Genetic parameters and responses associated with high temperature in potato wild relatives.

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Abstract

Crop wild relatives (CWRs) have significantly been used in potato (*Solanum tuberosum*, Solanaceae) breeding. Hence, introgression breeding may help in coping with the challenges posed by climate change. We used 20 accessions from Embrapa Potato Genebank, twelve belongs to wild specie *Solanum chacoense* and eight from *S. commersonii* and one, *S. tuberosum* commercial cultivar for their tolerance to two different temperature conditions CT as control temperature (14–24ºC) and HS as heat stress (24–37ºC). The evaluation was based on gas exchange (Pn, Gs and Tr), chlorophyll fluorescence analysis (Y(II), NPQ, Fv/Fm), chlorophyll A, B and carotenoid content and tuber yield related traits (FTW and DMC%) and measured after 1DAS (Days after stress), 15DAS and 35DAS. Mixed model methodologies were used to predict average genotypic value in the various environments and capitalize on an average interaction with all evaluated environments. Significant differences were observed between *Solanum* wild genotypes showed by 2-factorial for agronomic traits and 3-factorial ANOVA for physiological traits. The correlations among the accessed traits were found here significant for heat stress conditions. Mixed model methodology helps us ranking the genotypes based on measured variables according to their true genotypic values for both temperature conditions and after each measurement of days after applied stress.

Introduction

Temperature influences the internal biological reactions that control growth and development, influences photosynthesis and respiration, establishes crop cultivation boundaries (Geange et al. 2021), and is a worrying climate change factor (e.g., water stress, salinity, ozone, and CO_2) that will affect crop yields (Jin et al. 2017; Chaudhry and Sidhu 2022). Temperature increases are projected to range from 2.1°C to 5.7°C globally by the end of the 21st century (Pörtner et al. 2022). Temperature variability is a cause for concern because most cultivated species have lower heat tolerance limits (Geange et al. 2021). As a result, crops must be bred to perform well at higher temperatures.

Potato crop wild relatives (CWRs) are a valuable source of genetic diversity for potato improvement. They have been shown to contain genes for resistance to pests and diseases, tolerance to abiotic stresses such as drought and heat, and improved nutritional quality (Zhang et al. 2017). The importance of CWRs is becoming increasingly evident as the world faces the challenges of climate change (Dempewolf et al. 2017). Climate change is expected to lead to more extreme weather events, such as heat waves, droughts, and floods. These events can have a devastating impact on crop yields, and CWRs can provide the genetic diversity needed to develop new varieties that are more resilient to these stresses.

One of the challenges in using CWRs in breeding is that they often have undesirable traits, such as low yield or poor tuber quality (Kashyap et al. 2021). This is where estimating the genetic parameters under heat stress is important. Genetic parameters are the quantitative effects of genes on traits (Thompson 2008). By estimating these parameters, breeders can identify the genes that are responsible for heat tolerance and select for them in breeding programs. There are a number of methods that can be used to estimate genetic parameters under heat stress. One common method is to use field trials. In field trials, plants are grown under different heat stress conditions, and their yields and other traits are measured. The genetic parameters can then be estimated using statistical methods. The estimation of genetic parameters under heat stress is a complex and challenging task, but it is essential for developing new potato varieties that are more resilient to climate change (Bita and Gerats 2013). By understanding the genetic basis of heat tolerance, breeders can select for the genes that are most important for this trait and develop varieties that will be able to withstand the challenges of the future (Chapman et al. 2012).

Gas exchange and chlorophyll fluorescence are important physiological processes that can be affected by heat stress in potato plants. Understanding the genetic basis of these responses is crucial for developing strategies to enhance heat tolerance in potato crops. Gas exchange, through stomatal regulation, ensures the uptake of carbon dioxide essential for photosynthesis while facilitating the release of oxygen (Harrison et al. 2020). This process supports the production of energy and vital compounds required for growth and development. On the other hand, chlorophyll fluorescence offers deep insights into the health of the photosynthetic apparatus. Under heat stress conditions, it becomes a dynamic tool for assessing the efficiency of Photosystem II, the primary driver of photosynthesis, and detecting potential damage (Schreiber 2004). A decline in chlorophyll fluorescence parameters, notably the maximum quantum yield of Photosystem II (Fv/Fm), can signify impairment in photosynthetic performance (Baker 2008). Moreover, chlorophyll fluorescence acts as an early stress indicator (Moustaka and Moustakas 2023), enabling prompt interventions to mitigate damage and sustain plant productivity. Additionally, this process aids in the controlled dissipation of excessive light energy, averting oxidative stress and maintaining cellular integrity. Ultimately, a comprehensive understanding of the interplay between gas exchange and chlorophyll fluorescence equips scientists, researchers, and agriculturists with valuable tools to decipher potato plant responses to heat stress and devise strategies for crop improvement in the face of changing climatic conditions.

Potato is a nutritious crop which can be grown in many environments and could be an important food to help with the world's increasing demand for food due to its growing population (Birch et al. 2012). Tuber yield and quality of potato reduces with high temperatures, one of the main hurdles for increasing potato yield in warmer areas and seasons (Dahal et al. 2019). One important factor for the potato crop is minimal

night temperatures as, potato tuberization is decreased when temperatures at night are above 20°C and if they are 25°C and above, no tuberization will occur (Ewing 1981). Injuries due to high temperature stress may eventually result in growth suppression, starvation, reduced iron flux and might even result in generation of reactive oxygen species and/or toxic substances (Schöffl et al. 1999; Sabina and Sameena 2021). After exposure to elevated temperature, heat shock proteins are activated; this is known to be an important environmental adaptive strategy in this regard (Feder and Hofmann 1999; Janni et al. 2020). The tolerance caused due to exposure to so, results in many benefits, such as better photosynthesis, water use and nutrient use efficiency, assimilate partitioning and stability of cell membranes (Camejo et al. 2005; Ahn and Zimmerman 2006; Percival 2023). Due to these adaptations, plants can grow and develop under heat stress. Successful attempts have already been made to strengthen heat tolerance through traditional crop breeding methods (Ehlers and Hall 1998; Camejo et al. 2005; Driedonks et al. 2016). There is a huge amount of variation between and within species, this provides an opportunity to improve the tolerance of crops for heat stress through genetic means. Hence, the objective of this research was carried out to investigate the morphological and physiological parameters of wild potato accessions of various nature in order to rank and select the best fit ideotype with heat tolerant characteristic.

Material and methods

The experiment follows a randomized complete block design (RCBD) with 3 factors. Tubers from 20 genotypes (G) of uniform size were selected and acclimatized and grown in controlled condition (Table 1).

Table 1
Germplasm from Embrapa Potato Genebank evaluated for genotypic response under heat stress.

Sr. #	BGB	BRA	Species
01.	BGB001	00167007-4	*Solanum commersonii*
02.	BGB011	00167027-2	*Solanum commersonii*
03.	BGB048	00167400-1	*Solanum commersonii*
04.	BGB055	00167407-6	*Solanum commersonii*
05.	BGB068	00167420-9	*Solanum commersonii*
06.	BGB077	00167429-0	*Solanum commersonii*
07.	BGB094	00167446-4	*Solanum chacoense*
08.	BGB095	00167447-2	*Solanum chacoense*
09.	BGB097	00167449-8	*Solanum chacoense*
10.	BGB099	00167451-4	*Solanum chacoense*
11.	BGB100	00167017-3	*Solanum chacoense*
12.	BGB104	00167021-5	*Solanum chacoense*
13.	BGB105	00167022-3	*Solanum chacoense*
14.	BGB106	00167023-1	*Solanum chacoense*
15.	BGB108	00167025-6	*Solanum chacoense*
16.	BGB110	00167028-0	*Solanum chacoense*
17.	BGB111	00167029-8	*Solanum chacoense*
18.	BGB453	00183760-8	*Solanum commersonii*
19.	BGB460	00183766-5	*Solanum commersonii*
20.	BRSBEL	00167251-8	*Solanum tuberosum 4x*

After uniform growth they were transferred to growth chambers with two temperature (T) conditions (control-CT, 14–27°C; stress-HS, 24–34°C) in two replications of each accession, both chambers had controlled photoperiod of 12 hours (7:00 at 19:00h) with light intensity 400 µmol m^{-2} s^{-1} and relative humidity was maintained between 50–60% throughout the experiment (Fig. 1), and third factor was the data recorded after 1, 15 and 35 days after stress (DAS). Regular irrigation and pest scouting were performed daily.

Physiological traits:

Determination of Chlorophyll fluorescence (CF) variables

Chlorophyll fluorescence analysis were performed using the PAM-2500 fluorometer (Walz Heinz GmbH, Effeltrich, Germany). Before measurements, the plants were dark-adapted inside each growth chamber for at least 30 minutes. The chlorophyll fluorescence parameters were measured immediately after dark adaptation between 9:00 a.m. and 1:00 p.m. The maximal photochemical efficiency of photosystem II (PSII) (Fv/Fm), effective quantum yield of PSII (YII) and non-photochemical quenching (NPQ) were measured according to methods described in Maxwell and Johnson (2000). The response values for Y(II), NPQ, Fv/Fm were calculated by taking the average of the values obtained in light 281, 336, 396 and 461 µmol $m^{-2}s^{-1}$.

