Amax), stomatal conductance (gs), and water use efficiency calculated as the ratio of Amax and transpiration rate (E) (Amax/E) were determined at 1300 µmol m^{-2} s^{-1} photosynthetic photon flux density (PPFD). For each plot, three fully developed leaves from the upper strata of the canopy from independent plants were randomly selected for analysis. Additionally, chlorophyll fluorescence was measured in the same leaves used for photosynthesis evaluation using a pulse-modulated fluorimeter (Type FMS2, Hansatech Instruments, King's Lynn, UK). The leaves were dark-adapted for 30 min and then illuminated with a first pulse of saturating light at 15,000 µmol m^{-2} s^{-1} followed by a constant intensity of actinic light (2000 µmol m^{-2} s^{-1})

for 1 min. A second saturating pulse of 15,000 µmol m^{-2} s^{-1} was subsequently applied. Maximum photochemical efficiency (Fv/Fm) was used as an indicator of the potential quantum yield (photochemical efficiency) of PSII (Maxwell and Johnson 2000). The optimal values for this parameter are around 0.83 (Björkman and Demming 1987). Additionally, the photochemical quenching coefficient (qP), non-photochemical quenching coefficient (NQP), and photosystem II efficiency (ΦPSII) were recorded. Measurements were performed between 10:00 am and 12:00 pm at four-time points, under ambient PAR levels fluctuating between 1000 and 1300 µmol m^{-2} s^{-1}. This timing coincided with the collection of leaves for pigment and soluble protein determination.

Furthermore, the net photosynthesis-light response curves were determined 20 days after the beginning of the thermal treatments at 10 PPFD (0, 150, 350, 550, 700, 1000, 1200, 1400, 1600, and 1800 µmol $m^{2\ s-1}$). The leaf photosynthetic light response curves were fitted using a non-rectangular hyperbola (NRH) model, as described by Marshall and Biscoe (1980):

$$\theta P_n^2 - \left(Pg_{max} + \alpha I - \theta R_d\right)P_n + \alpha I\left(Pg_{max} - (1-\theta)R_d\right) - R_d Pg_{max} = 0$$

where α is the photon-use efficiency of CO_2-assimilation on the incident light basis, θ is the convexity term, P_n is net photosynthesis rate, Pg_{max} is light-saturated gross photosynthetic rate, I is incident photosynthetic photon flux density and R_d is dark respiration rate. The Pn_{max} was calculated as $Pn_{max} = Pg_{max} - (1-\theta)R_d$ (Marshall and Biscone 1980). The parameters Pg_{max}, α, θ, and R_d were estimated using the non-linear least squares curve fitting procedure with the Solver routine in Microsoft Excel, through successive iterations to minimize the residual sum of squares (Lobo et al. 2013).

Rubisco content was measured in soluble protein extracts from frozen, fully expanded leaf samples harvested on the 26th day after the beginning of the thermal treatments, using the protocol modified by Bassi et al. (1987). The protein content of the extracts was determined using the Bradford method. According to Towbin et al. (1979) and Chen et al. (2014), SDS-PAGE and immunoblot analysis were performed. The immunoblot analysis was performed using a rabbit anti-Rubisco polyclonal antibody (Cusabio, China) as a primary antibody and anti-rabbit IgG-alkaline phosphatase (Sigma-Aldrich) as the secondary antibody. Rubisco standard was prepared from spinach (Ma et al. 2009) and to quantify the signal intensities in the immunoblots, ImageJ 1.53 k software was used.

At the same time as Rubisco content samples were taken, the leaf's relative water content (RWC%) was determined. Twenty-seven 6-mm leaf discs were collected from each plot between 11:00 am and 12:00 pm and weighed immediately to estimate their fresh weight (FW). The turgid weight (TW) was determined after immersing the leaf discs in distilled water for 6 h, and the dry weight (DW) was measured after drying the leaf discs at 70 °C in an oven for 24 h. The relative water content (RWC%) was calculated as follows: RWC% = [(FW-DW) / (TW-DW)] × 100 (Steubing et al. 2002). Additionally, the DW and leaf area of the samples were used to calculate the specific leaf area (SLA) as cm^2 g^{-1} DW (Sun et al. 2014).

Statistical Analysis

A split-plot analysis of variance (ANOVA) was used to assess treatments effects on crop variables. The LSD test was used to identify significant differences ($P < 0.05$). All data were tested for normality and homogeneity of variance, and when appropriate, ln or square-root transformation was used. To compare the physiological data obtained in this experiment with previously published agronomic data from the same study (Avila-Valdés et al. 2020), a principal component analysis (PCA) was conducted with R 4.3.2 Statistics software ('FactoMineR' package).

Results

Environmental Conditions

During the crop cycle, the incident PAR averaged 11.03 MJ m^{-2} d^{-1} and accumulated rainfall was 296.7 mm with 50.9% of the total rainfall occurring between emergence and flowering (Fig. 1). The mean air temperature during the growing season was 14.7 °C, and the mean maximum and minimum temperatures were 20.8 ± 0.3 °C and 8.6 ± 0.2 °C, respectively.

