

Phenotyping wild potatoes for photosynthesis associated traits under heat stress

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Abstract

Heat stress is one of the major factors reducing potato yield by limiting the plant photosynthesis activity, production and partitioning of assimilates to the sink. Potato wild relatives (*Solanum* sect. *Petota*, Solanaceae) are a natural reservoir of valuable traits for abiotic stress resistance. However, it is necessary to assess the response of wild potato genotypes based on physiological features such as gas exchange, chlorophyll index and chlorophyll fluorescence that are promising candidates to improve crop photosynthesis under adverse conditions. Multivariate approaches on two factor experimental design were used to phenotype the best performing genotypes for most important traits under control and heat stress treatments. From the results, the most important traits to be focused on are net photosynthetic rates, transpiration rates, and stomatal conductance along with effective photochemical yield of PSII, Coefficient of photochemical yield of PSII and dry matter content, which are highly associated with heat stress conditions. *Solanum commersonii* accession (BGB451) and *S. chacoense* (BGB467, BGB113, BGB444, BGB083) are the top five genotypes of the heat stress tolerant group. However, BRSBEL, BGB003, BGB091 and BGB101 are most susceptible to heat stress. From our study, we concluded that most genotypes phenotyped for heat stress resistance belong to *S. chacoense*. The assessment of wild accessions for photosynthetic traits under heat stress is a reliable way to discriminate the most promising sources of abiotic stress resistance even though they do not have best quality tuber traits for the breeding of the potato crop.

Key Points

- Wild potato genotypes were explored for heat tolerance.
- Multivariate methods were utilized to select the optimum genotypes based on photosynthetic activity traits.
- *Solanum chacoense* accessions are more likely to be tolerant to heat stress.
- Effective photochemical yield and non-photochemical quenching could be used as stress indicators,
- Positive relationship among net photosynthetic rates, transpiration rates, and stomatal conductance were found.

Introduction

Plant regulatory mechanisms have evolved to adapt to various weather changes, such as fluctuating irradiation, limited and excessive precipitation, or low and high temperatures. Despite the inhibition of their photosynthetic processes, these adaptations allow plants to thrive even in rapidly changing conditions (Zivcak et al. 2017). As a result, the success of crop species and genotypes is determined by the efficiency of the photosynthetic apparatus (Zahra et al. 2023).

The increase in average global temperature is modeled to reach 0.3–4.8°C by the end of the XXI century (IPCC et al., 2021), which directly affects the growth and development of plants by changing photosynthesis and growth period. This scenario will lead agriculture to a challenge, especially in arid regions. Basically, this temperature increase can cause a reduction in the stomatal conductance and rate of photosynthesis (Urban et al. 2017) by warming up mesophyll cell and causing increase in the temperature of the stroma and thylakoid membrane within the chloroplasts (Scafaro et al., 2011). However, Havaux (1992) stated that exposure of potato (*Solanum tuberosum* L., Solanaceae) leaves to heat stress (HS) caused an increase in activity of photosystem II (PSII) in stressed plants due to the quick adaptation of the potato leaves to elevated temperature conditions. This happens because photosynthesis and gas exchange involve several processes related to the conversion and transformation of radiation into the photochemical energy powering CO₂ fixation and the formation of assimilates, which is essential for the plant's survival during heat stress.

Therefore, non-invasive technique such as chlorophyll fluorescence (CF) and infra-red gas analyzer (IRGA) has become a well-established and commonly used to assess the photosynthetic performance of plants by physiologists and eco-physiologists (Maxwell and Johnson, 2000). The CF and IRGA has been used to detect and quantify the damage in photosystem II (PSII) in several crops including potato (Sundbom et al. 1982), wheat (Wu and Bao 2011; Sharma et al. 2015), rice (Gu et al. 2017) and oats (Rizza et al. 2001) under various abiotic stress conditions. This technique allows rapid and early phenotyping of genotypes to identify existing genetic variation in responses of the stomatal conductance (Gs) and rate of photosynthesis (Pn) (Urban et al. 2017) associated with heat stress tolerance. During heat stress, high temperatures can cause damage to photosynthetic components, leading to a decline in chlorophyll fluorescence, which could be observed with decline in the effective photochemical efficiency of photosystem (YII) (Guidi et al. 2019; Muhie 2022). This decline in photochemical yield suggests that the plant is undergoing stress, and its ability to carry out photosynthesis is being compromised (Allel et al., 2018; Huang et al., 2011), which can be indicated by an important stress indicator (Baker 2008) called maximum chlorophyll fluorescence (Fv/Fm). Additionally, it has been postulated that non-photochemical quenching (NPQ) plays a key role in determining plant productivity (Demmig-Adams et al. 2014). According to (Hubbart et al. 2018), NPQ may contribute to enhance productivity by decreasing the photoinhibition, but may also reduce the plant yield by overly protective persistence, lowering quantum yield when a plant is submitted to low light unnecessarily (Kromdijk et al. 2016). Several authors have suggested that chlorophyll fluorescence can be more efficiently used as a suitable selection criterion for genotype screening and as an indicator of the effects of climate change on crop species (Rodenburg et al. 2008; Bussotti et al. 2020; Cai et al. 2020; Barboricova et al. 2022; Lauterberg et al. 2023). The ability of plants to adapt photosynthetic response in changing environments depends on the level of genetic variation within a population. One of the major approaches for improving photosynthetic efficiency of crop species could be through exploitation of natural variation for photosynthesis rates in crop wild relatives (Crop Trust 2023). Therefore, geographically widely distributed potato genepool comprises more than 100 wild relative species (Spooner et al. 2014) and containing valuable reservoir of allelic genetic diversity for various biotic and abiotic stresses incorporated into potato breeding program over time (Bashir et al. 2021).

Hence, climate change, especially the increase of temperature, requires identifying new sources of heat tolerance and breeding new potato cultivars able to cope with supraoptimal temperatures. Physiological phenotyping approaches such as gas exchange in combination with chlorophyll fluorescence may help to identify and phenotype best performing genotypes, aiming define new plant ideotype to face future climate scenarios. Thus, the aim of this study was to identify the ideal wild potato ideotype for heat stress which likely will achieve maximize photosynthesis, be effective at utilizing available water by accessing more water and fixing more carbon per unit of water taken up, hence will be resulted in maintaining tuberization under conditions of high temperature.

However, wild potatoes tuber traits were not focused in this study because high heterosis of bad tuber quality traits such as secondary growth, high levels of glycoalkaloids, difference in tuberization timing are the drawback for the potato breeding program.

Material and methods

Plant material and temperature treatments:

The experiment was carried out in controlled environment, at the Phenotyping Platform from Embrapa Clima Temperado, in Pelotas, Rio Grande do Sul, Brazil (32°45' S and 52°30' W). Phenotyping was performed for 24 accessions (Table 1) of Embrapa Potato Gene Bank which belong to *Solanum commersonii*, wild; *Solanum chacoense*, wild; *Solanum tuberosum*, di-haploid and one commercial cultivar of *Solanum tuberosum* 4x (BRSIPR-BEL) developed by Embrapa. Uniform tubers from the available accessions were selected and taken out from cold chambers and placed on phenolic sponges for 20 days. After acclimatization, tubers were transplanted to plastic bags filled with approximately 4 kg of organo-mineral substrate. The plants were kept in a greenhouse until the next 15 days until they reached the emergence stage. Subsequently, they were taken to growth chambers and exposed to two temperature gradients: control temperature (CT) treatment, with a thermal amplitude of 14 to 27°C, which is the temperature range for optimum growth for potato crop (Struik 2007) and heat stress (HS) treatment, with an amplitude of 24 to 34°C, (Fig. 1). The photoperiod was 12 hours (7:00 to 19:00h) with a light intensity of 400 µmol m⁻²s⁻¹, approximately. The used accession remained under these conditions for 60 days, until the time of harvest.

Table 1
List of potato germplasm evaluated from the Embrapa Potato Genebank at Embrapa Clima Temperado, Pelotas, RS, Brazil.

Sr. #	Accession #	Genesys #	Species	Origin
1.	BGB003	BRA 00167009-0	<i>S. commersonii</i> Dunal	Wild, Rio Grande do Sul, Brazil
2.	BGB008	BRA 00167014-0	<i>S. commersonii</i> Dunal	Wild, Rio Grande do Sul, Brazil
3.	BGB009	BRA 00167015-7	<i>S. commersonii</i> Dunal	Wild, Rio Grande do Sul, Brazil
4.	BGB027	BRA 00167203-9	<i>S. commersonii</i> Dunal	Wild, Rio Grande do Sul, Brazil
5.	BGB045	BRA 00167397-9	<i>S. commersonii</i> Dunal	Wild, Rio Grande do Sul, Brazil
6.	BGB083	BRA 00167435-7	<i>S. chacoense</i> Bitter	Wild, Santa Catarina, Brazil
7.	BGB086	BRA 00167438-1	<i>S. chacoense</i> Bitter	Wild, Minas Gerais, Brazil
8.	BGB088	BRA 00167440-7	<i>S. tuberosum</i> L. 2x	Di-haploid of cv. Mountain
9.	BGB089	BRA 00167441-5	<i>S. tuberosum</i> L. 2x	Di-haploid of cv. Sowa
10.	BGB091	BRA 00167443-1	<i>S. tuberosum</i> L. 2x	Di-haploid of cv. Anchieta
11.	BGB093	BRA 00167445-6	<i>S. tuberosum</i> L. 2x	Di-haploid of unknown origin
12.	BGB096	BRA 00167448-0	<i>S. chacoense</i> Bitter	Wild, Tucumán, Argentina
13.	BGB098	BRA 00167450-6	<i>S. chacoense</i> Bitter	Wild, Unkown origin, South America
14.	BGB101	BRA 00167018-1	<i>S. chacoense</i> Bitter	Wild, Salta, Argentina
15.	BGB102	BRA 00167019-9	<i>S. chacoense</i> Bitter	Wild, San Luis, Argentina
16.	BGB103	BRA 00167020-7	<i>S. chacoense</i> Bitter	Wild, Córdoba, Argentina
17.	BGB107	BRA 00167024-9	<i>S. chacoense</i> Bitter	Wild, Argentina
18.	BGB109	BRA 00167026-4	<i>S. chacoense</i> Bitter	Wild, Argentina
19.	BGB113	BRA 00167031-4	<i>S. chacoense</i> Bitter	Wild, Salta, Argentina
20.	BGB444	BRA 00167395-3	<i>S. chacoense</i> Bitter	Wild, Santa Catarina, Brazil
21.	BGB451	BRA 00183759-0	<i>S. commersonii</i> Dunal	Wild, Rio Grande do Sul, Brazil
22.	BGB467	BRA 00183774-9	<i>S. chacoense</i> Bitter	Wild, Santa Catarina, Brazil
23.	BGB472	BRA 00183779-8	<i>S. chacoense</i> Bitter	Wild, Santa Catarina, Brazil
24.	BRSIPR-BEL	BRA 00167251-8	<i>S. tuberosum</i> L. 4x	Commercial cultivar, Brazil

Chlorophyll fluorescence and photosynthesis components

Before measurements, the plants were adapted to the dark within each growth chamber for at least 30 minutes, and the temperature was maintained at 24°C for control condition and 34°C for stress condition. For chlorophyll index, we used SPAD values of leaves that were determined by a portable chlorophyll meter (SPAD 502 Plus, Minolta, Spectrum Technologies Inc., Illinois, USA). The net photosynthesis rate (Pn) µmol C₂O_m⁻²s⁻¹, stomatal conductance (Gs) mol H₂O m⁻²s⁻¹, transpiration (E) mmol H₂O m⁻²s⁻¹, and intracellular and ambient CO₂ assimilation ratios (Ci/Ca) were measured by using the LI-6400XT

photosynthesis system (6400-02B; Li-Cor, Lincoln, NE, USA) on the third expanded leaf from the top of the stem in a plant of each genotype previously irrigated and adapted for at least 30 minutes at a temperature of 24°C for control condition, and 34°C for stress condition. The CO₂ concentration used in the chamber was 400 $\mu\text{mol mol}^{-1}$ and a photon flux density of 400 $\mu\text{mol of photons m}^{-2}\text{s}^{-1}$, and relative humidity 50–65%. We also used the ratios of Pn, E and Gs to calculate the water-use efficiency (WUE) and intrinsic WUE as suggested by (Pimentel et al., 1999; (Farquhar and Richards 1984)).