Leaf gas Exchange Responses

The leaf gas exchange parameters such as, net photosynthetic rate (Pn) and stomatal conductance (Gs) and transpiration rate (Tr) were measured by using portable photosynthesis system LI-6400XT (Li-COR Inc., Lincoln, NE, USA) equipped with an open-flow infrared gas analyzer was used at a steady state (PAR of 100–800 µmol $m^{-2}s^{-1}$, reference CO_2 concentration of 400 µmol mol^{-1}, air flow rate of 500 µmol s^{-1}. Measurements were performed on the third expanded leaf from the top of the stem on a plant of each genotype previously irrigated and adapted for at least 30 minutes at a temperature of 24°C for plants in the control temperature condition, and 34°C for plants in the stress condition.

Determination of chlorophyll traits

Chlorophyll A, B, and carotenoids were determined as described by Wellburn (1994) with small modifications. The absorption was measured at 480, 649, and 665nm using a microplate reader SpectraMax® M3. Contents of chlorophyll A, chlorophyll B and carotenoid were calculated by the formulas:

Chlorophyll-A (Chl-A) = $(12.19 \times \mathrm{A}_{665}) - (3.45 \times \mathrm{A}_{649})$

Chlorophyll-B (Chl-B) = $(21.99 \times \mathrm{A}_{649}) - (5.32 \times \mathrm{A}_{665})$

Carotenoid Contents (Carot) = $((10^3 \times A480) - (2.14 \times Chl\text{-}A) - (70.16 \times Chl\text{-}B)) \div 220$

Agronomic traits

At the end of the potato plant life cycle, fresh shoot weight (g) was measured and after oven drying at 70°C for three days dry shoot weight (g) was measured. Tubers were collected and fresh tuber weight (g) was taken and dry matter content (DMC %) determined by oven-dry method (Bashir et al. 2022) and calculated by taking difference of oven dry weight ÷ initial fresh weight × 100.

Statistical Models

Physiological data were subjected to three-way factorial analysis of variance (ANOVA) for treatment and genotype, DAS, and their interaction effects, while morphological data analyzed by two-way factorial for treatment and genotypes as factors and their interaction effects.

Two statistical mixed models were used to estimates of the variance components, heritability (Fehr, 1987) and predictions of the genotypic values made using the REML/ BLUP (Restricted Maximum Likelihood/Best Linear Unbiased Predicted) procedure (Resende and Duarte 2007). The first model ($Y = X_r + Z_g + W_i + e$) use for agronomic data, considered the genotype × environment interaction, where "*Y*" is the data vector, '*r*' is the vector of repetition effects (assumed to be fixed) added to the overall mean, '*g*' is the vector of genotypic effects (random) and '*e*' is the vector of residuals (random) and '*i*' is the vector of the effects of the genotype × treatment (random).

Whereas, REML/BLUP components for physiological traits measured by data $Y = X_f + Z_g + Q_a + T_i + W_t + e$, where "*Y*" is the data vector, '*f*' is the vector of the effects of the repetition-treatment-DAS combinations (assumed to be fixed) added to the general mean, '*g*' is the vector of the genotypic effects (assumed as random), '*a*' is vector of the effects of the interaction of genotypes with years (random), '*l*' is the vector of the effects of genotypes x local interaction, '*t*' is the vector of the effects of triple interaction genotypes x treatment x DAS (assumed as random) and '*e*' is the vector of errors or residuals (random). The capital letters represent the incidence matrices for these effects.

Correlation Analysis

Based on the estimated genotypic value for each genotype, Pearson's correlation analysis was made for all measured variables under CT and HS conditions for 1DAS, 15DAS and 35DAS. To carry out these analyzes the statistical R package "corrplot" (Wei and Simko 2017) was implemented in R program (R Core Team 2023).

RESULTS

Restricted maximum likelihood (REML)

The estimation of genetic parameter of all studied traits is shown in Table 2. The three factorial ANOVA for physiological traits showed significant ($_{*\leq 0.05, **\leq 0.01, ***\leq 0.001}$) differences among genotypes, treatments, DAS, and their interaction effect, except for the pigment parameters (Chl-A, Chl-B, Carot) which showed non-significant ($_{NS}$) differences for the interaction effects (**G × T; G × DAS; G × T × DAS**), while two factorial ANOVA for agronomic traits also showed significant differences for genotypic and treatment effects while non-significant for interaction effects (**G × T**) except for DMC%. In physiological observed traits, the highest broad sense heritability was observed for NPQ (0.48) followed by Gs, Tr, and lowest by Chl-B. For agronomic traits heritability ranges between 0.67 – 0.34 for FTW and DSW, respectively. PCV values observed were higher than the GCV for all studied traits. The highest PCV, GCV and ECV percentage observed for FTW (86.28, 68.56, 46.10) followed by Gs and lowest for Fv/Fm (PCV, ECV) and Chl-B showed the lowest GCV (1.32). Coefficient of determination (R^2) for the G × T interaction effect showed highest for the Fv/Fm (0.37) and followed by the DMC (0.26). R^2 for the G × DAS interaction effect showed moderate proportion of total variability for Pn and lowest for all traits under both interaction effects. However, proportion of the total variable explained for the G×T×DAS interaction effect, showed moderate coefficient of determination for gas exchange and chlorophyll fluorescence traits ranged between 0.2–0.5% and pigment traits (Chl-A, Chl-B and Carot) showed low R^2 percentage. Most of the traits showed strong degree to which the genotypic values of two traits are associated within a population. Genotypic correlation values showed in Table 2 indicate a consistent relationship between between genetic makeup under all treatment and their interaction effects (T, DAS, T×DAS, DAS×T). However, under genotypic correlation under the effect across Treatment and DAS have moderate (Gs) to low (Chl-B) degree of association (0.57 – 0.01), respectively.

Table 2
REML (restricted maximum likelihood) components of variance estimates under control (CT) and heat stress (HS) conditions for net photosynthesis rate (Pn), stomatal conductance rate (Gs), transpiration rate (Tr), effective photochemical quantum yield of PSII (YII), non-photochemical quenching (NPQ), maximum quantum efficiency of the PSII (Fv/Fm), chlorophyll-A (Chl-A), chlorophyll-B (Chl-B), carotenoid contents (Carot), measured on 1DAS, 15DAS, 35DAS and fresh short weight (FSW), dry shoot weight (DSW), fresh tuber weight (FTW), dry matter content % (DMC) at the end of the plant life cycle of potato genotypes (*Solanum* sect. Petota, *Solanaceae*) from Embrapa Potato Genebank.

REML	Pn	Gs	Tr	Y(II)	NPQ	Fv/Fm	Chl-A	Chl-B	Carot	FSW	DSW	FTW	DMC
G	**0.00*****	**0.00*****	**0.00*****	**0.00*****	**0.00*****	**0.00*****	**0.01****	0.07^{NS}	**0.01****	**0.00*****	**0.00*****	**0.00*****	**0.00*****
T	0.40^{NS}	**0.00*****	**0.00*****	**0.00*****	**0.00*****	**0.00*****	**0.00*****	**0.00*****	**0.00*****	**0.01****	0.56^{NS}	**0.00*****	**0.03***
G × T	**0.00*****	**0.00*****	**0.00*****	**0.00*****	**0.00*****	**0.00*****	0.18^{NS}	0.11^{NS}	0.13^{NS}	0.23^{NS}	0.32^{NS}	0.14^{NS}	**0.03***
DAS	**0.00*****	**0.00*****	**0.00*****	**0.00*****	**0.00*****	**0.00*****	**0.05***	0.17^{NS}	**0.03***				
G × DAS	**0.00*****	**0.00*****	**0.00*****	**0.00*****	**0.00*****	**0.00*****	0.18^{NS}	0.17^{NS}	0.20^{NS}				
T × DAS	**0.00*****	**0.00*****	**0.00*****	**0.00*****	**0.00*****	**0.00*****	**0.02***	**0.01****	0.15^{NS}				
G × T × DAS	**0.00*****	**0.00*****	**0.00*****	**0.00*****	**0.00*****	**0.00*****	0.66^{NS}	0.70^{NS}	0.72^{NS}				
PCV (%)	42.27	80.11	69.46	47.49	17.85	6.61	35.03	36.01	30.03	33.14	19.42	86.28	42.28
GCV (%)	15.02	46.95	32.08	17.85	12.13	1.35	3.82	1.32	4.70	20.52	11.59	68.56	10.94
ECV (%)	21.21	36.79	25.08	13.82	4.58	1.35	28.50	31.13	25.17	24.51	15.66	46.10	7.99
H^2_{BS}	0.15	0.43	0.36	0.19	0.48	0.02	0.02	0.00	0.03	0.38	0.34	0.67	0.48
$R^2_{G \times T}$	0.15	0.05	0.10	0.01	0.05	0.37	0.08	0.06	0.07	0.07	0.04	0.02	0.26
$R^2_{G \times DAS}$	0.21	0.01	0.10	0.19	0.08	0.17	0.04	0.05	0.06				
$R^2_{G \times T \times DAS}$	0.20	0.26	0.21	0.51	0.31	0.39	0.01	0.01	0.01				
R_T	0.51	0.90	0.78	0.96	0.90	0.06	0.17	0.03	0.29	0.85	0.89	0.97	0.65
R_{DAS}	0.42	0.99	0.79	0.50	0.86	0.12	0.29	0.03	0.32				
$R_{T \times DAS}$	0.71	0.90	0.82	0.98	0.91	0.34	0.41	0.45	0.56				
$R_{DAS \times T}$	0.59	0.99	0.83	0.51	0.88	0.70	0.71	0.57	0.62				
$R_{T \times DAS\, \bar{x}}$	0.66	0.92	0.82	0.98	0.92	0.36	0.29	0.26	0.43				
$R_{DAS \times T\, \bar{x}}$	0.61	0.99	0.84	0.70	0.90	0.70	0.61	0.44	0.54				
$R_{T \times DAS}$	0.21	0.57	0.47	0.21	0.52	0.02	0.11	0.01	0.17				
$\bar{x}$	**9.38**	**0.16**	**2.46**	**0.13**	**0.65**	**0.74**	**1.83**	**0.76**	**0.37**	**194.95**	**31.41**	**69.13**	**24.66**