During the thermal treatments, initiated 40 days after the beginning of tuber bulking, the mean ambient temperature outside the chambers was 16.5 ± 0.9 °C. Within the chambers, the mean temperature increased significantly, reaching 22.5 ± 1.1 °C in the rainfed plots (T1H0) and 21.5 ± 1.1 °C in the irrigated plots (T1H1) (Table 1). Heated plots experienced temperatures above 30 °C (< 34 °C – mean 3.8 h day^{-1}) for approximately 34.0 ± 1.4 days (Fig. 2), while plots maintained at ambient temperature experienced temperatures above 30 °C only for 2 days (< 32 °C – mean 4.5 h d^{-1}).

Temperature regimes increased the air temperature by c. 5.9 ± 0.7 °C in T1H0 and 5.0 ± 0.5 °C in T1H1 (Table 1). The mean air temperatures between 7:00 am and 21:00 pm during the 40 days of thermal treatments were 20.1 ± 0.8 °C (T0),

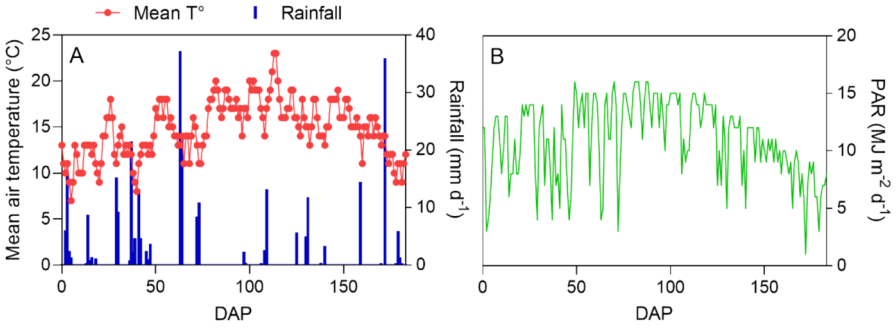


Fig. 1 Environmental conditions during the 2015/2016 growing season in Valdivia, Chile. (A) Mean daily ambient temperature and rainfall, (B) Photosynthetically active radiation (PAR). DAP: day after planting

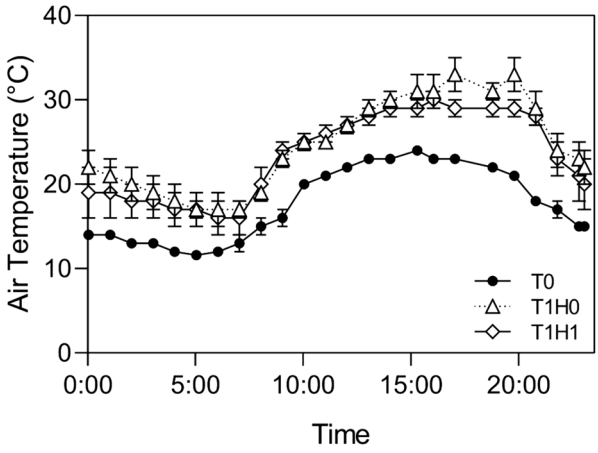


Fig. 2 Hourly air temperature variation along the thermal treatment period. Closed symbols show ambient temperature (T0), and open symbols show air temperature inside the polyethylene chambers (T1H0 and T1H1). Treatments: T1H0, high temperature under rainfed conditions; T1H1, high temperature under irrigation conditions. Values are means of three replications ± standard error

25.0 ± 1.2 °C (T1H0), and 24.6 ± 1.1 °C (T1H1) (Table 1). At night (21:00 – 7:00), the mean air temperatures were 13.2 ± 0.4 °C, 20.0 ± 0.7 °C and 18.5 ± 0.5 °C, respectively (Table 1). Increased heating within the chambers was mainly due to higher maximum temperatures without heat shock temperatures (Fig. 2).

Leaf Pigment Contents

The total chlorophyll content (i.e., Chl a + b) varied widely between genotypes, with Karú INIA showing the lowest average values (0.253 ± 0.03 mg g^{-1} FW) compared to Desiree (0.491 ± 0.05 mg g^{-1} FW) and Chona Negra (0.548 ± 0.03 mg g^{-1} FW) (Fig. 3A, B, C). All genotypes showed a higher total chlorophyll content and a higher Chl a + b/carotenoids ratio under ambient temperature and irrigation (T0H1). During the crop cycle, the commercial potato genotypes exhibited a similar decline in leaf total chlorophyll content across treatments (Fig. 3A, B). However, Chona Negra under irrigation (i.e., T0H1 and T1H1) reached higher contents, which declined more slowly compared to rainfed conditions (i.e. T0H0 and T1H0), independent of thermal treatment (Fig. 3C). The canopy-green maintenance for a longer period in Chona Negra was at the same time accompanied by a higher rate of Chl a + b/carotenoids (Fig. 3F). The total soluble protein content was similar across all potato genotypes (approximately 27.2 ± 2.6 mg g^{-1} FW) and showed a similar decline across treatments, except for Chona Negra, which exhibited a sustained increase of around 30% under T1H1 (Fig. 3I).