Chlorophyll fluorescence (CF) analyses were performed using the IMAGING-PAM M-Series 500 fluorometer (Walz Heinz GmbH, Effeltrich, Germany). To measure the different states of CF, an actinic light of 7000 $\mu\text{mol m}^{-2}\text{s}^{-1}$ photon was activated. The following parameters were measured: minimum fluorescence of dark-adapted leaves (F_M), minimum fluorescence of light-adapted leaves (F_O), maximum fluorescence of dark-adapted leaves (F_M), maximum fluorescence of light-adapted leaves (F_M'), and steady-state chlorophyll fluorescence in light-adapted leaves (F_S). The following ratios shown below were calculated by these parameters according to Genty et al. (1989). All the physiological data were recorded after 15 days after stress (DAS), 28DAS and 42DAS, respectively.

Maximum photochemical quantum yield of PSII ($\frac{F_v}{F_m} = \frac{F_M' - F_O}{F_M'}$)

Effective photochemical quantum yield ($\frac{F_v}{F_m} = \frac{F_M' - F_O}{F_M'}$)

Nonphotochemical quenching ($\frac{F_N}{F_m} = \frac{F_M' - F_M}{F_M'}$)

Proportion of oxidized or 'open' state PSII reaction centers ($\frac{F_0}{F_m} = \frac{F_O - F_M}{F_M'}$)

Biomass and yield components:

At the end of the crop cycle, biomass and yield production components were measured in terms of fresh shoot weight (g), dry shoot weight (g), fresh tuber weight (g), and dry matter content (%) as suggested by Bashir et al. (2022).

Experimental design and data analysis:

The experiments were carried out in a factorial design with 2 factors. Genotype (G) or used accession in three replication and temperature treatment (CT and HS) were considered as factors for interaction effect. However, for physiological traits data, average was calculated for replicated data and data measured at 15DAS, 28DAS and 42DAS were used in analysis. Data were analyzed in R (R Core Team 2023) for two-way ANOVA to determine the main and interaction effects by using the *easynova* v9.0 package (Arnhold 2013) and, subsequently, the means of each treatment and genotypes were compared to each other using the Scott-Knot grouping test ($P \leq 0.05$). Pearson's correlation and visualization for both treatments (CT & HS) were performed separately by using *Corrplot* v0.92 (Wei and Simko 2021) for traits relationship. The principal component analysis (PCA) biplots were created using R packages, Factoextra (Kassambara and Mundt 2021) and FactoMineR (Lê et al. 2008). Ward's method of HCA, which is based on squared Euclidean distance of transformed z-score values was utilized to classify the genotypes into different clusters. Descriptive statistics of physiological and morphological traits under both treatments of different clusters were calculated. Relative importance of all traits associated with heat tolerance was calculated using PCA. To designate the cluster on their tolerance level, cluster score was calculated as weighted linear combination of all traits as suggested by Nagar et al. (2015). Based on cluster score, clusters were nominated as highly heat tolerant, intermediate, sensitive. Within the cluster, most tolerant and sensitive genotypes were also identified using individual score of cultivars. The individual score of each cultivar was calculated similarly as calculated for cluster score.

Results

Performance of studied germplasm

Gas exchange and related traits:

Analysis of variance (ANOVA) results for all examined traits is presented in Table 3, which shows significant difference among the genotypes and treatment. However, for DAS, significant differences were observed for SPAD, Pn, Gs, and E. The mean comparison of all studied variables related to physiological and morphological traits was shown in Fig. 2 under both CT and HS conditions.

Table 2

Results from analysis of variance (degree of freedom, DF; means square, MS) for physiological and morphological variables considering 24 potato germplasm genotypes (G) and two temperature treatments (T) as sources of variation, and their interaction. NS, *, **, *** significant at $P > 0.05$, $P \leq 0.05$, $P \leq 0.01$, $P \leq 0.001$, respectively.

Source of variance	DF	Chlorophyll Index		Gas exchange traits					
		SPAD		Pn [§]	Gs	E	Ci/Ca	iWUE	WUE
Genotype (G)	23	3.56***		56.67***	1.68***	11.51***	0.53 ^{NS}	0.81 ^{NS}	0.99*
Treatment (T)	1	9.03***		47.50*	20.65***	0.53 ^{NS}	69.96***	19.74***	50.39***
DAS (Rep)	2	11.13***		112.73***	5.34***	18.80**	1.08 ^{NS}	0.92 ^{NS}	0.90 ^{NS}
G × T	23	0.36*		9.41 ^{NS}	0.44 ^{NS}	5.29 ^{NS}	0.50 ^{NS}	1.27*	0.41 ^{NS}
Photochemistry traits				Morphological traits					
Source of variance	DF	Y(II)	NPQ	qP	Fv/Fm	FSW	DSW	FTW	DMC
Genotype (G)	23	0.0001***	0.0250***	0.0294***	1.73***	14914***	3.66***	4.82***	3.84***
Treatment (T)	1	0.0059 ^{NS}	0.1096***	0.0476**	23.51***	29958***	5.59***	7.56***	3.10***
DAS (Rep)	2	0.0408***	0.0227 ^{NS}	0.1047***	12.38***	85.00 ^{NS}	1.94***	0.04 ^{NS}	0.00 ^{NS}
G × T	23	0.0019 ^{NS}	0.0108 ^{NS}	0.0068 ^{NS}	0.45 ^{NS}	249***	0.55 ^{NS}	0.55***	0.32 ^{NS}

[§] Pn = net photosynthesis rates. Gs = stomatal conductance. E = net transpiration rate. Ci/Ca = intracellular and ambient CO₂ assimilation ratio. WUE = water use efficiency. iWUE = intrinsic photosynthetic water use efficiency. Y(II) = Effective photochemical quantum yield of PSII. NPQ = non-photochemical quenching. Fv/Fm = maximum photochemical quantum yield of PSII. FSW = fresh shoot weight. DSW = dry shoot weight. FTW = fresh tuber weight. DMC = dry matter content.

The chlorophyll index (SPAD), Pn, WUE and iWUE were higher under HS temperature range, (Table 2) but all the gas exchange related traits gradually reduced with the advancement in heat stress period, which is shown by the significant differences in trait measurements at 14, 28 and 42DAS (Table 2), respectively. While stomatal conductance (Gs) and transpiration rate (E) were reduced under HS condition but differences between treatments for E were not significant (Table 2). However, SPAD, Pn, Gs and E showed reduction when measured at 14, 28 and 42DAS but Pn increased at 28DAS (Fig. 2). Ci/Ca, WUE and iWUE showed no significant differences of days after stress (Table 1). BGB109 (*S. chacoense*) genotype showed the highest SPAD values, along with WUE and iWUE in HS. BGB091 (*S. tuberosum* 2x) was the highest among the used germplasm for stomatal conductance under HS. *S. commersonii* genotype BGB003, was found to be the highest performer under HS for Gs, E and Ci/Ca (Table 2).

Table 3
Chlorophyll index and gas exchange traits by genotypes of wild potato germplasm under Control and Heat Stress conditions.