G: Genotype; **T**: Treatment; **DAS**: Days after stress; **G×T**: Genotype × Treatment interaction effect; **G×DAS**: Genotype × DAS interaction effect; **T×DAS**: Treatment × DAS interaction effect; **G×T×DAS**: Genotype × Treatment × DAS interaction effect; **PCV**: Phenotypic Coefficient of Variation; **GCV**: Genotypic Coefficient of Variation; **ECV**: Environmental Coefficient of Variation; H^2_{BS}: heritability of individual plots in the broad sense, that is, of the effects total genotypes; $R^2_{G \times DAS}$: Coefficient of determination of the effects of the genotypes x DAS interaction; $R^2_{G \times T}$: Coefficient of determination of the effects of the genotype x Treatment interaction; $R^2_{G \times T \times DAS}$: Coefficient of determination of the effects of the genotype x Treatment x DAS interaction; R_T: Genotypic correlation across Treatment, valid for any DAS; R_{DAS}: Genotypic correlation across DAS, valid for any Treatment; $R_{T \times DAS}$: Genotypic correlation across Treatment in a given DAS; $R_{DAS \times T}$: Genotypic correlation across DAS at a given Treatment; $R_{T \times DAS\, \bar{x}}$: Genotypic correlation across Treatment, averaged over all DAS; $R_{DAS \times T\, \bar{x}}$: Genotypic correlation across DAS, averaged over all Treatment; $R_{T \times DAS}$: Genotypic correlation across Treatment and DAS; $\bar{x}$: General mean; Significant levels (* ≤ 0.05, ** ≤ 0.01, *** ≤ 0.001, ^{NS}: non-significant).

Predicted genotypic performance.

Photosynthesis components:

The accessed genotypes were ranked for each evaluated variable based on the predicted genotypic value (*μ + g + gem*) under both CT and HS conditions and capitalized on an average interaction with traits measured after 1, 15 and 35 DAS. Genotypes with the highest predicted genotypic value under HS condition were ranked first and with low value ranked last as shown in Fig. 2–8. In the bar graph, accessions belong to different species (*S. commersonii*, *S. chacoense* and *S. tuberosum 4x*) represented with three different bar fillings. To demonstrate the mean differences among used genotypes tukey test, mean comparison test was applied which represents with the lettering along the bars in Fig. 2–10. Mean performance of variables (Pn, Gs, Tr, Y(II), NPQ, Fv/Fm) after 1DAS, 15DAS and 35DAS were shown in Fig. 2–7b and overall average performance of the trait were shown in Fig. 2–7c.

For gas exchange traits, such as Pn, Gs, Tr (Fig. 2a, 3a, 4a) average of the genotypic values for the used germplasm were 9.38, 0.16 and 2.46, respectively. So, the accession which achieved predicted genotypic values higher than the mean are considered good performers of the respected traits. For gas exchange traits Pn, Gs and Tr, BRSBEL showed the highest predicted genotypic value and ranked first among the evaluated accessions. However, BGB077 (*S. commersonii*) was ranked first among all wild germplasm for Pn, Gs, Tr and BGB110 (*S. chacoense*) has the lowest predicted genotypic value hence ranked last. Additionally, nine genotypes showed higher values than the overall mean of the μ + g + gem. While there are significant differences among the Pn measured at 1, 15, 35DAS but there was no difference on the performance under control (CT) and stress (HS) conditions. Potato germplasm showed significant differences of stomatal conductance and transpiration rate among CT and HS however, only significant differences when measured after 1DAS vs 35DAS and 15DAS vs 35DAS (Fig. 2b, 3b, 4b, 2c, 3c, 4c).

For chlorophyll fluorescence traits the average mean of predicted genotypic values for all genotypes were 0.13 for YII, 0.66 for NPQ and 0.74 for Fv/Fm. Genotype BRSBEL, commercial cultivar showed the highest predicted genotypic value followed by BGB111 (*S. chacoense*) among the wild genotypes while BGB100 ranked last while observing effective photochemical quenching of PSII (Fig. 5a). Genotypes have high predicted genotypic values for YII showed low values for NPQ (Fig. 6a). BGB110 (*S. chacoense*) ranked first and BGB460 (*S. commersonii*) ranked last in prediction of genotypic performance for NPQ. For the stress indicator (Fv/Fm), only seven genotypes including commercial cultivar (BELBRS) predicted to have higher genotypic values than the mean (Fig. 7a). *S. commersonii* accessions BGB001 and BGB068 ranked first and last with prediction of genotypic values, respectively. In the actual overall performance of the chlorophyll fluorescence traits, only Fv/Fm ratio showed significant differences among both CT and HS conditions (Fig. 7c). Moreover, Y(II) were significantly different when measured and compared at 1DAS vs 35DAS and 15DAS vs 35DAS (Fig. 5b). There were no differences in the performance of NPQ among all stages of measurement 1, 15, 35DAS (Fig. 6b). Stress indicator for potato germplasm showed significant differences at 1DAS vs 15DAS and 1DAS vs 35DAS (Fig. 7b).

Average predicted genotypic values for Chl-A (Fig. 8a), Chl-B (Fig. 8b), and Carotenoids (Fig. 8c) were 1.83, 0.76 and 0.37. For all the three traits *S. chacoense* genotypes BGB099 ranked first according to the however, *S. commersonii* genotype BGB011 ranked last for Chl-A and Chl-B and BGB111 (*S. chacoense*) in the case of carotenoid contents. Under CT and HS condition Chl-A and carotenoid contents have significant differences (**Supplementary Fig. 1a, c**). Chlorophyll A, B and Carotenoid showed significant increase when measured at 1DAS and 15DAS but there was non-significant difference found at 35DAS (**Supplementary Fig. 1a, b, c)**.

For the agronomic traits, we calculated predicted the genotypic values for vegetative part traits such as fresh shoot weight and dry shoot weight (Fig. 9a, b). The average mean for the predicted genotypic values were 194.95, 31.41 respectively for FSW and DSW. Genotypes belong to *S. commersonii* (BGB001, BGB055) were ranked first while BGB099 was ranked last for the vegetative traits. FSW showed a significant decrease under HS condition as compared to CT, while DSW remained unchanged under both conditions. Average predicted genotypic values of the tuber traits were 69.13 and 24.66 for fresh tuber weight and dry matter content, respectively (Fig. 10a, b). However, *S. chacoense* genotypes BGB097 and BGB100 ranked first for both tuber traits respectively, while genotypes BGB460 and BGB110 ranked last according to the genotypic values predicted for the FTW and DMC%. Both measured tuber traits showed significant reduction under HS conditions.

Correlation between variables:

Predicted genotypic values under both treatments were used to visualize the correlation present among the traits observed in this study shown in **Fig. 11**. Gas exchange traits, net photosynthesis rate (Pn), transpiration rates (Tr) and stomatal conductance (Gs) were highly positively associated with each other, also positively correlated with the effective photochemical quenching (YII). However, all these traits (Pn, Gs, Tr, YII) negatively correlated with non-photochemical quenching (NPQ). In pigment analysis, chlorophyll-B and Carotenoid have strong positive significant association. In agronomic traits, FSW and DSW have significant positive correlation, while FSW has negative significant association with FTW and DMC and these two traits also showed negative significant correlation with DSW.

Discussion

Genetic basis of studied traits:

Any breeding effort focused on boosting yield and other characteristics must include variability. As a result, knowledge of both genotypic and phenotypic coefficients of variation is essential. The information on phenotypic coefficient of variation and heritability is very useful in predicting possible genetic advances via genotype selection for a character. The relevance of variability parameters such as GCV, PCV, Heritability, and Genetic Gain were investigated. In general, phenotypic coefficients of variation (PCV) were slightly higher than genotypic coefficients of variation (GCV), indicating the importance of environment in character expression. Similarly, higher values for PCV than the GCV were observed in our study indicated that studied traits are influenced by environmental or temperature treatments applied during this experiment. The ultimate goal of exploring the variability and heritability of any trait is to provide insight into the viability of selection. However, only heritability-based trait selection may not be successful sometimes, as the broad sense of heritability counts on total genetic variance, which involves additive, dominant, and epistatic variances.

Therefore, estimation of the heritability of a group of genotypes coupled with high genetic advance is more reliable and efficient for the selection of desirable traits for a group of the population (Rasheed et al. 2023). The improvement in mean performance of progenies of selected families over the base population is referred to as genetic advance, and when stated as a percentage of mean, it is referred to as genetic gain (Rutkoski 2019). Usually, heritability associated with genetic advance would be used as a clue in most selection programs and the traits which showed high genetic gain along with heritability were predominantly governed by additive gene action and can be improved through simple selection (Mishra et al. 2006).