Photosynthetic and Fluorescence Parameters

Contrasting photosynthetic and fluorescence performances were observed between potato genotypes during the crop cycle (Fig. 4). Commercial genotypes under irrigation reached higher photosynthesis rates and stomatal conductance before thermal treatments. At the same time, Chona Negra did not show

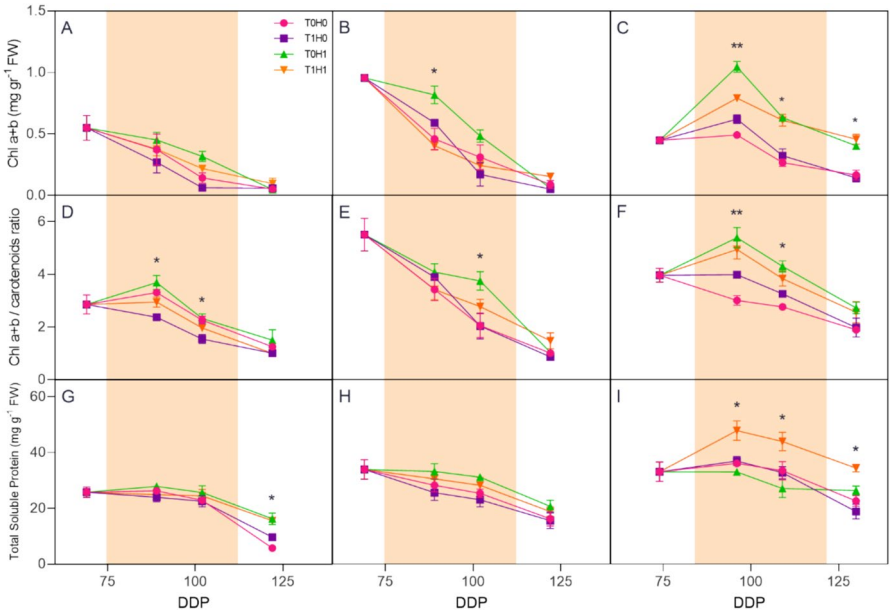


Fig. 3 Total chlorophyll content (Chl a + b) (**A**, **B**, **C**), total chlorophyll content/carotenoids ratio (**D**, **E**, **F**), and total soluble protein content (**G**, **H**, **I**) of fully expanded leaves of Karú INIA (left panels), Desiree (central panels) and Chona Negra (right panels) during the growing cycle by treatment. The colored area indicates the duration of thermal treatment according to genotypes. Treatments: T0H0, ambient temperature under rainfed conditions; T1H0, high temperature under rainfed conditions; T0H1, ambient temperature under irrigated conditions; T1H1, high temperature under irrigated conditions. Values are means of three replications ± standard error, and the asterisks indicate significant differences between treatments for each sampling date ($P < 0.05 = *$; $P < 0.01 = **$). DAP: day after planting

significant differences between water scenarios. Throughout the evaluation period, higher temperatures did not induce substantial changes in the photosynthesis and fluorescence performance of Karú INIA and Desiree. Despite both commercial genotypes responding quickly to the increase in temperature under rainfed conditions (i.e., T1H0), their photosynthesis, stomatal conductance, and Amax/E subsequently behaved similarly to the values observed under T0H0 (Fig. 4A, B, D, E, G, H). On the other hand, Chona Negra increased its photosynthesis rate by approximately 32% under higher temperatures and irrigation (i.e., T1H1) compared to the other treatments (Fig. 4C). This increase was accompanied by a significant rise in stomatal conductance (approximately 37%) and quantum yield of PSII (approximately 22%) (Fig. 4F,O). Notably, this improvement was not associated with a decrease in NPQ, which remained relatively constant over time (Fig. 4U).

The photosynthetic light-response curves differed between potato genotypes and treatments (Table 2). Under both water conditions, higher temperatures (i.e., T1H0 and T1H1) decreased the maximum net photosynthetic rate by approximately 43% in both commercial potatoes. This reduction was accompanied by a significant decrease in the photon-use efficiency of CO_2-assimilation on the

incident light basis. Conversely, irrespective of the water availability scenario, higher temperatures enhanced the maximum photosynthetic rate in Chona Negra; resulting in a threefold increase under irrigation. Additionally, only the commercial potatoes increased their dark respiration rates at higher temperatures, depending on the water scenario, while Chona Negra did not show significant changes.

Rubisco Content

The Rubisco content in leaves was significantly affected by the water regime ($P < 0.01$), temperature ($P < 0.001$), and potato genotype ($P < 0.001$), as well as their interactions (Fig. 5). Chona Negra exhibited approximately 2.3 times more Rubisco than commercial genotypes on average. Higher temperature only decreased Rubisco content in Karú INIA under rainfed conditions (c. 42%), while Desiree did not show significant changes. Conversely, Chona Negra nearly doubled its leaf Rubisco content at high temperatures regardless of water availability (i.e. T1H0 and T1H1).