Genotype	SPAD		Pn ($\mu\text{mol C}_2\text{Om}^{-2}\text{s}^{-1}$)		Gs ($\text{mol H}_2\text{O m}^{-2}\text{s}^{-1}$)		E ($\text{mmol H}_2\text{O m}^{-2}\text{s}^{-1}$)		Ci/Ca		WUE ($\mu\text{mol (C}_2\text{O) mol (H}_2\text{O)}^{-1}$)		iWUE ($\mu\text{mol CO}_2 \text{mol}^{-1} \text{H}_2\text{O}$)	
	CT	HS	CT	HS	CT	HS	CT	HS	CT	HS	CT	HS	CT	HS
BRS-BEL	41.5 $\pm 2.7^a$	49.2 $\pm$ 1.8 ^a	14.4 $\pm 1.7^a$	16.5 $\pm 1.2^a$	0.75 $\pm$ 0.3 ^a	0.55 $\pm$ 0.3 ^a	5.6 $\pm 1.1^a$	7.5 $\pm$ 1.3 ^a	0.82 $\pm$ 0.04 ^a	0.68 $\pm$ 0.1 ^a	2.7 $\pm$ 0.4 ^a	2.3 $\pm$ 0.2 ^b	22.7 $\pm$ 4.9 ^a	46.1 $\pm$ 16.4 ^b
BGB003	35.6 $\pm 2.0^b$	35.1 $\pm$ 1.9 ^c	14.9 $\pm 1.7^a$	16.6 $\pm 1.5^a$	0.58 $\pm$ 0.1 ^a	0.66 $\pm$ 0.3 ^a	5.7 $\pm 0.3^a$	7.9 $\pm$ 1.5 ^a	0.85 $\pm$ 0.004 ^a	0.78 $\pm$ 0.07 ^a	2.6 $\pm$ 0.3 ^a	2.2 $\pm$ 0.2 ^b	25.6 $\pm$ 0.8 ^a	38.9 $\pm$ 15.2 ^b
BGB008	33.9 $\pm 1.9^b$	35.4 $\pm$ 3.5 ^c	11.9 $\pm 2.2^a$	12.6 $\pm 2^b$	0.55 $\pm$ 0.2 ^a	0.32 $\pm$ 0.1 ^a	5.2 $\pm 0.9^a$	5.4 $\pm$ 1.1 ^a	0.85 $\pm$ 0.01 ^a	0.60 $\pm$ 0.07 ^a	2.3 $\pm$ 0.2 ^a	2.4 $\pm$ 0.2 ^b	24.3 $\pm$ 3.7 ^a	51.0 $\pm$ 17.2 ^b
BGB009	33.2 $\pm 1.6^b$	31.5 $\pm$ 1.6 ^d	15.0 $\pm 1.1^a$	15.9 $\pm 1^a$	0.59 $\pm$ 0.1 ^a	0.34 $\pm$ 0.1 ^a	5.6 $\pm 0.5^a$	7.1 $\pm$ 0.8 ^a	0.84 $\pm$ 0.01 ^a	0.71 $\pm$ 0.06 ^a	2.7 $\pm$ 0.3 ^a	2.3 $\pm$ 0.2 ^b	26.5 $\pm$ 3.2 ^a	53.3 $\pm$ 13.9 ^b
BGB027	39.8 $\pm 0.6^a$	42.0 $\pm$ 1.8 ^b	6.8 $\pm$ 1.7 ^b	10.8 $\pm 1.5^b$	0.32 $\pm$ 0.1 ^a	0.19 $\pm$ 0.1 ^a	4 $\pm$ 1.2 ^a	5.0 $\pm$ 1.6 ^a	0.85 $\pm$ 0.04 ^a	0.60 $\pm$ 0.1 ^a	1.9 $\pm$ 0.4 ^a	2.4 $\pm$ 0.4 ^b	27.9 $\pm$ 9.5 ^a	78.6 $\pm$ 21.9 ^b
BGB045	32.2 $\pm 1.5^b$	22.5 $\pm$ 11.2 ^d	10.8 $\pm 0.3^a$	9.0 $\pm$ 4.5 ^b	0.53 $\pm$ 0.03 ^a	0.18 $\pm$ 0.1 ^b	5.6 $\pm 0.4^a$	3.8 $\pm$ 2 ^b	0.88 $\pm$ 0.003 ^a	0.47 $\pm$ 0.2 ^a	1.9 $\pm$ 0.2 ^a	1.6 $\pm$ 0.9 ^b	20.6 $\pm$ 0.8 ^a	37.9 $\pm$ 22 ^b
BGB083	30.8 $\pm 0.3^b$	36.8 $\pm$ 0.7 ^c	6.6 $\pm$ 2.8 ^b	5.4 $\pm$ 0.7 ^b	0.36 $\pm$ 0.2 ^a	0.03 $\pm$ 0.01 ^b	4.2 $\pm 1.6^a$	1.1 $\pm$ 0.4 ^b	0.87 $\pm$ 0.03 ^a	0.08 $\pm$ 0.1 ^b	1.8 $\pm$ 0.5 ^a	5.6 $\pm 1^a$	26.5 $\pm$ 9.4 ^a	211.1 $\pm$ 38.7 ^a
BGB086	32.0 $\pm 1.4^b$	34.9 $\pm$ 0.8 ^c	9.0 $\pm$ 0.6 ^b	11.2 $\pm 1.2^b$	0.39 $\pm$ 0.1 ^a	0.23 $\pm$ 0.1 ^a	4.1 $\pm 0.5^a$	4.6 $\pm$ 0.7 ^a	0.83 $\pm$ 0.01 ^a	0.66 $\pm$ 0.08 ^a	2.2 $\pm$ 0.1 ^a	2.4 $\pm$ 0.1 ^b	27.4 $\pm$ 5.9 ^a	58.0 $\pm$ 16.3 ^b
BGB088	34.8 $\pm 2.7^b$	38.9 $\pm$ 1.6 ^b	8.7 $\pm$ 0.9 ^b	12.4 $\pm 2^b$	0.40 $\pm$ 0.2 ^a	0.22 $\pm$ 0.1 ^a	4.1 $\pm 1.1^a$	5.2 $\pm$ 1.6 ^a	0.82 $\pm$ 0.06 ^a	0.62 $\pm$ 0.1 ^a	2.4 $\pm$ 0.6 ^a	2.7 $\pm$ 0.6 ^b	34.8 $\pm$ 14.1 ^a	75.1 $\pm$ 26.3 ^b
BGB089	35.3 $\pm 3.8^b$	40.1 $\pm$ 1.2 ^b	9.9 $\pm$ 1.6 ^b	11.1 $\pm 4.2^b$	0.46 $\pm$ 0.3 ^a	0.27 $\pm$ 0.2 ^a	4.5 $\pm 1.3^a$	5.2 $\pm$ 2.4 ^a	0.83 $\pm$ 0.04 ^a	0.59 $\pm$ 0.1 ^a	2.3 $\pm$ 0.2 ^a	2.6 $\pm$ 0.5 ^b	31.5 $\pm$ 9.1 ^a	78.9 $\pm$ 29.2 ^b
BGB091	41.0 $\pm 2.8^a$	48.2 $\pm$ 0.7 ^a	14.1 $\pm 2.2^a$	17.5 $\pm 1.4^a$	0.44 $\pm$ 0.1 ^a	0.37 $\pm$ 0.1 ^a	5 $\pm$ 0.3 ^a	7.6 $\pm$ 0.7 ^a	0.82 $\pm$ 0.005 ^a	0.73 $\pm$ 0.02 ^a	2.8 $\pm$ 0.3 ^a	2.3 $\pm$ 0.04 ^b	32.2 $\pm$ 1.4 ^a	49.3 $\pm$ 6.7 ^b
BGB093	35.7 $\pm 3.6^b$	42.9 $\pm$ 1.9 ^b	8.4 $\pm$ 3.5 ^b	12.0 $\pm 3.9^b$	0.40 $\pm$ 0.3 ^a	0.29 $\pm$ 0.2 ^a	3.7 $\pm 2.1^a$	5.4 $\pm$ 2.8 ^a	0.76 $\pm$ 0.08 ^a	0.41 $\pm$ 0.3 ^a	2.8 $\pm$ 0.7 ^a	4.2 $\pm$ 2.2 ^b	48.9 $\pm$ 19.7 ^a	129.7 $\pm$ 84.1 ^a
BGB096	30.6 $\pm 1.1^b$	32.6 $\pm$ 1.5 ^d	12.9 $\pm 1.7^a$	8.4 $\pm$ 1.1 ^b	0.46 $\pm$ 0.1 ^a	0.09 $\pm$ 0.02 ^b	5.3 $\pm 0.9^a$	2.9 $\pm$ 0.7 ^b	0.83 $\pm$ 0.03 ^a	0.51 $\pm$ 0.06 ^a	2.5 $\pm$ 0.5 ^a	3.0 $\pm$ 0.5 ^a	30.6 $\pm$ 6.8 ^a	101.4 $\pm$ 15.5 ^a
BGB098	35.5 $\pm 1.7^b$	38.0 $\pm$ 0.5 ^c	7.1 $\pm$ 3.6 ^b	12.3 $\pm 2.3^b$	0.31 $\pm$ 0.2 ^a	0.22 $\pm$ 0.1 ^a	3.6 $\pm 1.8^a$	5.0 $\pm$ 1.6 ^a	0.80 $\pm$ 0.06 ^a	0.59 $\pm$ 0.1 ^a	2.2 $\pm$ 0.3 ^a	2.8 $\pm$ 0.5 ^b	35.4 $\pm$ 11.6 ^a	83.9 $\pm$ 35.1 ^b
BGB101	43.6 $\pm 1.7^a$	42.9 $\pm$ 0.9 ^b	13.3 $\pm 1.7^a$	17.1 $\pm 2^a$	0.41 $\pm$ 0.1 ^a	0.41 $\pm$ 0.1 ^a	4.8 $\pm 0.4^a$	7.2 $\pm$ 1.6 ^a	0.82 $\pm$ 0.01 ^a	0.68 $\pm$ 0.1 ^a	2.8 $\pm$ 0.4 ^a	2.5 $\pm$ 0.3 ^b	32.2 $\pm$ 2.1 ^a	59.3 $\pm$ 24.2 ^b
BGB102	32.1 $\pm 2.7^b$	34.5 $\pm$ 0.9 ^c	4.0 $\pm$ 2.1 ^b	6.4 $\pm$ 2 ^b	0.12 $\pm$ 0.1 ^a	0.05 $\pm$ 0.03 ^b	2.2 $\pm 1.0^a$	1.9 $\pm$ 0.9 ^b	0.82 $\pm$ 0.01 ^a	0.30 $\pm$ 0.1 ^b	1.7 $\pm$ 0.2 ^a	3.9 $\pm$ 0.9 ^a	32.2 $\pm$ 1.4 ^a	148.4 $\pm$ 32.7 ^a
BGB103	42.2 $\pm 3.6^a$	40.2 $\pm$ 3.6 ^b	9.4 $\pm$ 2.5 ^b	9.0 $\pm$ 2 ^b	0.38 $\pm$ 0.1 ^a	0.09 $\pm$ 0.04 ^b	4.6 $\pm 0.1^a$	2.9 $\pm$ 1.1 ^b	0.86 $\pm$ 0.02 ^a	0.32 $\pm$ 0.3 ^b	2.0 $\pm$ 0.5 ^a	4.3 $\pm$ 1.8 ^a	24.1 $\pm$ 4.2 ^a	147.8 $\pm$ 66.8 ^a
BGB107	39.4 $\pm 2.2^a$	40.0 $\pm$ 1.2 ^b	10.5 $\pm 0.3^a$	11.3 $\pm 2.8^b$	0.72 $\pm$ 0.5 ^a	0.15 $\pm$ 0.1 ^b	5.5 $\pm 2.1^a$	4.1 $\pm$ 1.5 ^b	0.84 $\pm$ 0.07 ^a	0.52 $\pm$ 0.1 ^a	2.4 $\pm$ 0.7 ^a	3.3 $\pm$ 0.8 ^a	32.8 $\pm$ 14.1 ^a	99.0 $\pm$ 31.8 ^a
BGB109	46.8 $\pm 2.8^a$	53.7 $\pm$ 1.9 ^a	7.3 $\pm$ 4.4 ^b	10.6 $\pm 4.9^b$	0.10 $\pm$ 0.05 ^a	0.24 $\pm$ 0.2 ^b	3.2 $\pm 2.1^a$	4.0 $\pm$ 2.8 ^b	0.81 $\pm$ 0.04 ^a	-0.10 $\pm$ 0.7 ^b	2.3 $\pm$ 0.1 ^a	6.8 $\pm$ 3.8 ^a	61.0 $\pm$ 11.9 ^a	300.5 $\pm$ 212.6 ^a

Genotype	SPAD		Pn ($\mu\text{mol C}_2\text{O m}^{-2}\text{s}^{-1}$)		Gs ($\text{mol H}_2\text{O m}^{-2}\text{s}^{-1}$)		E ($\text{mmol H}_2\text{O m}^{-2}\text{s}^{-1}$)		Ci/Ca		WUE ($\mu\text{mol (C}_2\text{O mol (H}_2\text{O)}^{-1}$)		iWUE ($\mu\text{mol CO}_2 \text{mol}^{-1} \text{H}_2\text{O}$)	
	CT	HS	CT	HS	CT	HS	CT	HS	CT	HS	CT	HS	CT	HS
BGB113	41.0 ± 3.3 ^a	46.3 ± 2.2 ^a	11.2 ± 2.2 ^a	7.2 ± 1.9 ^b	0.36 ± 0.1 ^a	0.09 ± 0.1 ^b	4.4 ± 1.0 ^a	1.1 ± 0.3 ^b	0.8 ± 0.03 ^a	-0.05 ± 0.1 ^b	2.7 ± 0.4 ^a	6.6 ± 1.1 ^a	36.5 ± 8.3 ^a	162.0 ± 66.3 ^a
BGB444	30.8 ± 2.1 ^b	35.2 ± 3.2 ^c	7.9 ± 1.5 ^b	7.2 ± 1.1 ^b	0.31 ± 0.1 ^a	0.06 ± 0.02 ^b	4.1 ± 0.9 ^a	2.0 ± 0.6 ^b	0.84 ± 0.02 ^a	0.08 ± 0.3 ^b	2.0 ± 0.2 ^a	4.4 ± 1.3 ^a	27.8 ± 3.6 ^a	144.0 ± 46.1 ^a
BGB451	31.9 ± 0.1 ^b	34.1 ± 2.1 ^c	7.7 ± 1.3 ^b	6.7 ± 1.2 ^b	0.26 ± 0.1 ^a	0.03 ± 0.01 ^b	3.5 ± 1.2 ^a	1.1 ± 0.2 ^b	0.77 ± 0.08 ^a	-0.08 ± 0.07 ^b	2.7 ± 0.8 ^a	6.3 ± 0.6 ^a	45.1 ± 19.5 ^a	245.8 ± 14.5 ^a
BGB467	34.1 ± 2.2 ^b	41.2 ± 3.6 ^b	7.5 ± 1.4 ^b	9.7 ± 2.9 ^b	0.29 ± 0.1 ^a	0.13 ± 0.1 ^b	3.7 ± 1.2 ^a	3.2 ± 1.8 ^b	0.82 ± 0.04 ^a	0.29 ± 0.3 ^b	2.2 ± 0.3 ^a	4.5 ± 1.6 ^a	35.3 ± 9 ^a	154.3 ± 64.2 ^a
BGB472	32.9 ± 2.4 ^b	38.2 ± 3.4 ^c	8.1 ± 2.1 ^b	8.0 ± 0.8 ^b	0.28 ± 0.1 ^a	0.04 ± 0.004 ^b	3.8 ± 1.0 ^a	1.6 ± 0.2 ^b	0.83 ± 0.03 ^a	0.20 ± 0.01 ^b	2.2 ± 0.5 ^a	4.9 ± 0.4 ^a	32.9 ± 8 ^a	179.5 ± 2.3 ^a

Genotype marginal means with letter within a studied trait are significantly different by the Scott-Knott at the 5% level of significance

Photochemistry of studied germplasm:

As shown in Table 2, HS doesn't significantly affect the Y(II) and qP, thus showed an increase by 7.12% and 9.91%, respectively (Table 4). A significant reduction due to heat stress was observed for the NPQ and Fv/Fm ratios by 9.40% and 3.96% as compared to CT conditions.

However, there was significant reduction in the Y(II), qP and Fv/Fm ratio responses while observed at 14, 28 and 42DAS (Fig. 2). The germplasm maintained the NPQ responses and did not show any significant difference in responses observed after DAS (Table 2).

Commercial cultivar BRSIPR-BEL recorded for the highest Y(II) and qP under HS (Table 4). *S. chacoense* (BGB096) showed highest NPQ under both CT and HS conditions. HS effect the 92% of the germplasm studied but two genotypes of *S. chacoense* BGB083 and BGB109 have increased Fv/Fm ratio as compared to CT conditions (Table 4).