In our study, only FTW showed high heritability followed by high genetic gain while stomatal conductance, transpiration rates, fresh shoot weight, dry shoot weight and dry matter contents showed moderate heritability with high genetic advance, which suggests that simple selection would be effective in later generation advancement. However, low heritability followed by poor genetic advance for traits Pn, Chl-A, Chl-B and carotenoids contents were observed, suggests that nonadditive gene action plays a major effect. Similar overall results also been reported in different crops by many studies (Johnson et al. 1955; Olakojo and Olaoye 2011; Aminu and Izge 2012; Azam et al. 2015; Zeleke et al. 2021). The information from the current study related to heritability is helpful for selecting the best traits for the improvement of potato crop. Wild potato accession with high estimated genotypic values than the overall mean of population presented a high genetic potential, since the BLUP method relies on the estimating of genotypic values. Hence, genetic values are more important for breeders because they represent true values in predicted and represent the genetic potential of individuals. For this purpose, true genotypic values were used to check the association of studied traits and discussed their role in the next section.

Physiological responses of germplasm:

The results obtained confirm the effect of increasing temperature on the gas exchange, chlorophyll fluorescence and chlorophyll contents in potato genotypes and show that there are differences between the evaluated accessions. Photosynthetic efficiency is among the physiological mechanisms related to heat tolerance in potatoes (Wolf et al. 1990). In tomatoes, changes in photosynthetic activity clearly demonstrate susceptibility to high temperature (Camejo et al. 2005). In species such as wheat, good yield under heat stress is associated with maintenance of photosynthesis rate, chlorophyll content and stomatal conductance at elevated temperatures (Yang et al. 2002). In potatoes, the optimal temperature for photosynthesis is around 24°C, above which there is a reduction in the efficiency of the PSII, an increase in maintenance of respiration and a reduction of the leaf area (Prange et al. 1990; Aien et al. 2011). According to Burton (1981), an increase of 5°C in the optimal temperature causes a decrease of about 25% in the photosynthetic rate. Other studies with higher temperatures reductions in the photosynthetic rate ranging from 37–45% in heat-sensitive genotypes, when evaluated after heat treatment at 40°C compared to the rate at 20°C, were observed (Hammes and De Jager 1990; Reynolds et al. 1990). However, Hancock et al. (2014) evaluating potato plants exposed to slightly higher temperatures, 30 and 20°C (day/night), observed an increase in the net rate of carbon assimilation, which agrees with results previously observed by Dwelle et al. (1983), who suggest that moderately high growing temperatures, up to approximately 30°C, have a positive impact on photosynthesis of cultivars described as heat tolerant. The elevated temperature of 34°C used in this experiment did not significantly affects the photosynthesis rate of the wild genotypes in relation to the temperature of the control condition, however these genotypes increased the stomatal conductance and the transpiration rate. The increase in stomatal conductance observed, mainly in the genotypes belonging to S. commersonii, was also observed by other authors in several potato genotypes (Dwelle et al. 1983; Hancock et al. 2014a; Demirel et al. 2017). According to Demirel et al. (2017), the increase in stomatal conductance under hot conditions may be related to the transpiration cooling mechanism under high temperature conditions, favored by the required water availability in which the plants grow.

Higher temperature conditions possibly cause damage to the PSII reaction centers, as confirmed by the response to the maximum quantum efficiency of the PSII (Doğru 2021). Changes in fluorescence emission from chlorophyll-A in photosynthetic organisms are the result of changes in photosynthetic activity, mainly changes in mesophyll capacity, which depend on Rubisco activity and photosynthetic electron transport capacity to regenerate Rubisco (Feller et al. 1998; Baker and Rosenqvist 2004). The wild genotypes, when cultivated in higher temperature conditions, had not shown a significant reduction in the effective quantum yield of the PSII Y(II), when compared to the control condition, indicating that the temperature did not influence the photochemical efficiency of the given genotypes evaluated here. Therefore, the dissipation of light energy captured by chlorophyll directed to photosynthesis is higher, with lower dissipation in the form of heat (Goltsev et al. 2016). In this study the effect of heat stress temperature on the photosynthetic activity of the wild genotypes was not reflected in reductions in both shoot

and tuber yield, as well as in dry matter content. However, in general, the reduction of the photosynthetically active area due to the reduced efficiency of PSII in plants under heat stress directly affects the final tuber production (Prange et al. 1990; Fagundes et al. 2010). Hence, it is possible to say that reduction in the tuber yield or other agronomic traits in wild genotypes under heat stress involved some tuber mechanisms because addition to the decline in photosynthesis, the increase in stomatal conductance and transpiration under high temperature conditions result in a decrease in tuber production (Demirel et al. 2017) as was shown in this study.

In industry, characteristics that confer frying quality, such as high dry matter content, low reducing sugar content and absence of disturbances physiological factors are important (Silva et al. 2019). The dry matter content varies according to the genotype and is influenced by the growing conditions. Under conditions of high temperature there is stimulation of shoot development, reducing the partition of photoassimilates to the tubers, producing smaller tubers with low dry matter content (de Menezes et al. 2001).

The maximum effective quantum yield of PSII (Fv/Fm) is a parameter of chlorophyll fluorescence, which has been used to monitor the physiological status of plants after a period of high temperature treatment (Rykaczewska 2015). For unstressed leaves, values above 0.8 are considered optimal (Murchie and Lawson 2013). Among evaluated wild potato genotypes, Solanum chacoense genotypes showed values near to optimal values to estimate whether leaves were stressed or not. In the following evaluations, the average values for the Gs and Fv/Fm became higher in the stress condition in relation to the control condition, thus demonstrating the effect of the genotypic resistance of wild genotypes. In high temperature environments, the increase in Tr usually occurs as a cooling mechanism, as the loss of water helps to remove heat from the leaves (Taiz et al. 2015). In all the evaluations carried out, the Tr was superior in the heat stress condition in relation to the control condition, demonstrating that all genotypes are losing more water, possibly allowing reducing their temperature.

Chlorophyll-A is the main pigment involved in light collection in PSI; in PSII, both chlorophyll a and b are important. The increase in the chlorophyll a/b ratio in plants exposed to stress indicates possible changes in the PSI/PSII ratio, due to mechanisms of adaptation of chloroplasts to stress (Takabayashi et al. 2005). Increases in the PSI ratio increase cyclic electron transport, which is involved in the dissipation of excess energy, thus preventing further damage to the PSII (Li et al. 2006). In addition, the light curve made it possible to confirm the strong limitation of photosynthetic reactions that respond to the increase in light intensity, a fact corroborated by the reduction in the electron transport rate. The excess of absorbed energy was dissipated through regulated energy dissipation mechanisms, that is, through the xanthophyll cycle (Muller et al. 2001), since there was inhibition of non-regulated mechanisms.

It has been shown that the mechanism of energy dissipation through the xanthophyll cycle can be effective in defending against different types of stress (García-Plazaola et al. 2019). Moreover, since chlorophyll content is an indicator of early senescence, it is positively correlated with crop yield (Araus et al. 1997; Rharrabti et al. 2001). In this study, wild potato genotypes showed higher production of chlorophyll a, b and carotenoids content under heat stress conditions as compared to control conditions, which also explain higher rate of Pn and other stress indicators evaluated in this experiment. Moreover, carotenoids protect plants from photooxidative stress (Lohr 2023). In recent years, metabolic engineering efforts have also been undertaken with the aim to improve plant resistance to abiotic stress through overproduction of carotenoids (Giuliano et al. 2008).

Conclusion

The present study revealed that there exists an adequate amount of variability in the germplasm studied in almost all traits. Phenotypic coefficients of variation were slightly higher than the estimates of genotypic coefficients of variation for all traits under study implying that besides genetic factors some seasonal factors are having their role in expression of characters. These results indicate the operation of additive gene action in the inheritance of these studied traits and improvement of these traits are possible through simple selection in later stages. Based on the importance of the traits and selection of wild accession according to predicted genotypic and incorporated into potato breeding program for improvement of heat tolerance.