Relative Water Content (RWC%) and Specific Leaf Area (SLA)

Higher temperatures did not significantly modify the RWC% of leaf tissue. However, it was significantly modified by available water ($P < 0.001$) and potato genotype ($P < 0.001$) (Fig. 6A). As expected, all irrigated genotypes showed a higher RWC%, with the commercial genotypes reaching the highest levels.

The interaction between the thermal regime, water scenario, and genotype induced changes in the SLA ($P < 0.001$) (Fig. 6B). On average, the native genotype Chona Negra showed a lower SLA (84.2 ± 3.3 cm^2 g^{-1}) than the commercial varieties Karú INIA (116.5 ± 5.8 cm^2 g^{-1}) and Desiree (98.3 ± 3.3 cm^2 g^{-1}). Higher temperatures increased the SLA of Karú INIA (c. 25%) under rainfed conditions (T1H0) and the SLA of Chona Negra (c. 32%) under irrigation conditions (T1H1); only Desiree decreased its SLA under high temperature and rainfed conditions.

Principal Components

To understand the association between the unpublished physiological response data and agronomic parameters previously published by Ávila-Valdés et al. (2020) for potato genotypes subjected to high temperatures and contrasting water conditions, we conducted a principal component analysis (PCA). PCA showed that 62.3% of the total variability in the data was explained by the principal component 1 (PC1) and the principal component 2 (PC2) (Fig. 7A, B). The PC1 revealed that yield, HI, mean tuber weight, RWC%, photosynthesis rate, stomatal conductance, Fv/Fm, and ΦPSII were positively correlated. On the positive side of PC1, starch, total phenols, total soluble protein of tubers, and dry matter tuber content were also positively correlated (Fig. 7A). PC2 revealed a negative correlation between proline content in tubers and photosynthesis rate, Fv/Fm, and ΦPSII. The second plot (Fig. 7B) showed the position of the three potato genotypes in response to thermal treatments under two water availability scenarios in the multivariate space of the first two PCs.

Fig. 4 Light-saturated net assimilation rate (Amax) (**A**, **B**, **C**), stomatal conductance (gs) (**D**, **E**, **F**), water use efficiency (Amax/E) (**G**, **H**, **I**), maximum quantum yield of PSII (Fv/Fm) (**J**, **K**, **L**)), quantum yield of PSII (ΦPSII) (**M**, **N**, **O**), photochemical quenching (qP) (**P**, **Q**, **R**) and non-photochemical quenching (NPQ) (**S**, **T**, **U**) of fully expanded leaves of Karú INIA (left panels), Desiree (central panels) and Chona Negra (right panels) during the growing cycle by treatment. The colored area indicates the duration of thermal treatment according to genotypes. Treatments: T0H0, ambient temperature under rainfed conditions; T1H0, high temperature under rainfed conditions; T0H1, ambient temperature under irrigated conditions; T1H1, high temperature under irrigated conditions. Values are means of three replications ± standard error, and the asterisks indicate significant differences between treatments for each sampling date ($P < 0.05 = *$; $P < 0.01 = **$). DAP: day after planting ▶