Table 4
Chlorophyll fluorescence traits by genotypes of wild potato germplasm under Control and Heat Stress conditions

Genotype	Y(II)		NPQ		qP		Fv/Fm	
	CT	HS	CT	HS	CT	HS	CT	HS
BRS-BEL	0.25 ± 0.06 ^a	0.29 ± 0.02 ^a	0.58 ± 0.1 ^a	0.49 ± 0.1 ^a	0.51 ± 0.09 ^a	0.57 ± 0.02 ^a	0.757 ± 0.008 ^a	0.754 ± 0.002 ^a
BGB003	0.20 ± 0.05 ^a	0.27 ± 0.03 ^a	0.60 ± 0.1 ^a	0.47 ± 0.03 ^a	0.38 ± 0.06 ^a	0.52 ± 0.04 ^a	0.766 ± 0.009 ^a	0.754 ± 0.002 ^a
BGB008	0.14 ± 0.04 ^a	0.15 ± 0.05 ^b	0.66 ± 0.1 ^a	0.63 ± 0.1 ^a	0.30 ± 0.07 ^b	0.33 ± 0.1 ^b	0.751 ± 0.027 ^a	0.715 ± 0.03 ^b
BGB009	0.21 ± 0.06 ^a	0.22 ± 0.03 ^a	0.63 ± 0.1 ^a	0.56 ± 0.05 ^a	0.45 ± 0.08 ^a	0.47 ± 0.03 ^a	0.746 ± 0.01 ^a	0.741 ± 0.007 ^a
BGB027	0.19 ± 0.001 ^a	0.23 ± 0.004 ^a	0.55 ± 0.04 ^a	0.48 ± 0.1 ^a	0.38 ± 0.02 ^a	0.47 ± 0.03 ^a	0.756 ± 0.01 ^a	0.733 ± 0.019 ^a
BGB045	0.21 ± 0.02 ^a	0.18 ± 0.09 ^b	0.56 ± 0.02 ^a	0.26 ± 0.1 ^a	0.45 ± 0.04 ^a	0.34 ± 0.17 ^b	0.748 ± 0.003 ^a	0.494 ± 0.247 ^b
BGB083	0.13 ± 0.03 ^a	0.16 ± 0.01 ^b	0.51 ± 0.04 ^a	0.58 ± 0.1 ^a	0.27 ± 0.05 ^b	0.35 ± 0.04 ^b	0.731 ± 0.008 ^a	0.734 ± 0.001 ^b
BGB086	0.19 ± 0.04 ^a	0.17 ± 0.03 ^b	0.49 ± 0.05 ^a	0.54 ± 0.1 ^a	0.36 ± 0.08 ^b	0.34 ± 0.06 ^b	0.774 ± 0.002 ^a	0.757 ± 0.001 ^a
BGB088	0.15 ± 0.04 ^a	0.22 ± 0.04 ^a	0.50 ± 0.1 ^a	0.49 ± 0.1 ^a	0.29 ± 0.07 ^b	0.44 ± 0.07 ^a	0.744 ± 0.01 ^a	0.735 ± 0.014 ^a
BGB089	0.20 ± 0.05 ^a	0.19 ± 0.03 ^b	0.56 ± 0.02 ^a	0.58 ± 0.1 ^a	0.43 ± 0.08 ^a	0.43 ± 0.07 ^a	0.741 ± 0.017 ^a	0.717 ± 0.004 ^b
BGB091	0.23 ± 0.04 ^a	0.25 ± 0.05 ^a	0.54 ± 0.1 ^a	0.45 ± 0.1 ^a	0.46 ± 0.03 ^a	0.51 ± 0.04 ^a	0.744 ± 0.017 ^a	0.722 ± 0.021 ^b
BGB093	0.24 ± 0.03 ^a	0.23 ± 0.02 ^a	0.48 ± 0.04 ^a	0.47 ± 0.03 ^a	0.46 ± 0.05 ^a	0.46 ± 0.02 ^a	0.758 ± 0.016 ^a	0.746 ± 0.001 ^a
BGB096	0.15 ± 0.01 ^a	0.16 ± 0.02 ^b	0.74 ± 0.1 ^a	0.68 ± 0.05 ^a	0.37 ± 0.03 ^a	0.40 ± 0.06 ^a	0.73 ± 0.003 ^a	0.711 ± 0.004 ^b
BGB098	0.18 ± 0.03 ^a	0.26 ± 0.04 ^a	0.54 ± 0.02 ^a	0.47 ± 0.1 ^a	0.37 ± 0.04 ^a	0.50 ± 0.05 ^a	0.753 ± 0.017 ^a	0.743 ± 0.002 ^a
BGB101	0.21 ± 0.02 ^a	0.21 ± 0.01 ^a	0.59 ± 0.05 ^a	0.54 ± 0.1 ^a	0.41 ± 0.03 ^a	0.44 ± 0.02 ^a	0.764 ± 0.01 ^a	0.746 ± 0.003 ^a
BGB102	0.14 ± 0.03 ^a	0.12 ± 0.04 ^b	0.64 ± 0.1 ^a	0.60 ± 0.05 ^a	0.31 ± 0.05 ^b	0.37 ± 0.01 ^b	0.754 ± 0.006 ^a	0.724 ± 0.019 ^b
BGB103	0.2 ± 0.05 ^a	0.20 ± 0.02 ^a	0.60 ± 0.05 ^a	0.48 ± 0.04 ^a	0.40 ± 0.08 ^a	0.41 ± 0.03 ^a	0.758 ± 0.013 ^a	0.741 ± 0.012 ^a
BGB107	0.14 ± 0.02 ^a	0.14 ± 0.02 ^b	0.69 ± 0.03 ^a	0.60 ± 0.03 ^a	0.30 ± 0.03 ^b	0.35 ± 0.02 ^b	0.757 ± 0.007 ^a	0.68 ± 0.04 ^b
BGB109	0.19 ± 0.02 ^a	0.22 ± 0.04 ^a	0.62 ± 0.01 ^a	0.56 ± 0.1 ^a	0.41 ± 0.03 ^a	0.44 ± 0.05 ^a	0.75 ± 0.01 ^a	0.756 ± 0.004 ^a
BGB113	0.17 ± 0.04 ^a	0.10 ± 0.01 ^b	0.51 ± 0.1 ^a	0.62 ± 0.03 ^a	0.34 ± 0.05 ^b	0.23 ± 0.02 ^b	0.75 ± 0.012 ^a	0.68 ± 0.014 ^b
BGB444	0.14 ± 0.02 ^a	0.11 ± 0.01 ^b	0.58 ± 0.03 ^a	0.51 ± 0.1 ^a	0.30 ± 0.05 ^b	0.23 ± 0.03 ^b	0.749 ± 0.008 ^a	0.732 ± 0.012 ^b
BGB451	0.14 ± 0.05 ^a	0.17 ± 0.01 ^b	0.58 ± 0.1 ^a	0.63 ± 0.03 ^a	0.29 ± 0.09 ^b	0.40 ± 0.02 ^a	0.742 ± 0.011 ^a	0.727 ± 0.011 ^b
BGB467	0.14 ± 0.03 ^a	0.17 ± 0.03 ^b	0.64 ± 0.1 ^a	0.53 ± 0.02 ^a	0.27 ± 0.05 ^b	0.34 ± 0.06 ^b	0.777 ± 0.005 ^a	0.751 ± 0.005 ^a
BGB472	0.15 ± 0.03 ^a	0.18 ± 0.03 ^b	0.68 ± 0.1 ^a	0.53 ± 0.1 ^a	0.31 ± 0.06 ^b	0.35 ± 0.06 ^b	0.763 ± 0.005 ^a	0.756 ± 0.001 ^a

Genotype marginal means with letter within a studied trait are significantly different by the Scott-Knott at the 5% level of significance

Vegetative and yield production under HS:

Long term heat stress considerably affects the vegetative and tuber production of the studied potato germplasm. The FSW, DSW and FTW were significantly reduced due to HS, but the reduction in DMC observed under HS was not significant as compared to CT conditions (Table 5). BGB467 (*S. chacoense*) observed for highest FSW and DSW under CT and HS conditions. Three genotypes of *S. commersonii* (BGB003, BGB009, BGB027) did not produce any tubers under CT condition. However, BGB008 only produced one tuber under developing tuber with low weight at HS condition. Highest FTW was produced by BGB088 (*S. tuberosum* 2x) and BGB113 (*S. chacoense*) under CT and HS treatments, respectively. DMC was 23.5% and 20.5% for CT and HS conditions, respectively and genotypes belong to *S. commersonii* BGB451 and *S. chacoense* BGB444 measured for highest DMC % at CT and HS, respectively.

Table 5
Biomass and tuber yield traits by genotypes of wild potato germplasm under Control and Heat Stress conditions