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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Figures

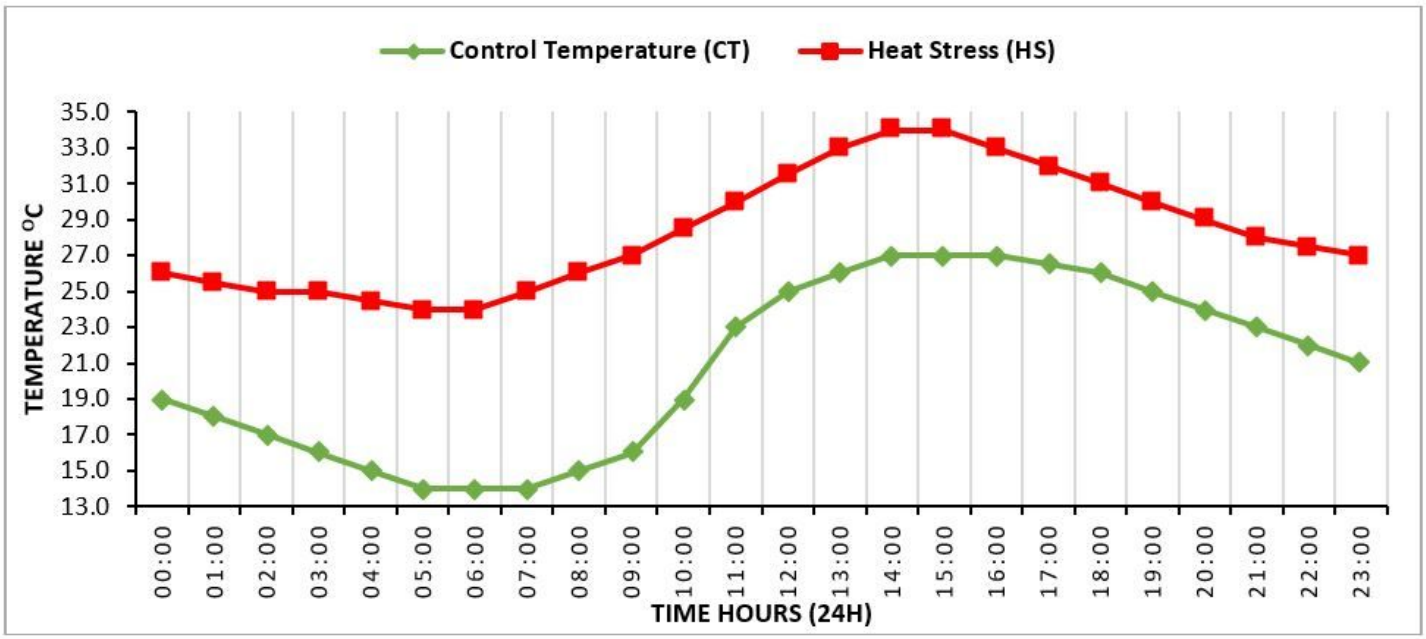

Figure 1

Growth chambers control and heat stress temperature environmental conditions

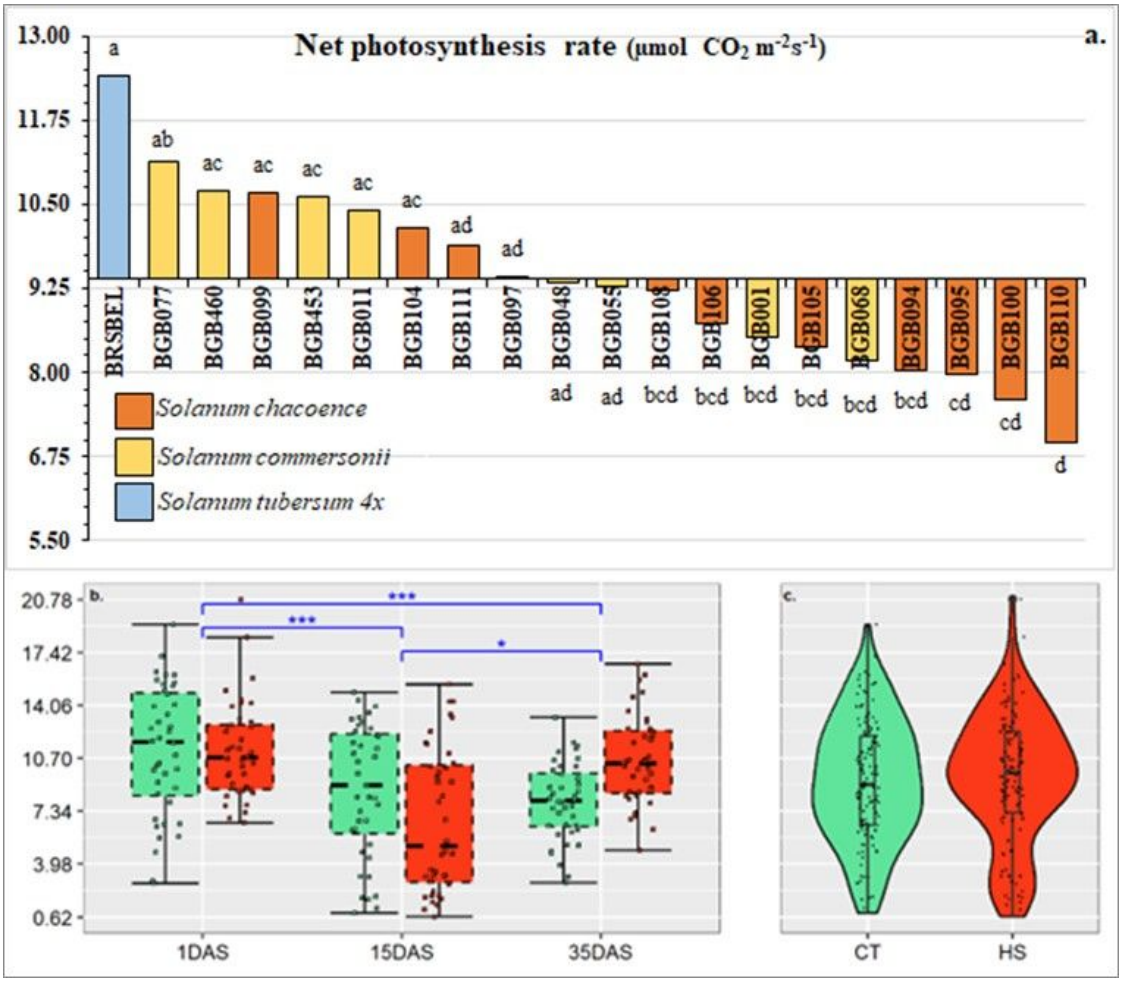

Figure 2

(a) Predicted genotypic values (µ+g+gem) for net photosynthesis rate of potato (*Solanum* sect. *Petota*, *Solanaceae*) germplasm accessions from Embrapa Potato Genebank under CT and HS and arranged according to highest to lowest (b) mean average performance of the trait measured after 1DAS, 15DAS and 35DAS (c) average performance under CT and HS conditions.

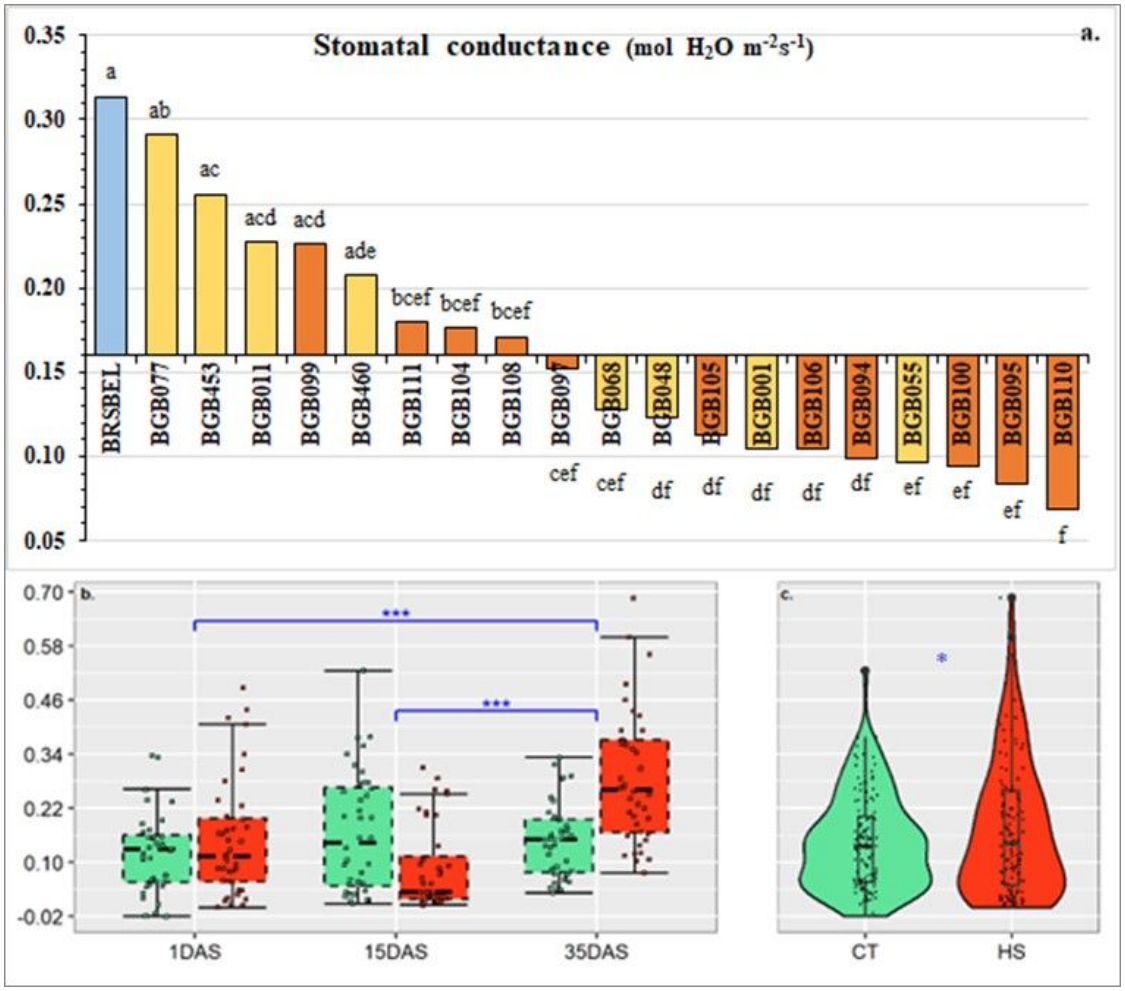

Figure 3

(a) Predicted genotypic values (μ+g+gem) for stomatal conductance of potato (*Solanum* sect. *Petota*, *Solanaceae*) germplasm accessions from Embrapa Potato Genebank under CT and HS and arranged according to highest to lowest (b) mean average performance of the trait measured after 1DAS, 15DAS and 35DAS (c) average performance under CT and HS conditions.