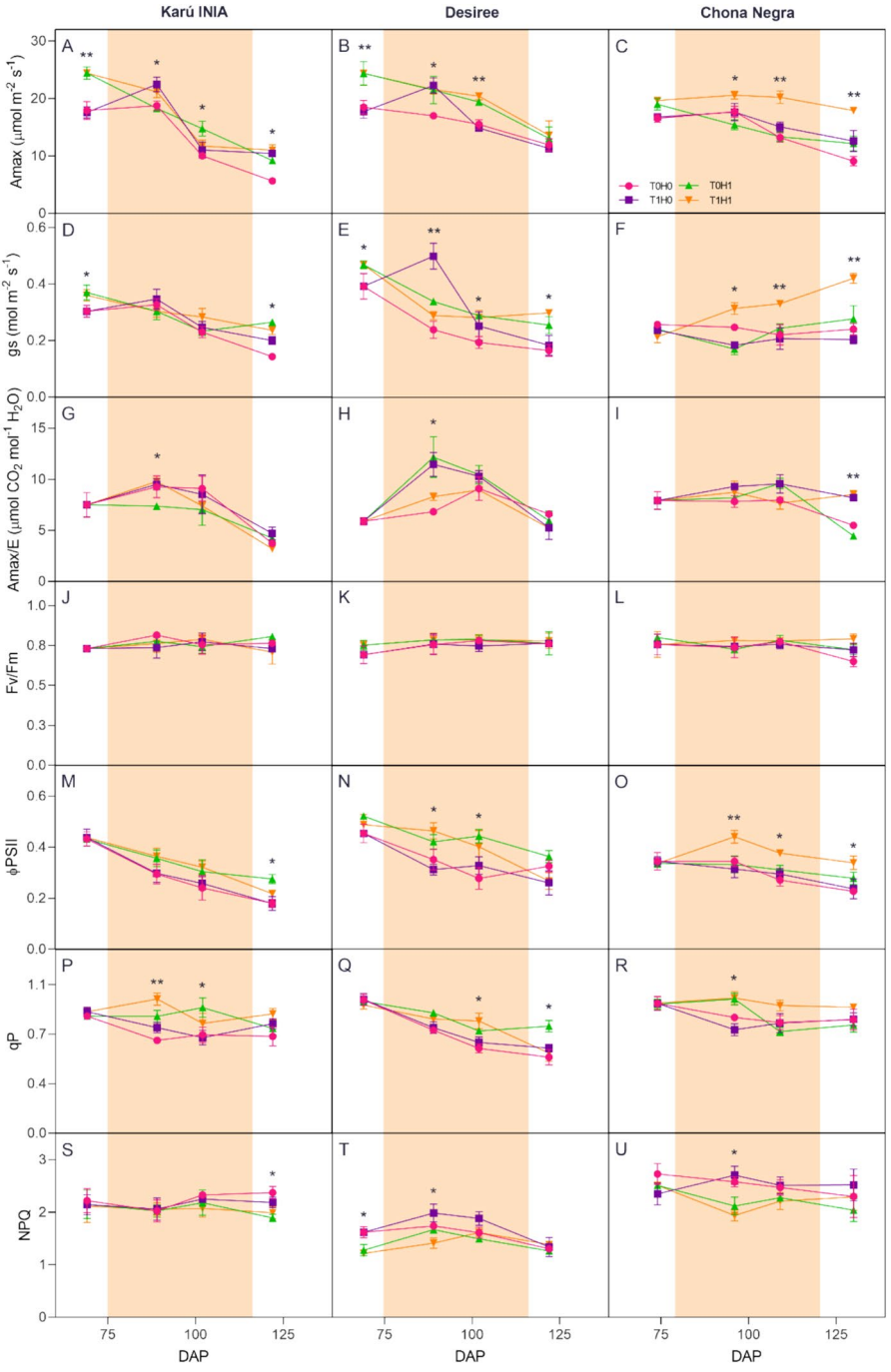
PC1 showed a clear opposition between commercial and native genotypes, with the commercial genotypes exhibiting higher yield, HI, mean tuber weight, RWC%, gs, ΦPSII, and photosynthesis rate. In contrast, the native genotype produced more tubers with higher total soluble protein, starch, and phenol contents. PC2 primarily separated the irrigation conditions, indicating a higher proline concentration in tubers under rainfed conditions.

Discussion

The potato crop is not tolerant to high temperatures and water deficit. In high-yielding environments, where crops grow near optimum temperatures, a slight increase in temperature can cause significant effects, especially under conditions of lower water availability. Few studies have investigated the impact of a moderate increase in air temperature (c. + 5 °C) during tuber bulking in high-yielding environments, especially at the physiological level, using open-closed polyethylene chambers under field conditions. In this field study, we investigated the differences between Chona Negra, a Chilean native genotype, and two commercial varieties regarding photosynthetic performance and chlorophyll fluorescence to identify traits associated with susceptibility or adaptation to future climate conditions.

Higher Temperatures Did Modify the Leaf Pigment Content But Did not Accelerate Canopy Senescence

During the heat period, the heated plots reached daily mean temperatures c. 22 °C (Table 1), optimal for the development of potato crops, including tuber bulking, starch synthesis, and photosynthetic carbon fixation (Wolf et al. 1991; Geigenberger et al. 1998; Struik 2007; Ku et al. 1977; Dwelle et al. 1981). However, these plots experienced temperatures above 30 °C (c. 4 h d^{-1}) during approximately 34 days. This cumulative thermal exposure and lower water availability induced a more rapid decline in total chlorophyll content (Fig. 4) in commercial potatoes without affecting the cycle length, as was published by Ávila-Valdés et al. (2020). In contrast, in the native potato Chona Negra, the maximum chlorophyll content attained and the reductions in cycle length were modulated primarily by water availability. These results suggest that commercial potatoes may be more susceptible to limitations


Karú INIA
Desiree
Chona Negra
A
B
C
D
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H
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L
M
N
O
P
Q
R
S
T
U
Amax (µmol m-2 s-1)
gs (mol m-2 s-1)
Amax/E (µmol CO2 mol-1 H2O)
Fv/Fm
ϕPSII
qP
NPQ
T0H0
T1H0
T0H1
T1H1
DAP
75
100
125

Table 2 Mathematical fitting results of light-response curves using non-rectangular hyperbola (NRH) model: maximum net photosynthetic rate (P_{nmax}), photon-use efficiency of CO_2-assimilation on the incident light basis (α), and dark respiration rate (R_d). Curves were performed 20 days after the beginning of the thermal treatments between 0 and 1800 µmol $m^{2\ s-1}$ PPFD. Treatments: T0H0, ambient temperature under rainfed conditions; T1H0, high temperature under rainfed conditions; T0H1, ambient temperature under irrigated conditions; T1H1, high temperature under irrigated conditions. Values are means of three replications ± standard error. Lower-case letters show significant differences for each potato genotype by Fisher's LSD test ($P < 0.05$)