Genotype	FSW (g)		DSW (g)		FTW (g)		DMC (%)	
	CT	HS	CT	HS	CT	HS	CT	HS
BEL	123.3 ± 17.8 ^c	99.5 ± 9.3 ^c	15.8 ± 0.6 ^c	13.4 ± 0.5 ^b	166.0 ± 13.6 ^a	49.0 ± 7.9 ^b	24.4 ± 0.6 ^b	15.8 ± 1.1 ^b
BGB003	137.0 ± 18.5 ^c	98.7 ± 5.2 ^c	19.2 ± 2 ^b	18.5 ± 0.7 ^b	0.0 ± 0.0 ^d	0.0 ± 0.0 ^d	0.0 ± 0.0 ^d	0.0 ± 0.0 ^c
BGB008	138.8 ± 11.8 ^c	103.8 ± 5 ^c	19.2 ± 1.1 ^b	16.6 ± 0.1 ^b	0.0 ± 0.0 ^d	1.3 ± 0.7 ^d	0.0 ± 0.0 ^d	8.7 ± 1.9 ^b
BGB009	138.3 ± 17.1 ^c	92.3 ± 8.1 ^c	20.0 ± 1.4 ^b	15.4 ± 1.4 ^b	0.0 ± 0.0 ^d	0.0 ± 0.0 ^d	0.0 ± 0.0 ^d	0.0 ± 0.0 ^c
BGB027	116.7 ± 13.7 ^d	71.0 ± 8.1 ^c	16.9 ± 0.6 ^b	15.4 ± 2.2 ^b	0.0 ± 0.0 ^d	0.0 ± 0.0 ^d	0.0 ± 0.0 ^d	0.0 ± 0.0 ^c
BGB045	168.7 ± 9.4 ^b	92.0 ± 49.8 ^c	25.2 ± 1.8 ^a	9.3 ± 5.7 ^b	2.3 ± 1.6 ^d	0.0 ± 0.0 ^d	15.9 ± 8 ^c	0.0 ± 0.0 ^c
BGB083	130.7 ± 23.8 ^c	88.7 ± 5.8 ^c	20.6 ± 3.4 ^b	20.9 ± 2.5 ^a	17.2 ± 6.8 ^c	29.6 ± 4.1 ^b	27.2 ± 0.6 ^b	26.8 ± 0.8 ^a
BGB086	59.5 ± 13.7 ^e	43.6 ± 2.9 ^c	11.8 ± 2.3 ^c	13.2 ± 0.8 ^b	16.6 ± 8.5 ^c	10.6 ± 5.8 ^c	12.5 ± 4.1 ^c	17.3 ± 3.5 ^b
BGB088	42.0 ± 11.4 ^e	87.7 ± 24.4 ^c	12.2 ± 1 ^c	16.5 ± 0.9 ^b	187.6 ± 29.4 ^a	74.2 ± 22.2 ^a	15.9 ± 0.6 ^c	11.7 ± 1.9 ^b
BGB089	80.7 ± 11.3 ^d	71.3 ± 9.5 ^c	18.2 ± 1.3 ^b	17.7 ± 1.4 ^b	125.5 ± 21.6 ^a	15.4 ± 7 ^c	21.5 ± 0.6 ^c	15.2 ± 1.4 ^b
BGB091	36.3 ± 13 ^e	44.0 ± 27 ^c	15.4 ± 2.5 ^c	10.1 ± 5.3 ^b	140.6 ± 17.9 ^a	93.1 ± 2.9 ^a	16.0 ± 0.3 ^c	13.6 ± 0.5 ^b
BGB093	37.3 ± 4.7 ^e	79.3 ± 9.8 ^c	17.0 ± 1 ^b	20.1 ± 0.8 ^a	153.5 ± 17.2 ^a	56.0 ± 4.8 ^b	19.0 ± 0.7 ^c	19.2 ± 0.9 ^b
BGB096	70.0 ± 13.1 ^e	79.7 ± 32.9 ^c	13.1 ± 1.9 ^c	16.5 ± 3.2 ^b	6.4 ± 5.5 ^d	13.2 ± 9.7 ^c	16.4 ± 8.3 ^c	15.6 ± 7.8 ^b
BGB098	187.3 ± 18.4 ^b	157.3 ± 1.9 ^b	26.3 ± 3 ^a	22.2 ± 0.7 ^a	65.2 ± 26.3 ^b	23.7 ± 17.4 ^c	30.4 ± 2.8 ^a	19.3 ± 9.6 ^a
BGB101	147.0 ± 35.5 ^c	128.3 ± 16.4 ^b	25.3 ± 1.9 ^a	20.9 ± 0.9 ^a	57.9 ± 28.8 ^b	36.6 ± 5.6 ^b	27.0 ± 3.2 ^b	26.2 ± 1 ^a
BGB102	108.0 ± 12.5 ^d	102.3 ± 17.7 ^c	19.2 ± 0.4 ^b	16.3 ± 1.8 ^b	132.1 ± 15.3 ^a	76.0 ± 4.3 ^a	30.3 ± 0.7 ^a	27.3 ± 0.8 ^a
BGB103	166.7 ± 17.7 ^b	118.0 ± 10.6 ^b	21.1 ± 1.8 ^b	18.6 ± 1.3 ^b	116.5 ± 27.3 ^a	43.9 ± 8.7 ^b	30.7 ± 0.5 ^a	24.7 ± 0.8 ^a
BGB107	147.3 ± 33.7 ^c	55.0 ± 8.7 ^c	17.3 ± 2.5 ^b	16.1 ± 4.5 ^b	107.1 ± 14.3 ^a	13.8 ± 1.5 ^c	27.2 ± 0.8 ^b	25.0 ± 1.6 ^a
BGB109	153.7 ± 17.9 ^c	129.7 ± 2.6 ^b	23.7 ± 2.3 ^a	20.3 ± 0.6 ^a	95.0 ± 36.7 ^b	36.9 ± 9 ^b	27.3 ± 1.1 ^b	26.4 ± 0.7 ^a
BGB113	93.7 ± 22 ^d	145.7 ± 28.3 ^b	22.3 ± 1.6 ^a	18.7 ± 2.8 ^b	164.5 ± 21.1 ^a	97.2 ± 20.9 ^a	28.5 ± 1.7 ^b	25.5 ± 0.9 ^a
BGB444	206.8 ± 22.4 ^b	144.9 ± 5.7 ^b	27.9 ± 2.5 ^a	21.9 ± 1.3 ^a	25.2 ± 5.1 ^c	54.8 ± 1.4 ^b	28.3 ± 11.9 ^b	29.5 ± 0.2 ^a
BGB451	211.7 ± 14.8 ^b	145.0 ± 10.2 ^b	27.7 ± 1.7 ^a	22.2 ± 0.8 ^a	59.7 ± 16.5 ^b	67.2 ± 6.6 ^a	31.5 ± 1.2 ^a	28.0 ± 0.2 ^a
BGB467	318.3 ± 24.9 ^a	223.7 ± 36 ^a	39.7 ± 5.6 ^a	29.3 ± 3.3 ^a	4.0 ± 2 ^d	2.2 ± 2.2 ^d	14.2 ± 7.3 ^c	9.6 ± 9.6 ^b
BGB472	178.0 ± 6.6 ^b	87.3 ± 15.1 ^c	20.4 ± 1.4 ^b	17.1 ± 1.8 ^b	123.1 ± 18.2 ^a	75.2 ± 7.1 ^a	26.7 ± 0.5 ^b	23.6 ± 0.9 ^a

Genotype marginal means with letter within a studied trait are significantly different by the Scott-Knott at the 5% level of significance

Multivariate analysis:

Correlation of 24 genotypes for photosynthesis, chlorophyll fluorescence and morphological traits under CT and HS conditions were shown in Fig. 3A, 4B. Gas exchange traits (Pn, E, Gs, Ci/Ca) found highly positive and significant association with each other, but these traits were significant negative association with WUE and iWUE under both temperature treatments. Photochemistry traits YII, qP were also found significant correlated with gas exchange traits under HS. Fv/Fm ratio was positively associated with YII while positively correlated with WUE, iWUE and DMC under HS. Under control conditions, DMC found negatively correlated with Pn, Gs and E. however, under stress conditions, DSW and DMC positively correlated with iWUE, WUE and negatively correlated with all the other studied traits but significant negative correlation exist between DMC and Pn, Gs, E, qP, YII.

The principal component analysis (PCA) based on photochemistry, gas exchange parameters and morphological traits was used to explain the variation present among the used potato germplasms. The PCA identified the five and three principal components (PC) for CT and HS as significant with Eigen values > 1.0 accounted for 84.09% and 77.99% variability, respectively (Table 6) by the studied traits. Biplot and correlation plot of variable associated with their respective PC for HS shown in Fig. 5 and for CT in Supp. Figure 1. The biplot had four main axes, with the upper right axis having a positive impact on PC1 and PC2, and the genotypes located have demonstrated by different colors according to their corresponding species (Fig. 4).

The first PC explained the highest variation present among the genotypes by the studied traits under both conditions and accounted for 32% and 52% of cumulative percentage of variation explained for CT and HS, respectively (Fig. 4). Traits such as Pn, Gs, E, YII, qP and DMC were the common traits

contributing to the variance with first PC under CT (Supp. Figure 1) and HS has Ci/Ca and iWUE are additional contributing traits (Table 6). Dry matter had lower values of eigenvectors (7.70, 7.34) under CT and HS, respectively. As part of second main component, which account to (54.00, 67.00) for CT and HS, respectively of the total variability of the experiment. The Chlorophyll index (SPAD), YII, qP and Fv/Fm ratio, FTW and DMC have the high value for the eigenvector under HS and SPAD, Ci/Ca, iWUE, YII and FTW were the most contributing under CT condition (Table 6).

Table 6
Eigenvalues, the proportion of variance and cumulative variance associated with the first five and three main components (PCA) under CT and HS, respectively estimated from a 15-variable correlation matrix for 24 potato genotypes.

Principal component	Control					Heat stress		
	PC1	PC2	PC3	PC4	PC5	PC1	PC2	PC3
SPAD	1.22	10.62	5.11	7.11	2.21	0.12	25.05	5.77
Pn	16.60	0.00	3.90	3.41	2.27	10.24	2.95	0.15
Gs	15.75	3.67	0.22	0.01	2.04	10.91	1.09	0.01
E	15.49	3.70	1.32	0.08	5.29	11.65	1.11	0.03
Ci/Ca	0.43	17.99	3.89	13.41	1.80	11.74	0.14	0.01
WUE	8.90	6.01	7.33	9.46	0.01	10.55	4.20	0.58
iWUE	4.66	14.62	3.08	8.47	0.28	9.52	4.63	0.35
YII	9.52	7.60	0.05	14.32	0.90	8.11	10.20	0.36
NPQ	0.08	4.27	8.93	17.26	9.54	3.09	0.05	4.71
qP	10.05	5.93	0.05	8.60	0.30	7.29	8.35	0.25
Fv/Fm	0.01	0.12	15.17	2.55	31.35	1.31	12.92	6.13
FSW	4.21	5.33	25.32	4.38	0.88	2.15	4.46	33.44
DSW	4.92	0.58	22.28	8.17	2.26	3.59	6.41	26.80
FTW	0.48	16.34	3.31	0.28	10.94	2.39	11.46	19.82
DMC	7.70	3.23	0.04	2.49	29.94	7.34	6.97	1.60
Eigenvalue	4.87	3.23	2.01	1.31	1.19	7.79	2.26	1.65
% variance	32.49	21.51	13.43	8.74	7.93	51.94	15.08	10.98
cumulative % variance	32.49	54.00	67.42	76.16	84.09	51.94	67.01	77.99

The dendrogram was generated to examine the relationships among different genotypes based on Euclidean distances, calculated by the ward's method under control and stress conditions as presented in Fig. 4. Inertia gain pointed to the categorization of the genotypes into three clusters in CT and HS treatment according to measuring traits. The corresponding genotypes in each cluster are given in Fig. 5 and their characteristics are summarized below. Tolerance levels of different clusters were identified by summation of linear combination of selected physiological and yield traits under CT and HS. Total scores for each cluster were obtained and presented in **Supplementary Table 1**. Based on the value of cluster score, clusters are divided into three categories below under HS conditions.

Tolerant group: in Cluster-I comprised genotypes including BGB103, BGB472, BGB103, BGB467, BGB083, BGB451, BGB102, BGB444 and BGB113 (Fig. 5) under HS characterized by significant performance of Pn, Gs, E, WUE, Ci/Ca, WUE, iWUE, YII, qP, FSW, DSW, FTW and DMC (Fig. 6). Hence, the genotypes of this group attain the highest total cluster and designated as tolerant group.

Intermediate group: Cluster-III under heat stress condition attain the second highest total score are described as an intermediate tolerant to stress condition contains 46% of total potato genotypes evaluated (BGB088, BGB093, BGB027, BGB086, BGB101, BGB098, BGB089, BGB107, BGB096, BGB008, BGB045). These genotypes showed significant performance of WUE, FSW, FTW and DMC (Fig. 6). Among this group BGB045, BGB009, BGB008 belong to *S. commersonii* and BGB096 (*S. chacoense*) perform better under HS conditions.

Susceptible group: Under CT conditions, Cluster-II and under HS conditions, Cluster-III was estimated as the most sensitive group to HS conditions based on the cluster scoring (Table 7). Under CT ranges, 38% of total genotypes were assigned to this group while under HS conditions, only four genotypes, among which commercial cultivar BEL was also included to this group (Fig. 5). However, this group only significant performance of physiological traits which include Pn, Gs, E, Ci/Ca, iWUE, YII and qP (Fig. 6) under HS conditions.

Discussion

During heat stress, the photosynthesis reduction is linked to reduced antenna pigments in chlorophyll content (Camejo et al. 2006). Furthermore, changes in chloroplast ultrastructure can have a direct impact on the state of the photosynthetic apparatus and the rate of photosynthesis (Zhang et al. 2014). HS can damage the chloroplast structure by disordering the lamellae and increase the plastoglobulus number (Gao et al. 2018). On the other hand, in our study

chlorophyll content in the scale of SPAD value (Fig. 7) increased in heat stressed plants but however this increase does not significantly correlated with the increase other gas exchange or photochemistry parameters (Fig. 4) in used potato germplasm. These observations of increased SPAD values in heat stressed plants, although repeatable and consistent with the leaf color and morphology of potato plants (Tang et al. 2018), are contrary to the findings of reduced SPAD values in wheat (*Triticum aestivum*) and rice (*Oryza sativa*) plants under heat stress (Tiwari et al. 2017). Increased SPAD under HS are also contrary to the findings of decreased chlorophyll content (based on extraction with acetone and spectrophotometric readings) under mild heat stress reported in the potato cultivar 'Desiree' (Hancock et al. 2014) and an accession of the wild species *S. chacoense* (Reynolds et al. 1990). The reason for this inconsistency remains unknown, but it may be related to the differences in heat stress temperature conditions, measurement methods and used potato germplasm among the referred studies. Additionally, BGB101 and BGB103 slight reduction in chlorophyll content is consistent with (Hancock et al. 2014). This demonstrates the genotypic response of potato cultivars to heat stress and suggests that multiple genotypes must be used to investigate genetic diversity.