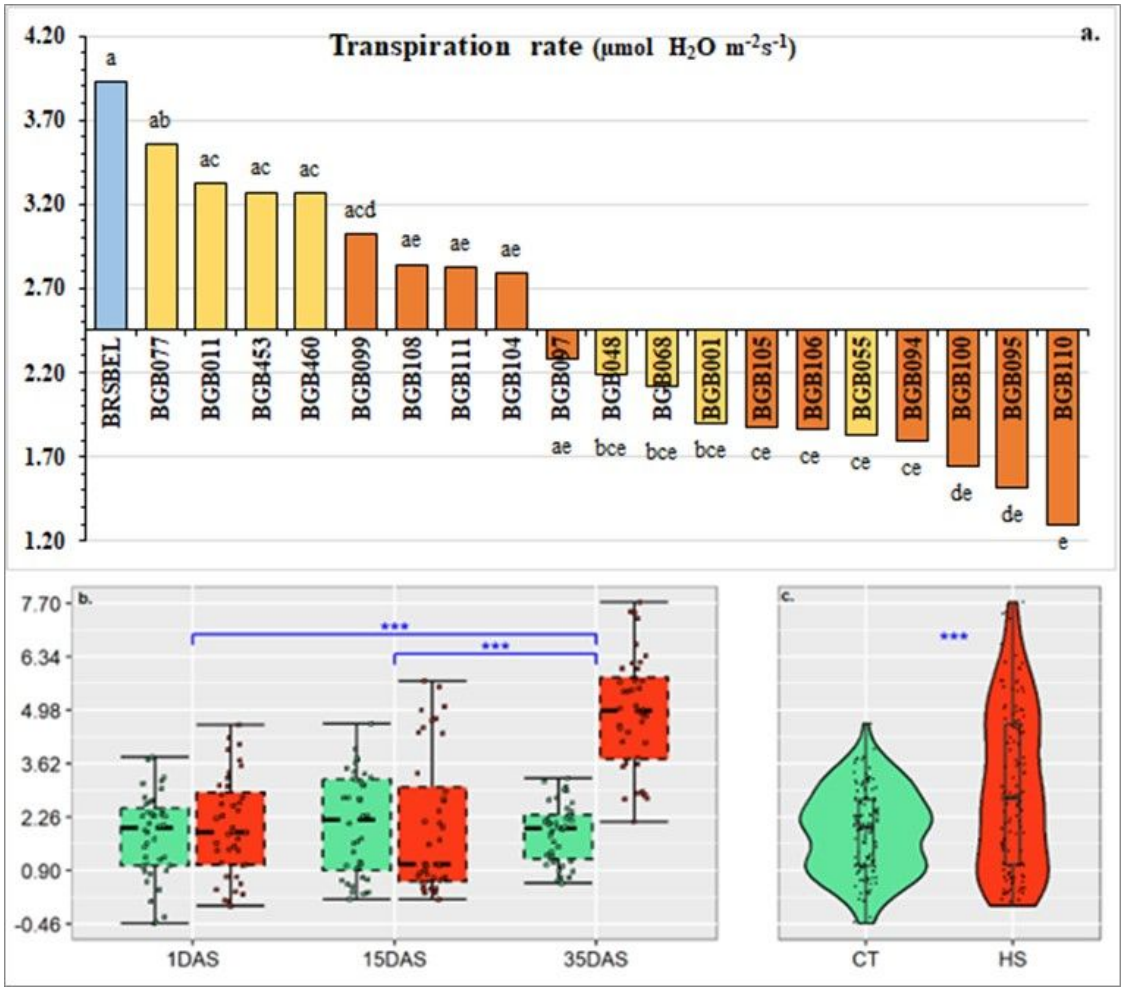

Figure 4

(a) Predicted genotypic values (µ+g+gem) for transpiration rate of potato (*Solanum* sect. *Petota*, *Solanaceae*) germplasm accessions from Embrapa Potato Genebank under CT and HS and arranged according to highest to lowest (b) mean average performance of the trait measured after 1DAS, 15DAS and 35DAS (c) average performance under CT and HS conditions.

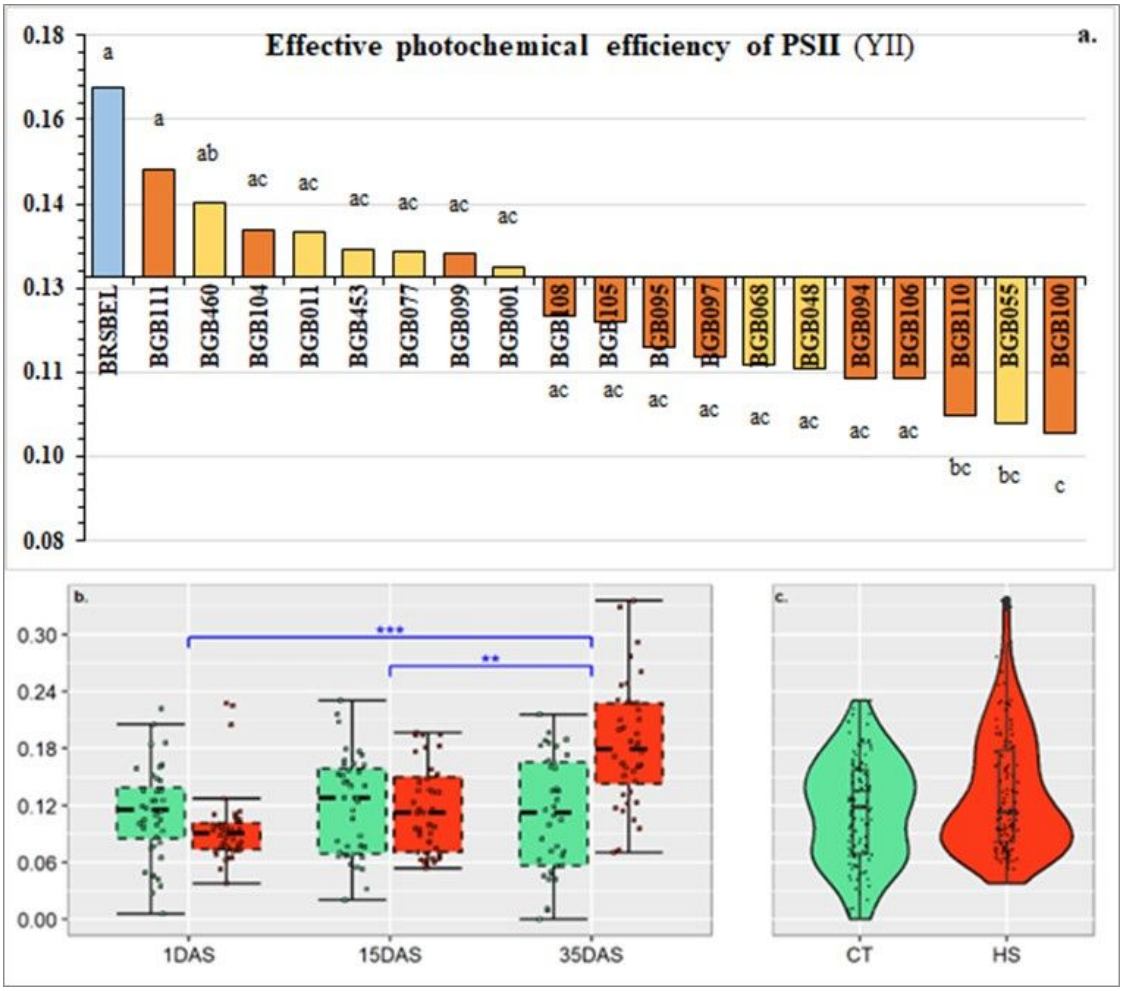

Figure 5

(a) Predicted genotypic values (μ+g+gem) for photochemical efficiency of photosystem II of potato (*Solanum* sect. *Petota*, *Solanaceae*) germplasm accessions from Embrapa Potato Genebank under CT and HS and arranged according to highest to lowest (b) mean average performance of the trait measured after 1DAS, 15DAS and 35DAS (c) average performance under CT and HS conditions.