Genotype	Treatment	Pn_{max}	α	R_d	R^{2a}
		µmol CO_2 m^{-2} s^{-1}	µmol CO_2 (µmol photon)$^{-1}$	µmol CO_2 m^{-2} s^{-1}	
Karú INIA	T0H0	11.3 ± 0.0 c	0.052 ± 0.000 b	0.31 ± 0.10 b	0.953
	T1H0	6.5 ± 0.1 d	0.042 ± 0.000 c	1.37 ± 0.49 a	0.930
	T0H1	25.6 ± 0.4 a	0.066 ± 0.001 a	1.31 ± 0.13 a	0.868
	T1H1	13.4 ± 0.2 b	0.055 ± 0.003 b	0.69 ± 0.29 b	0.926
Desiree	T0H0	17.6 ± 0.4 b	0.053 ± 0.001 b	1.39 ± 0.14 ab	0.904
	T1H0	8.6 ± 0.3 c	0.043 ± 0.001 c	1.74 ± 0.03 a	0.845
	T0H1	23.2 ± 0.5 a	0.063 ± 0.003 a	0.87 ± 0.36 b	0.920
	T1H1	16.4 ± 0.9 b	0.053 ± 0.001 b	1.78 ± 0.04 a	0.922
Chona Negra	T0H0	8.7 ± 0.1 c	0.044 ± 0.000 c	1.85 ± 0.07 a	0.861
	T1H0	13.6 ± 0.2 b	0.053 ± 0.001 b	1.46 ± 0.14 ab	0.922
	T0H1	11.8 ± 0.2 b	0.053 ± 0.000 b	1.19 ± 0.04 bc	0.874
	T1H1	34.6 ± 0.9 a	0.066 ± 0.001 a	1.03 ± 0.13 c	0.923
ANOVA	G	***	NS	*	
	I	***	***	NS	
	T	*	**	NS	
	GxI	***	NS	NS	
	GxT	***	***	NS	
	IxT	***	NS	NS	
	GxIxT	***	NS	*	

[a] coefficient of determination

[*] Significant at $P < 0.05$

[**] Significant at $P < 0.01$

[***] Significant at $P < 0.001$

in photosynthetic activity due to chlorophyll degradation and a shortened growing season under higher heat loads than those reached in this experiment from elevated temperatures and/or extended periods of high temperatures. In these scenarios, Karú INIA would have a comparative advantage over Desiree since it would have a lower mean Chl a + b/carotenoids ratio under T1H0, that is, a high proportion of carotenoids that would play a crucial role in protecting photosynthetic structures from oxidative stress caused by high temperatures and water deficit (Stra et al. 2022).

Throughout the crop cycle, a wide genotypic variance was observed among potato genotypes at photosynthetic level (Fig. 5). While Karú INIA showed minimal differences between treatments, the photosynthetic performance of Desiree was modulated mainly by water availability. In both commercial varieties, the higher temperatures

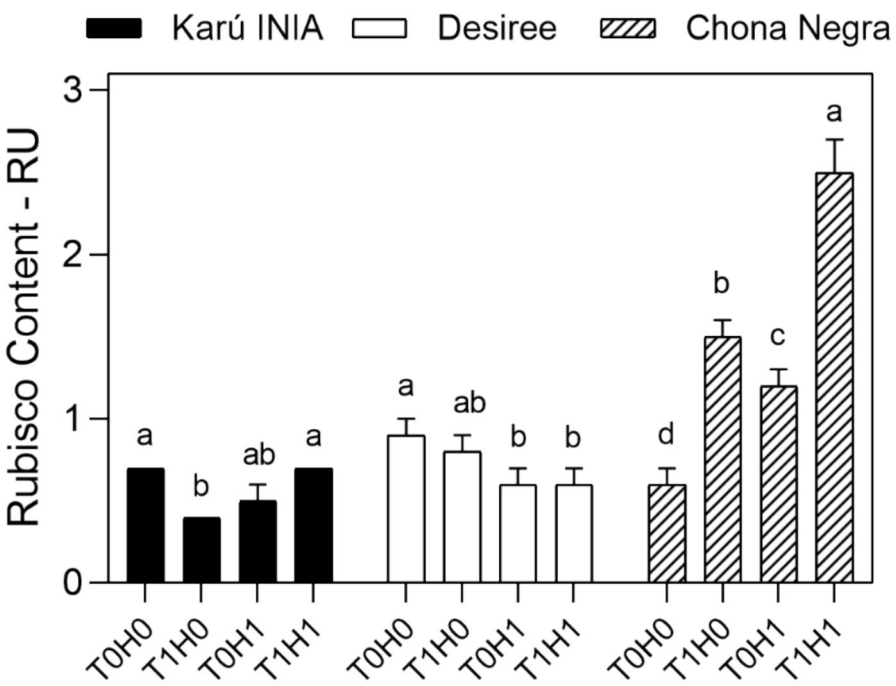

Fig. 5 Rubisco content in fully expanded leaves harvested 26 days after the beginning of the thermal treatments. Treatments: T0H0, ambient temperature under rainfed conditions; T1H0, high temperature under rainfed conditions; T0H1, ambient temperature under irrigated conditions; T1H1, high temperature under irrigated conditions. Values are means of three replications ± standard error. Lower-case letters indicate significant differences between treatments for each potato genotype ($P < 0.05$)