Photosynthesis serves as a global sensor of environmental stress (Biswal et al. 2011) and is highly sensitive to high temperature (Berry and Bjorkman 1980). Considering the objective of the study, the most distinctive observable fact is a shift in the optimum temperature of photosynthesis (Berry and Bjorkman 1980; Yamori et al. 2014) as the growth temperature changes by adaptive process explained by (Havaux 1993). The higher rate of net photosynthesis rate of studied wild germplasm in heat stress temperature (Fig. 7) observed and similar results reported for the heat-resistant potato genotypes such as Desirée and Norchip (Hancock et al. 2014) and summarized that heat-tolerant genotypes can longer maintain their photosynthesis at a higher level under elevated temperatures.. The increase in net photosynthesis rate indicated that the chloroplasts did not suffer damage and suggested that the genotypic response of potato cultivars to heat stress and presence of photosynthetic traits genetic diversity. Moreover, potato tubers are stem-derived organs which act as sink of starch produced by photosynthetically active source tissues (Hastilestari et al. 2018). Hence, higher rates of the Pn suggested that the presence of potential genes which stimulated under HS rather than CT. But this mechanism is contradicted in other agronomic crops such as wheat (Wahid et al. 2007). The difference in response to heat stress in our study may be due to the completely distinct morphology and biochemical machinery of the wheat and potato plants.

Stomatal conductance plays a vital role to avoid water loss (Goufo et al. 2017) and increase the ability of a plant to regulate internal temperature under heat stress (Schabow 2022). We found that, on average, potato plants closed stomata and decreased Gs significantly during the heat stress (Fig. 7). Stomatal responses to heat depended on species, however, and paradoxically, two accessions (BGB003, BGB109) opened stomata and significantly increased Gs (Table 4). Stomatal closure during heatwaves follows stomatal optimization theory (Cowan et al. 1977), and existence of strong significant correlation with Pn suggest us that the studied germplasm has the ability to create a balance between maximizing the CO₂ uptake to produce sugar for sink tissues. Whereas, in this study, 55% of used accessions (BGB003, BGB008, BGB009, BGB027, BGB086, BGB088, BGB089, BGB091, BGB093, BGB098, BGB101, BGB109, BRS-BEL) observed to be increasing transpiration rate to cooling the leaves by latent heat due to higher transpiration rates (Sadok et al. 2021) under the HS. There is also significant positive correlation present with Pn and Gs which explicit that potato germplasm with increasing photosynthesis and transpiration, tries to maintain its metabolic activity and cool its leaves, but it comes at the cost of water loss, which is compensated by daily manual irrigation. These findings also agrees with the findings of (Berry and Bjorkman 1980) who reported that transpiration is temperature dependent. This behavior is also in agreement with (Zhou et al 2016; Jolliet & Bailey 1992), who observed an increase in transpiration rate under HS in tomato genotypes. Overall, *S. chacoense* recorded a decrease in transpiration rate, which shows the intraspecies differences between genotypes in transpiration may be due to their differences in morphology. Plants that are able to regulate their internal CO₂ levels under heat stress conditions are more likely to be successful in survival and reproduction, and therefore, contribute to genetic diversity in the plant community. This highlights the importance of considering the role of C_i/C_a in screening potato germplasm under heat stress. Since, C_i/C_a varies throughout the day, it is necessary to understand correlation of gas exchange parameters effects on C_i/C_a variations (Tan et al. 2018). As we observed in this screening trail, genotypes belong to cluster-3 (BGB003, BGB009, BGB091, GB093, BGB101, BRS-BEL) showed relatively higher Gs values along with high Pn under heat stress, giving high C_i/C_a ratio. This indicates the less resistance to CO₂ entry into intercellular spaces (de Oliveira et al 2023). Therefore, these results suggest the use of C_i/C_a ratio to identify the heat tolerant germplasm but only combing with other gas exchange parameters such as CO₂ consumption and availability traits (Ji et al. 2022).

In general, rising temperatures cause an increase in WUE and iWUE, but this increase is not always related to increased crop productivity because it only gives plant breeders and physiologists an estimate of how efficiently the plant uses available water under the studied stress or high temperatures (Kilemo 2022). In our study, almost all used germplasm showed an increase in the WUE and iWUE (Table 4). However, it is also important to note that they are negatively significant linked with the other gas exchange and chlorophyll fluorescence parameters (Fig. 3). Hence, we can hypothesize that our germplasm is a water-saving strategy by closing stomata but transpiration rate where not reduced because of regular availability of daily irrigation. Genotypes with higher rates of WUE and iWUE also indicate the use of survival strategies varying intra and inter species. Some species may prioritize water conservation at the expense of photosynthesis, while others may try to maintain photosynthetic activity even at the expense of water loss in the form of higher transpiration rates (Griebel et al. 2020; Sadok et al. 2021; Gregory et al. 2023).

Concerning photochemistry, in the thylakoid membranes, photosystem II is the most vulnerable component to damage. As a result, the primary effect of abiotic stress is to make PSII susceptible to photoinhibition (Li et al. 2020). The positive correlations of YII, qP, ETR, and Fv/Fm with gas exchange parameters (such as Gs, Pn, and E) suggest that as photosynthetic activity increases, the efficiency of photochemical reactions in PSII also increases. This indicates that the plant is effectively using absorbed light energy for photosynthesis, resulting in higher rates of CO₂ uptake (Pn) and efficient water vapor exchange (E) through the stomata. From this study it is also observed that in wild potato germplasm demonstrate positive correlation among the photochemical quenching parameters which indicate that these parameters are closely related and collectively reflect the effective functioning of PSII and efficient electron transport during photosynthesis.

In this study, accessions belonging to distinct species group showed declining trend, in other words, which is obvious due to the presence of significant negative correlation between NPQ and photochemical quenching traits (Fig. 3). This indicates that the potato germplasm is efficiently utilizing the absorbed light energy for photosynthesis, reducing the need for protective mechanisms against excess light and avoiding photoinhibition to protect the photosynthetic machinery.

Taking these facts into account, we used possible photoinhibition indicators in this study to estimate the diversity of potato germplasm to tolerate heat stress. The Fv/Fm ratio was the first important parameter derived from the Kautsky curve (Krause 1988), and it later became a key parameter for detecting PSII photoinhibition caused by a stress factor (Krause and Weis 1991). The ratio Fv/Fm represents an estimate of maximum photochemical efficiency of PSII and is used to detect PSII reaction center function loss (Öquist et al. 1992). Fv/Fm values typically range between 0.75 and 0.85, and this ratio is proportional to photochemistry's quantum yield (Baker 2008). BGB003 of *S. commersonii*, BGB093 of *S. tuberosum* 2x, and five accessions of *S. chacoense* (BGB086, BGB101, BGB109, BGB467, BGB472) fall within the above-mentioned ratios under heat stress. A decrease in this ratio is thought to be a good indicator of photoinhibition (Ögren 1991; Krause and Winter 1996; Bertamini and Nedunchezian 2003; Santabarbara et al. 2019). As shown by 60% of assessed germplasm, whereas BGB107 and BGB113 were the most susceptible to heat stress genotypes due to photoinhibition. It can be caused by two different processes, first is a decrease in the rate constant of PSII photochemistry caused by damage to the PSII reaction centers and/or an increase in the rate constant of non-radiative excitation energy dissipation (Kitajima and Butler 1975). However, the decrease in Fv/Fm ratio is not always associated with photoinhibition, but it is also regarded as an indicator of PSII photoinactivation, which can occur due to the closure of PSII reaction centers or other processes such as thermal dissipation of absorbed light (Malnoë 2018).

In current study, accessions BGB113 (*S. chacoense*), BGB008 (*S. commersonii*) and BGB089 (*S. tuberosum* 2x) showed minimum values for effective photochemical yield (YII) in quenching analysis. Also, provides reliable data on the electron transport rate (ETR). In fact, this declining trend in YII along with ETR values talks about the inactivation of PSII which function as photoprotection by adjusting the photosynthetic photon density under heat stress conditions (Genty et al. 1989; Krause and Weis 1991). The results of Coefficient of photochemical quenching (qP) were also in accordance with the mechanism mentioned above because the same genotypes which showed the minimum effective photochemical yield, also maintains the maximum proportion of closed reaction center under heat stress.

The PCA under heat stress conditions (Fig. 4, Table 4) explain 78% of variability by the significant principal components in studied germplasm also suggesting the same results that the variability present in the germplasm is due to the same traits which were found significantly correlated under HS. Hence, gas exchange traits such as (Pn, Gs, E along with YII and qP) are worth screening the wild potato germplasm under heat stress conditions. Furthermore, studied germplasm were divided into three clusters based on the cluster scores Under both conditions, cluster-I contain 29% and 38% of total studied genotypes, which can be considered as tolerant group to their respective studied growth conditions.

Under HS conditions, cluster-I found to be maintaining the photosynthesis rates, while reducing the stomatal conductance and transpiration rates which is also proved by the chlorophyll fluorescence parameters YII and qP, showed higher mean values compare to CT condition for cluster-I. Therefore, our data suggest that under heat stress conditions, these genotypes are more efficient in transferring the light excitation energy to CO₂ fixation, thus producing a higher photosynthetic carbon gain, and resulted in higher biomass production and tuber yield and dry matter content as compared to the genotypes assigned to other clusters.

Conclusion

Gas exchange traits in combination with chlorophyll fluorescence traits (YII and qP) are key factors to phenotype the wild potato germplasm under heat stress. Through multivariate analysis it was confirmed these traits associated with HS conditions and further from cluster analysis, genotypes which are able to maintain their photosynthesis with reduction in stomatal conductance and transpiration rates and thus use of efficient use of available water to produce higher biomass and tuber production. These results concluded that the accession belong to *S. chacoense* could be a candidate genotypes to evaluate for the presence of resistant genes against HS in genotypes belong to tolerant group and could lead to further exploration and introduce to successful potato breeding and high-quality crop production.

Declarations

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Author Contributions

Conceptualization: IB, CC, GH; Methodology: IB, JH, GB; Software: Validation: IB; Formal analysis: IB; Resources: GH, CC; Data curation: IB and RN; Writing-original draft preparation: IB; Writing-review & editing: IB, RN, JH, CC, GH; Supervision: CC, GH; Project administration: CC, GH. All authors have read and agreed to the published version of the manuscript.

Declarations

I, Ikram Bashir, the corresponding author, declares on behalf of all authors that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper. There have been no involvements that might raise the question of bias in the work reported or in the conclusions, implications, or opinions stated.

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Table

Table 7 is not available with this version.

Supplementary Figure

Supplementary Figure 1 is not available with this version.

Figures

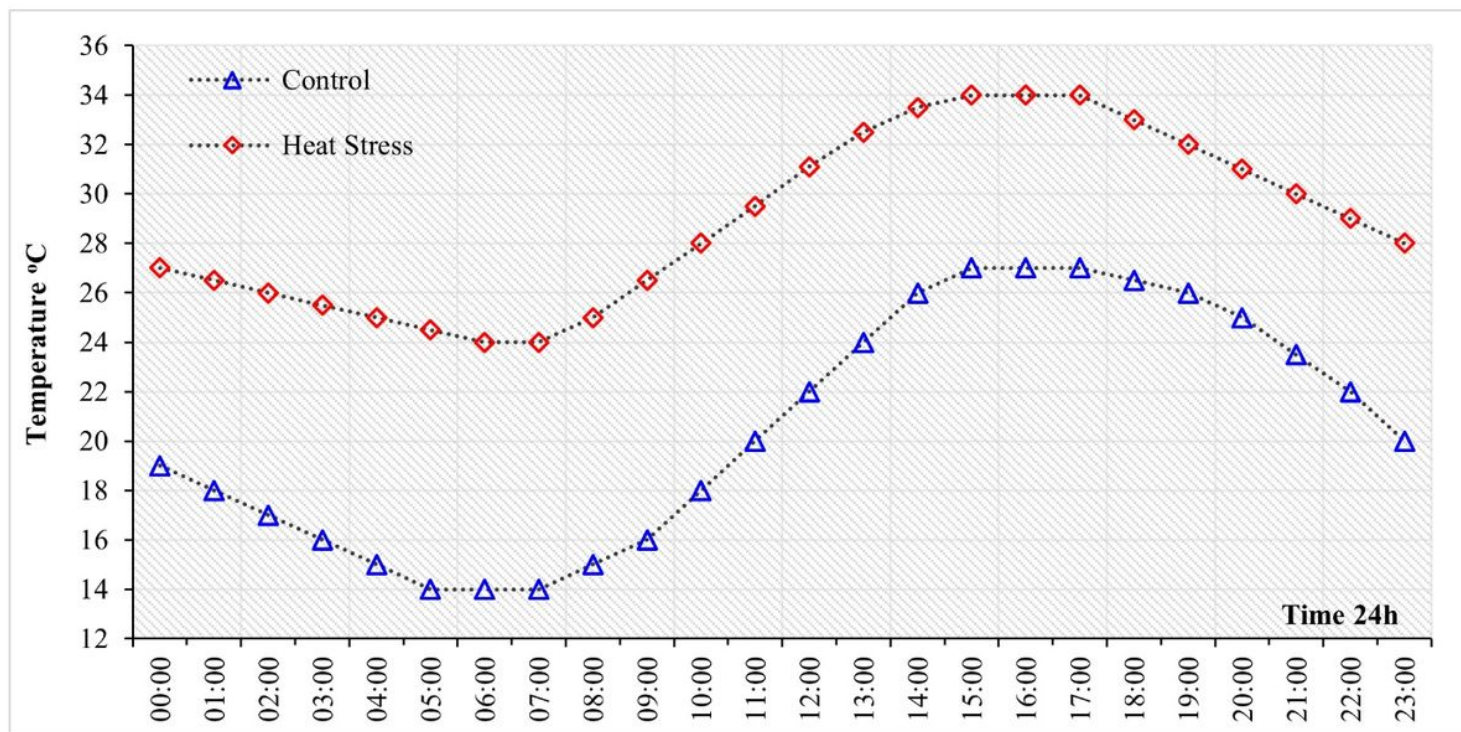


Figure 1
Growth chambers control and heat stress temperature environmental conditions 2021.