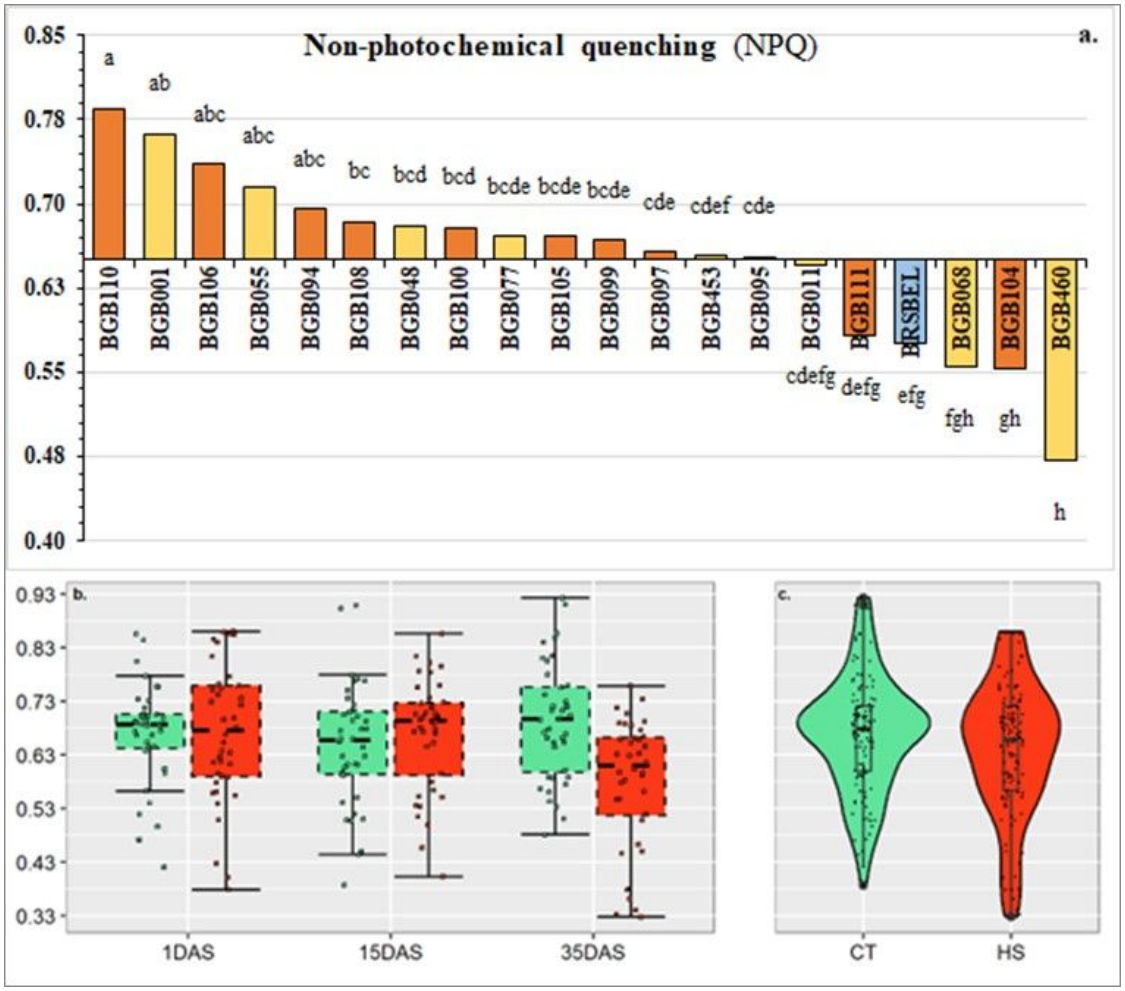

Figure 6

(a) Predicted genotypic values (μ+g+gem) for non-photochemical quenching of potato (*Solanum* sect. *Petota*, *Solanaceae*) germplasm accessions from Embrapa Potato Genebank under CT and HS and arranged according to highest to lowest (b) mean average performance of the trait measured after 1DAS, 15DAS and 35DAS (c) average performance under CT and HS conditions.

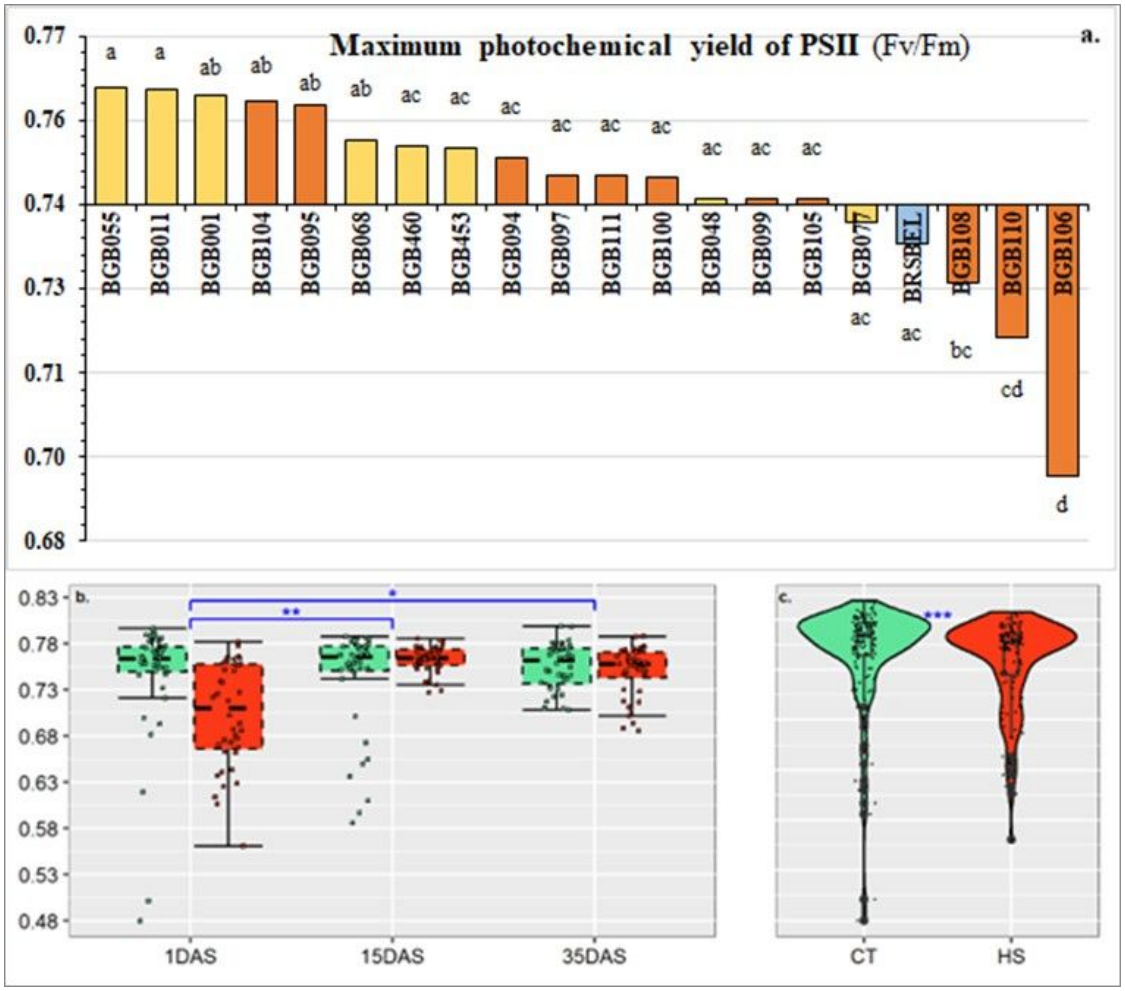

Figure 7

(a) Predicted genotypic values (μ+g+gem) for maximal photochemical efficiency of photosystem II of potato (*Solanum* sect. *Petota*, *Solanaceae*) germplasm accessions from Embrapa Potato Genebank under CT and HS and arranged according to highest to lowest (b) mean average performance of the trait measured after 1DAS, 15DAS and 35DAS (c) average performance under CT and HS conditions.

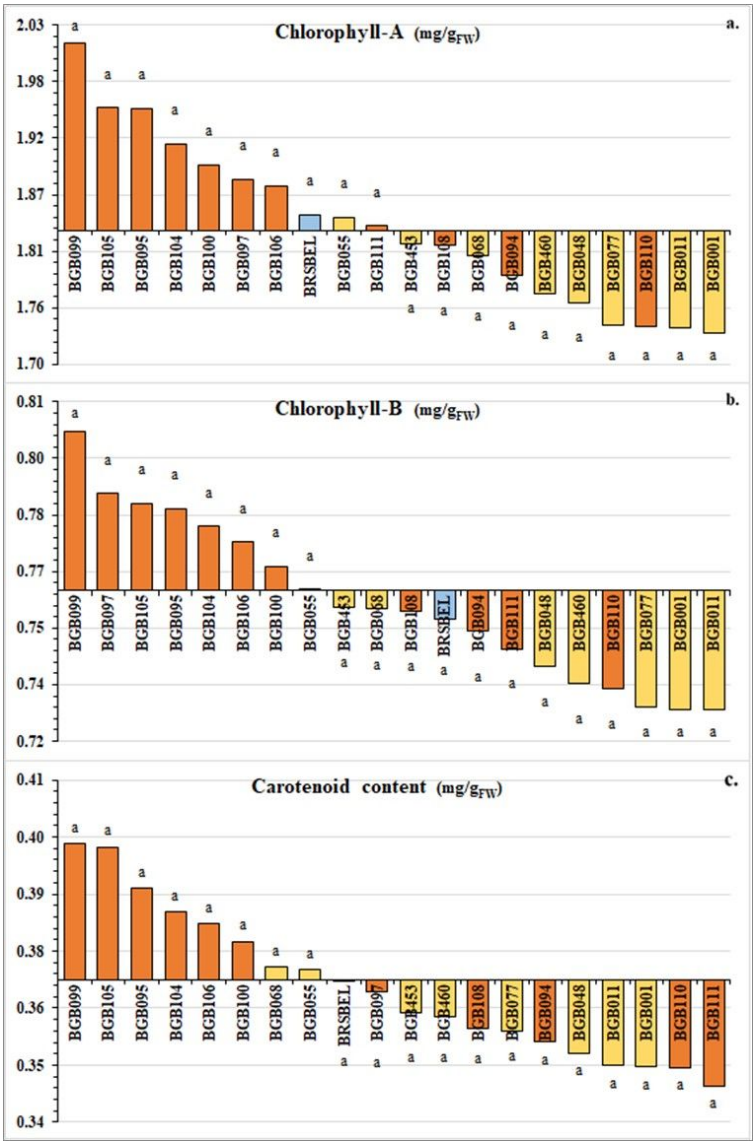

Figure 8

Predicted genotypic values (μ+g+gem) for (a.) Chlorophyll-A (b.) Chlorophyll-B (c.) Carotenoid content of potato (*Solanum* sect. *Petota*, *Solanaceae*) germplasm accessions from Embrapa Potato Genebank under CT and HS and arranged according to highest to lowest.