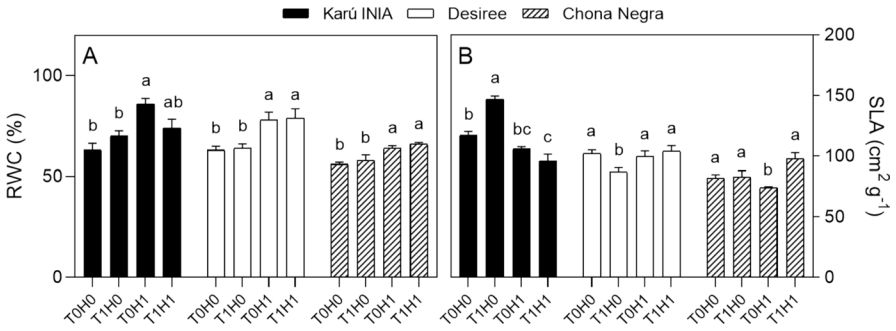

Fig. 6 Relative water content (RWC%) (**A**) and Specific Leaf Area (SLA) (**B**) of fully expanded leaves of three potato genotypes exposed to different thermal treatments and water regimens. Measurements were performed on fully expanded leaves 26 days after the beginning of the thermal treatments. Treatments: T0H0, ambient temperature under rainfed conditions; T1H0, high temperature under rainfed conditions; T0H1, ambient temperature under irrigated conditions; T1H1, high temperature under irrigated conditions. Values are means of three replications ± standard error. Lower-case letters indicate significant differences between treatments for each potato genotype ($P < 0.05$)

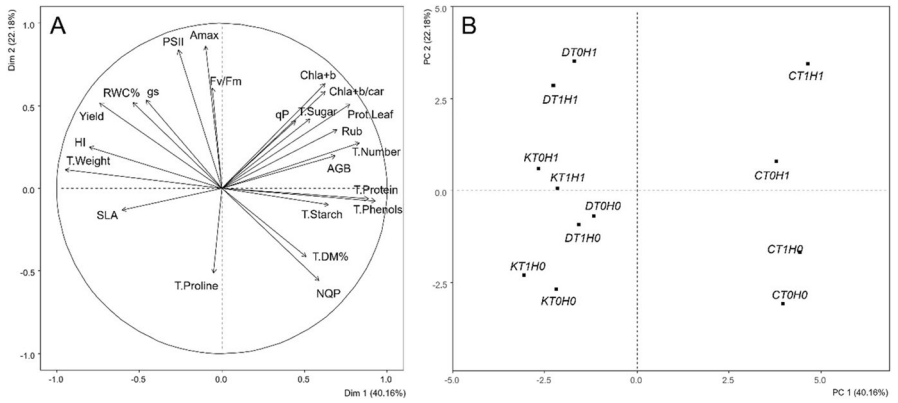

Fig. 7 Principal component analysis (PCA) plot scores for photosynthetic and fluorescence parameters (unpublished data), yield component, and tuber quality traits (previously published by Ávila-Valdés et al. (2020). (**A**) Variable graph and (**B**) individual graph of PCA showing the impact of treatments per genotype. Variables: Yield, tuber yield; HI, harvest index; T.DM%, dry matter content in tubers (%); AGB, above-ground biomass; T.Number, tuber number; T.Weight, mean tuber weight; T.Proline, proline content in tubers; T.Sugar, total soluble sugar in tubers; T.Protein, total soluble protein in tubers; T.Phenols, total phenolic content in tubers; T.Starch, starch content in tubers; Amax, photosynthesis rate; gs, stomatal conductance; Fv/Fm, maximum quantum yield of PSII; PSII, quantum yield of ΦPSII; qP, photochemical quenching; NQP, non-photochemical quenching; Rub, Rubisco content; Chla + b, total chlorophyll content (Chl a + b); Chla + b/car, total chlorophyll content/carotenoids ratio; Prot.Leaf, total soluble protein content in leaves; RWC%, relative water content of leaves (%); SLA, specific leaf area. Genotypes: K, Karú INIA; D, Desiree; C, Chona Negra. Treatments: T0H0, ambient temperature under rainfed conditions; T1H0, high temperature under rainfed conditions; T0H1, ambient temperature under irrigation conditions; T1H1, high temperature under irrigation conditions

reached did not negatively modify the photosynthetic and fluorescence performance under the evaluated water scenarios, suggesting that the primary processes of photosynthesis (i.e., leaf and chloroplast functions) were not inhibited by the thermal treatments. At the same time, our data provide evidence that the Chilean native potato Chona Negra has a higher capacity to improve its photosynthetic rate when exposed to a moderate increase in air temperature of c. + 5 °C. This higher rate was accompanied by high stomatal conductance, high quantum yield of PSII, and Rubisco content in leaves, which would partly explain this performance (Figs. 4, 5). Its higher ΦPSII values showed a weak inverse correlation with NPQ values, likely because adequate water availability minimized thermal stress and/or because photoprotective strategies developed by Chona Negra (e.g., antioxidant production) reduced the need for photoprotective mechanisms such as NPQ, thereby modifying the relationship between these two parameters. Additionally, these plants showed a higher SLA value at T1H1 (Fig. 6), an adaptation that can be advantageous for photosynthetic efficiency and heat dissipation. However, it may also increase susceptibility to dehydration and damage under severe heat stress and drought conditions (Craufurd et al. 1999; Delfin et al. 2021).