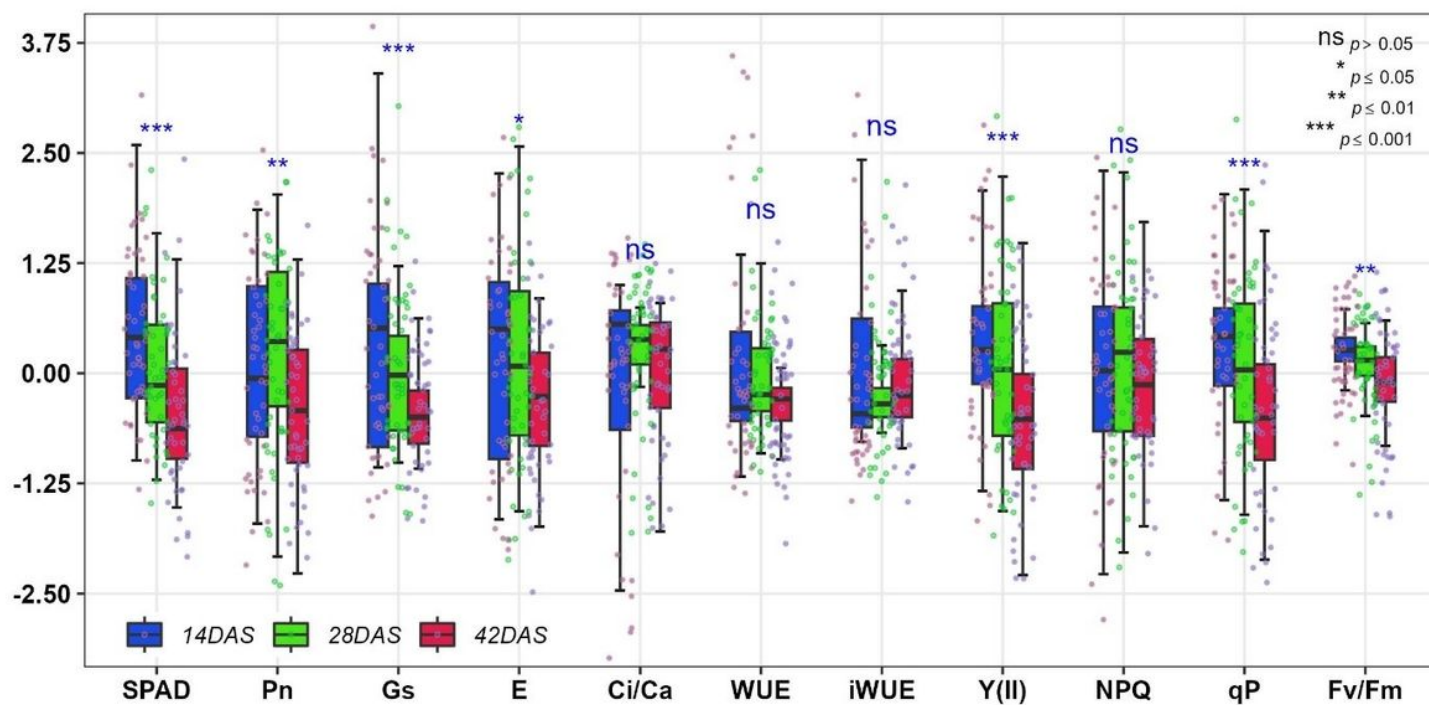


Figure 2
Mean comparison of physiological traits among 24 genotypes of potato (*Solanum*, *Solanaceae*) measured after 14 days after stress (DAS), 28DAS, 42DAS.

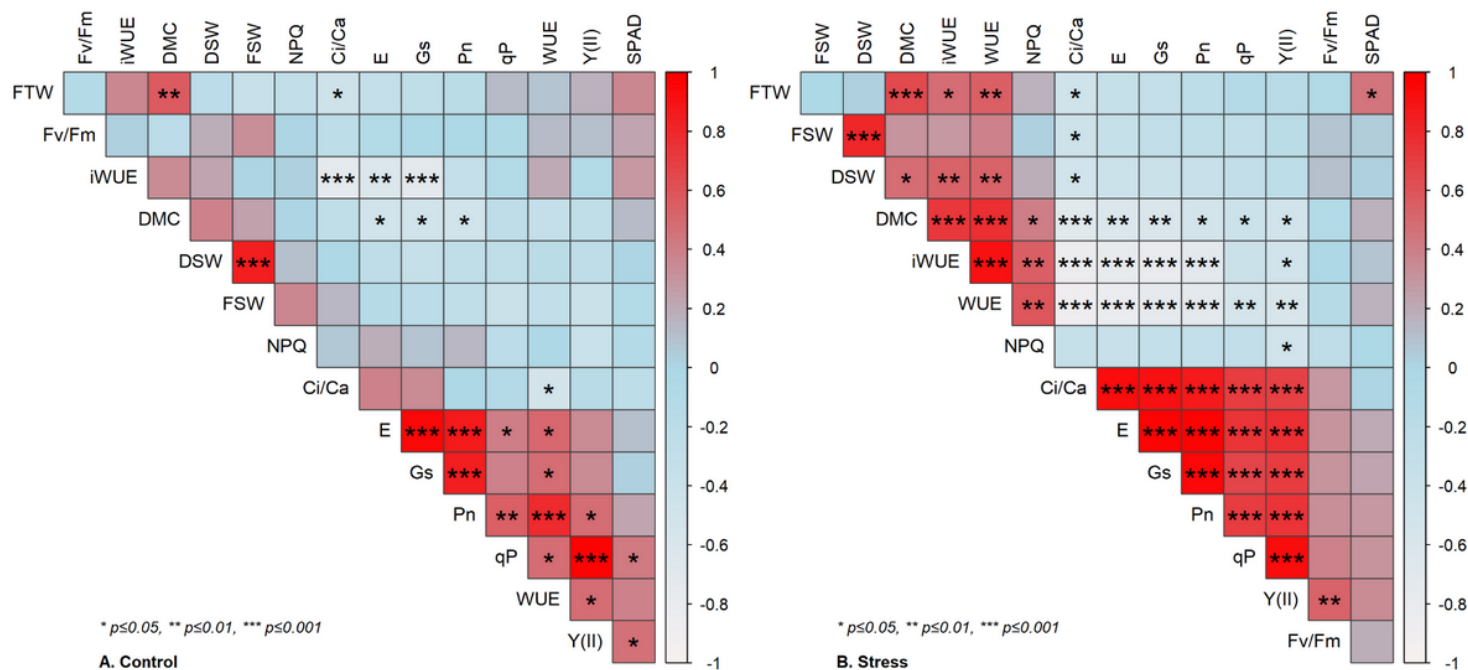


Figure 3

Correlation between different variables of chlorophyll fluorescence and photosynthesis traits in 24 potato (*Solanum*, Solanaceae) genotypes leaves in germplasm from Embrapa Potato Genebank. A. Control treatment (CT) 14-27°C, and B. Heat stress (HS) 24-34°C. * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$.

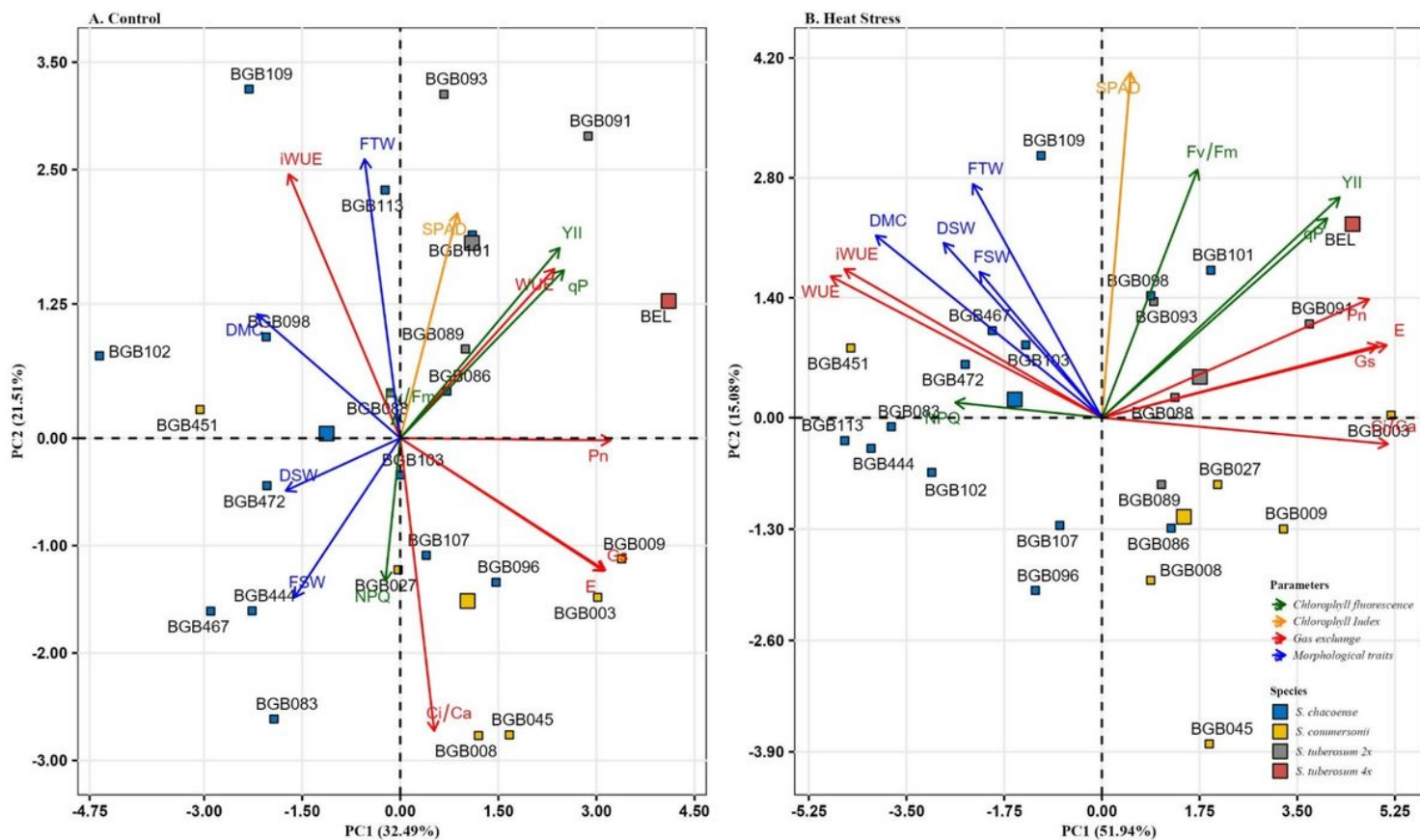


Figure 4

Dispersion of 24 potato (*Solanum*, *Solanaceae*) genotypes from Embrapa Potato Genebank by principal component analysis evaluated under A. Control and B. heat stress (HS) conditions, for the SPAD chlorophyll Index (SPAD), net photosynthesis rate (Pn), stomatal conductance (Gs), transpiration rate (E), water use efficiency (WUE), intrinsic water use efficiency (iWUE), intracellular and ambient CO₂ assimilation ratio (Ci/Ca), effective quantum yield of PSII (YII), nonphotochemical quenching (NPQ), Coefficient of photochemical quenching (qP), maximum efficiency of PSII 0(Fv/Fm), fresh shoot weight (FSW), dry shoot weight (DSW), fresh tuber weight (FTW) and dry matter content (DMC).

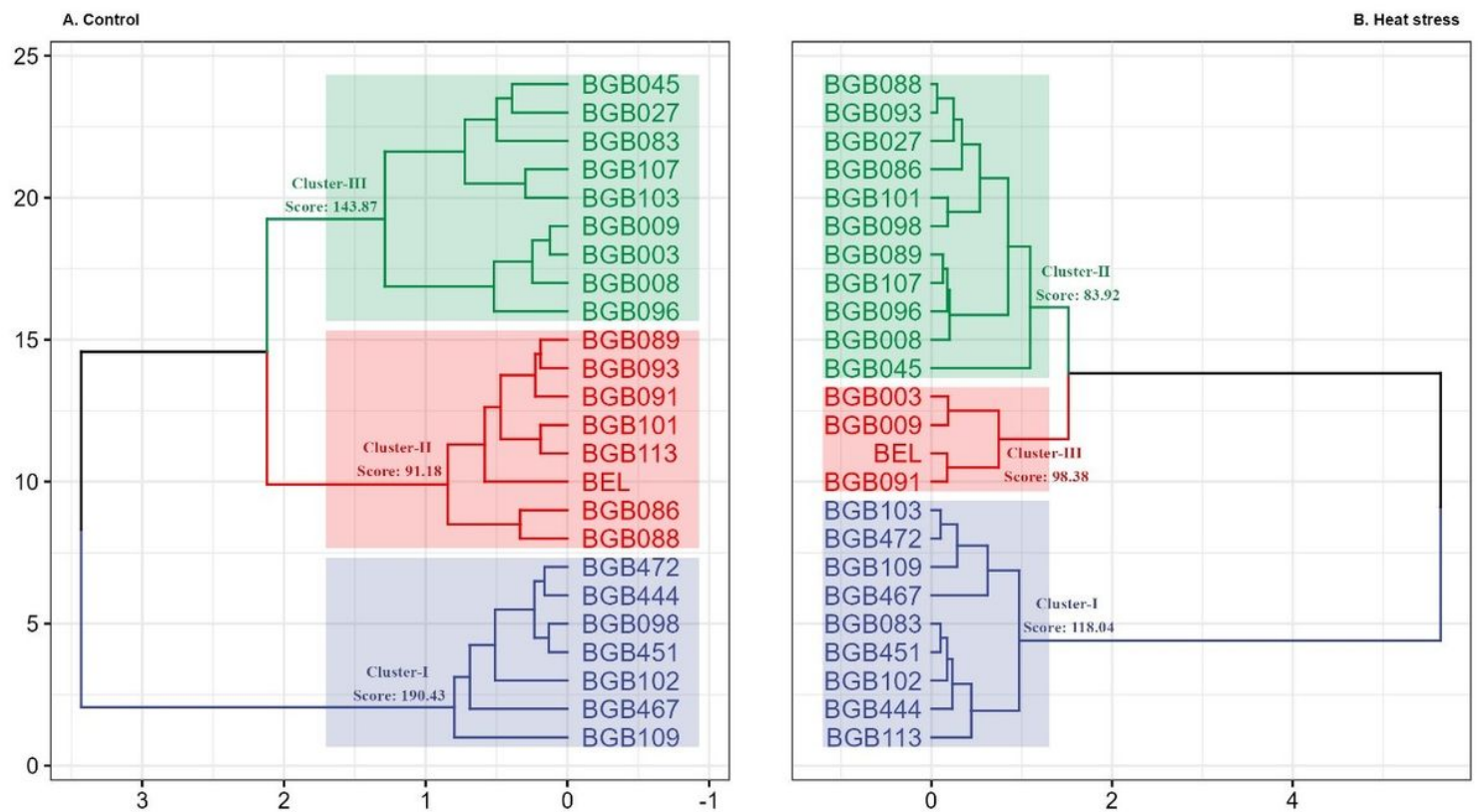


Figure 5

Dendrogram using Ward's method showing distribution of the 24 wild potato genotypes under A. Control; B. Heat stress on the basis of 15 quantitative characteristics.

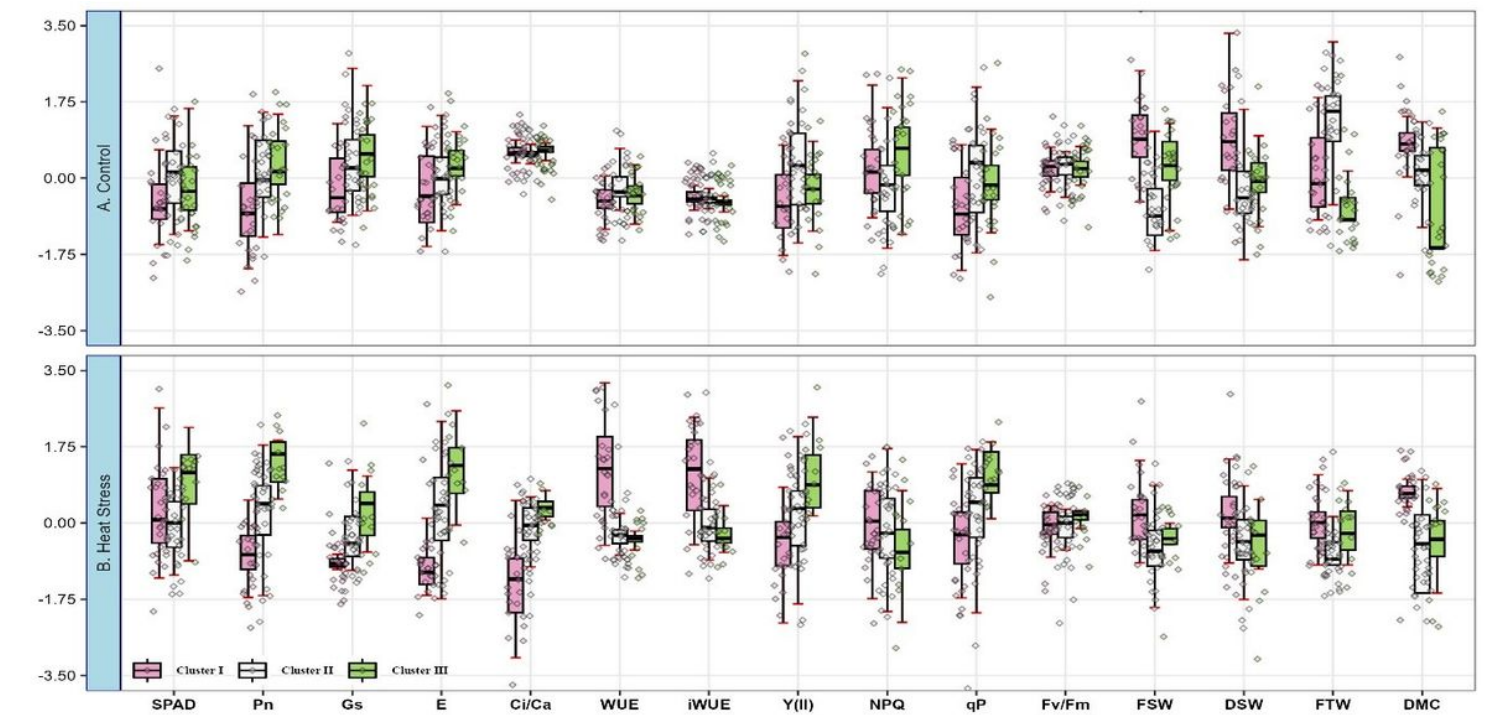


Figure 6

Phenotypic clusters. Box plots show median, 25 and 75 percentiles, and whiskers indicate 1.5 times the interquartile range of the variables assessed within each cluster. The x-axis shows the cluster performance of the respective traits to Y-axis. Each point represents genotype best linear unbiased predictor.

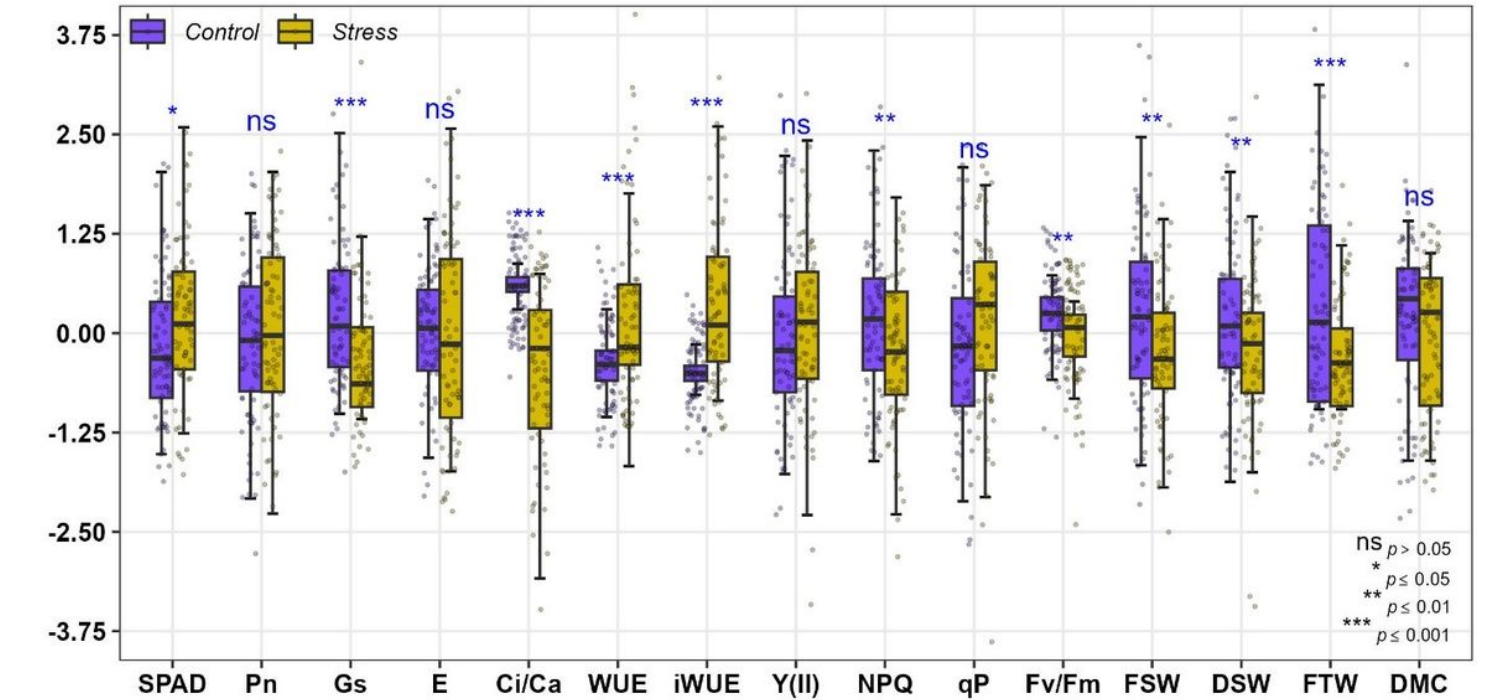


Figure 7

Mean comparison of gas exchange traits among 24 genotypes of potato (*Solanum*, Solanaceae) under control, CT, and HS stressed condition.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [SupplementaryTable1.docx](#)