The photosynthesis-light response curves showed that, at higher temperatures, only the commercial potato varieties exhibited a decrease in their maximum net photosynthetic rate and photon-use efficiency of CO_2 assimilation on the incident light basis, regardless of the water scenario (Table 2). Although this measurement

was taken at only one point in time during the heat treatment (i.e., day 20), it can be inferred that these restrictions on carbon assimilation capacity could be partly explained by a modification of key enzyme activity, an increase in photorespiration, and/or, as in the case of Karú INIA, a decrease in Rubisco content (Fig. 5) (Berry and Björkman 1980; Sharkey 2005). Additionally, a limited heat dissipation mechanism under thermal stress could partly explain the contrasting results between commercial and native potatoes under high temperatures and water deficit. In contrast, Chona Negra's maximum net photosynthetic rate was favoured by higher temperatures, regardless of the water scenario. The higher stomatal conductance and carotenoid concentrations in the leaves at T1H1 likely contributed to better leaf temperature regulation and the prevention of photoinhibition, partially explaining these results (Stra et al. 2022). Additionally, the likely higher leaf antioxidant content and the constitutively higher Rubisco concentration in the leaves (i.e., 2.3 times more Rubisco than in commercial varieties) could explain the stability or even the increase in photosynthetic rate observed under lower leaf water status and adverse environmental conditions (Camejo et al. 2006; Sharkey 2005).

Association Between Photosynthetic and Fluorescent Activity and Tuber Yield

As previously reported by Ávila-Valdés et al. (2020), the higher temperatures reached in the present study did not have a deleterious impact on the tuber yield of commercial potatoes across the evaluated water scenarios. These findings are consistent with our results, which showed that thermal treatments did not negatively affect the photosynthetic and fluorescence performance (Fig. 4, 7). Like tuber yield, the physiological parameters responded mainly to the availability of water (Fig. 7B), reaffirming that in southern Chile, water availability plays a critical role in determining potato yield under heat stress. It is not uncommon to observe a non-linear relationship between photosynthesis and tuber yield, as factors such as differing optimal temperatures for both processes, photosynthate translocation, and carbon partitioning to the tubers strongly influence the outcome. In this context, higher photosynthesis rates achieved by Chona Negra at T1H1 (Fig. 4) did not result in higher yields, as previously noted (Ávila-Valdés et al. 2020). However, this increase likely contributed to maintaining Chona Negra's yield without significant variation by triggering mitigating responses to higher temperatures under irrigation (T0H1 vs. T1H1). This suggests that a portion of the assimilates synthesized was probably diverted towards the production of antioxidant compounds and osmoprotectants as part of Chona Negra's stress-response mechanisms.

Potatoes native to Chile, specifically *Solanum tuberosum* spp. *tuberosum*, have evolved in cold environments at high latitudes in southern Chile (Contreras et al. 1993). As such, the favourable response of Chona Negra to higher temperatures is an unexpected finding of this research and is promising in terms of its potential adaptation to future climate change conditions. The effect of high temperatures on commercial potatoes highlights their limited ability to maintain photosynthetic functionality, particularly under temperature ranges higher than those reached in this study and under water restriction. The contrasting results between commercial and native potatoes emphasize the importance of genetic diversity in addressing climate change, as native varieties

have developed more robust adaptations to environmental stress. These findings could also guide future breeding programmes aimed at developing commercial cultivars with greater heat and water deficit resistance.

Conclusion

In conclusion, under field conditions in the high-yielding environment of southern Chile, water deficit and a moderate temperature increase (+5 °C) during the 40-day tuber bulking period affected the leaf pigment content, as well as the photosynthetic performance and chlorophyll fluorescence of both commercial and native potato genotypes evaluated. Although moderately high temperatures and lower water availability generally did not have stronger combined effects than each condition alone, our findings highlight the critical role of water availability in environments like southern Chile. Our results suggest that the Chilean native potato, Chona Negra, has a greater capacity to enhance its photosynthetic rate when exposed to higher temperatures under irrigation, which may prove advantageous in future unfavorable climatic conditions. In contrast, commercial potatoes appear more susceptible to limitations in photosynthetic activity under higher or prolonged periods of elevated temperatures.

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Data Availability The data that support the findings of this study are available from the corresponding author upon reasonable request.

Declarations

Competing Interests The authors declare no competing interests.

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