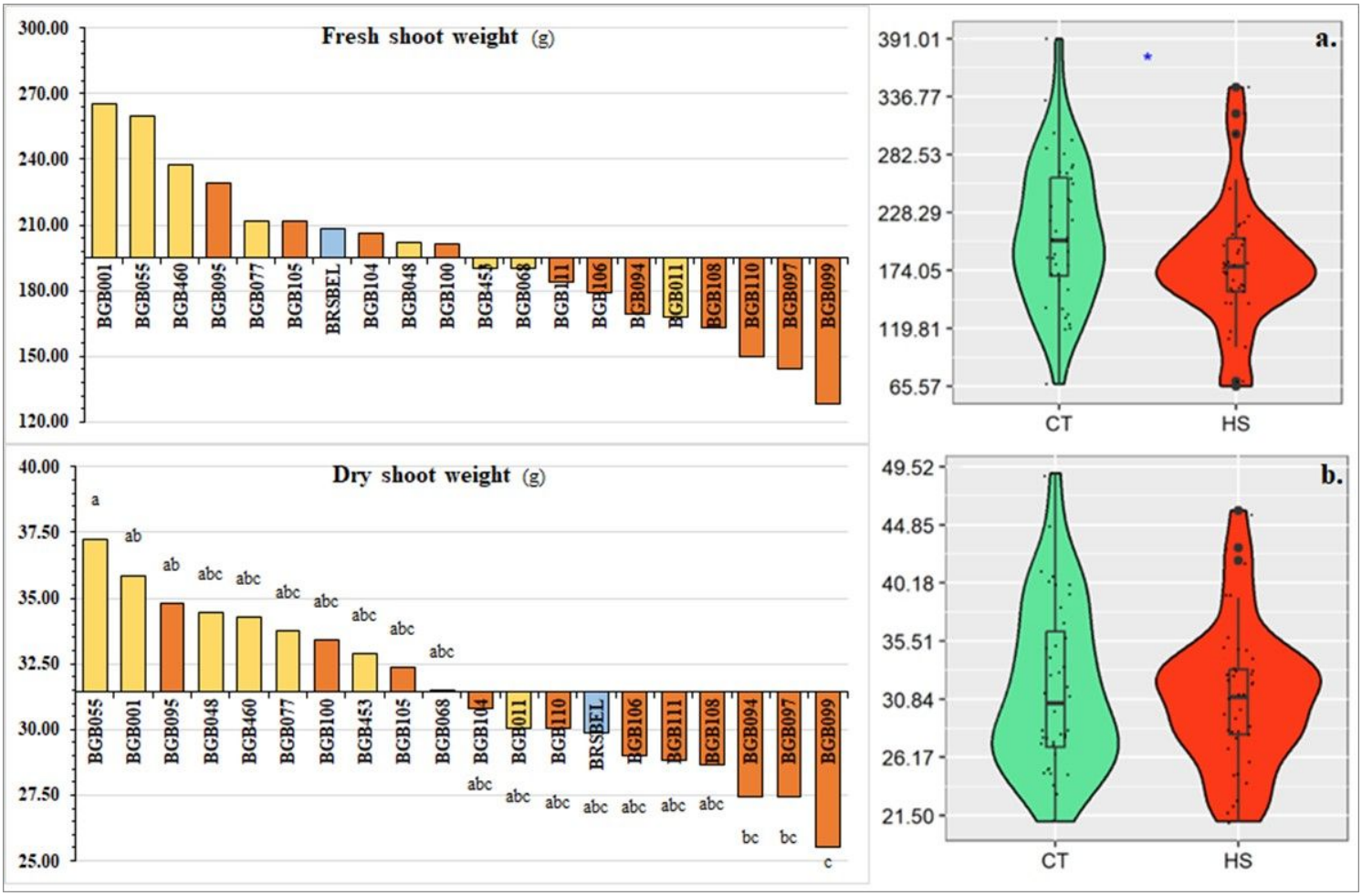

Figure 9

Predicted genotypic values (μ+g+gem) for (a) fresh shoot weight (b) dry shoot weight of potato (*Solanum sect. Petota, Solanaceae*) germplasm accessions from Embrapa Potato Genebank under CT and HS and arranged according to highest to lowest and mean actual performance of the accession measured under CT and HS conditions.

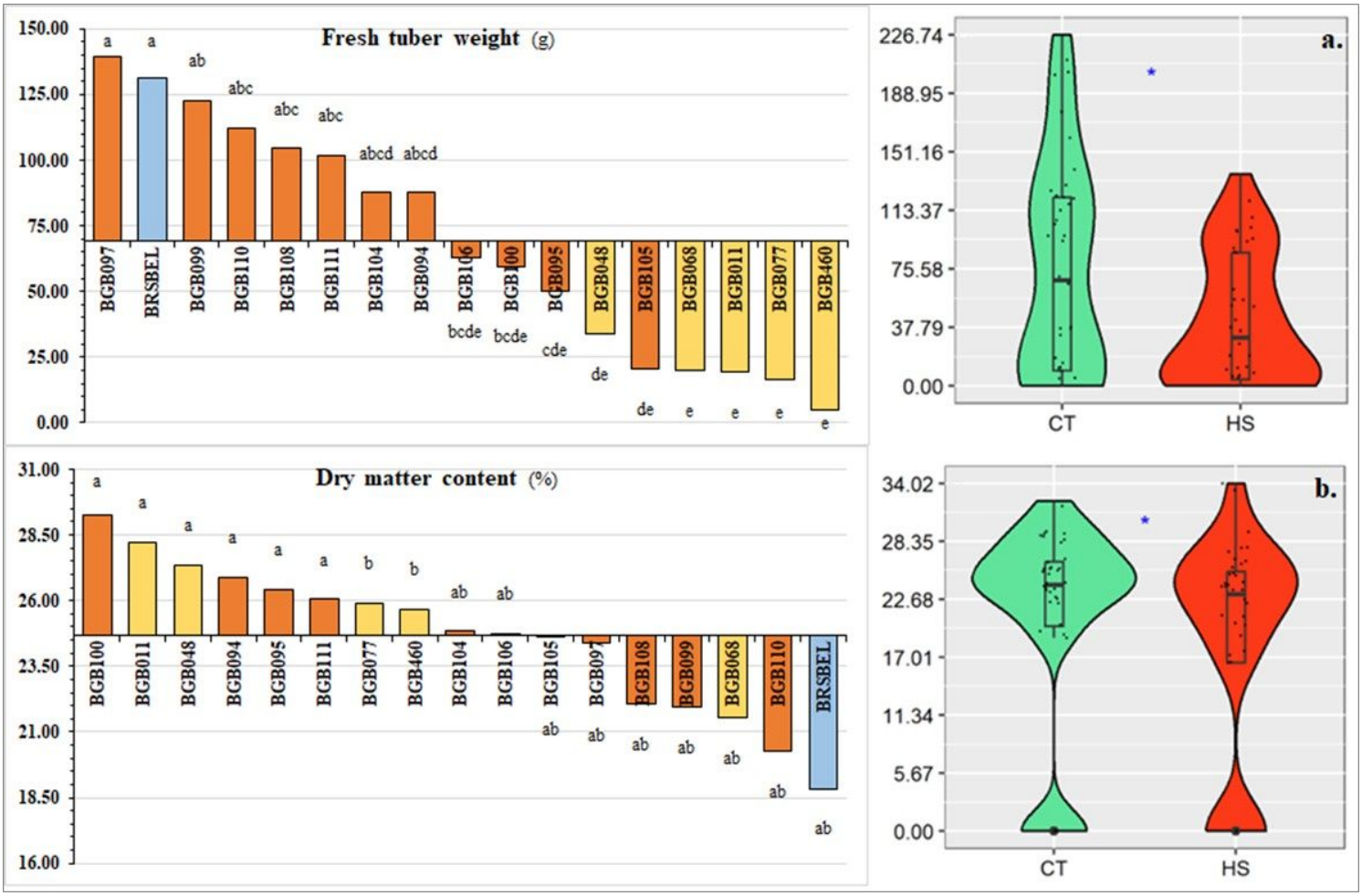

Figure 10

Predicted genotypic values (μ+g+gem) for (a) fresh tuber weight (b) dry matter content of potato (*Solanum sect. Petota, Solanaceae*) germplasm accessions from Embrapa Potato Genebank under CT and HS and arranged according to highest to lowest and mean actual performance of the accession measured under CT and HS conditions.

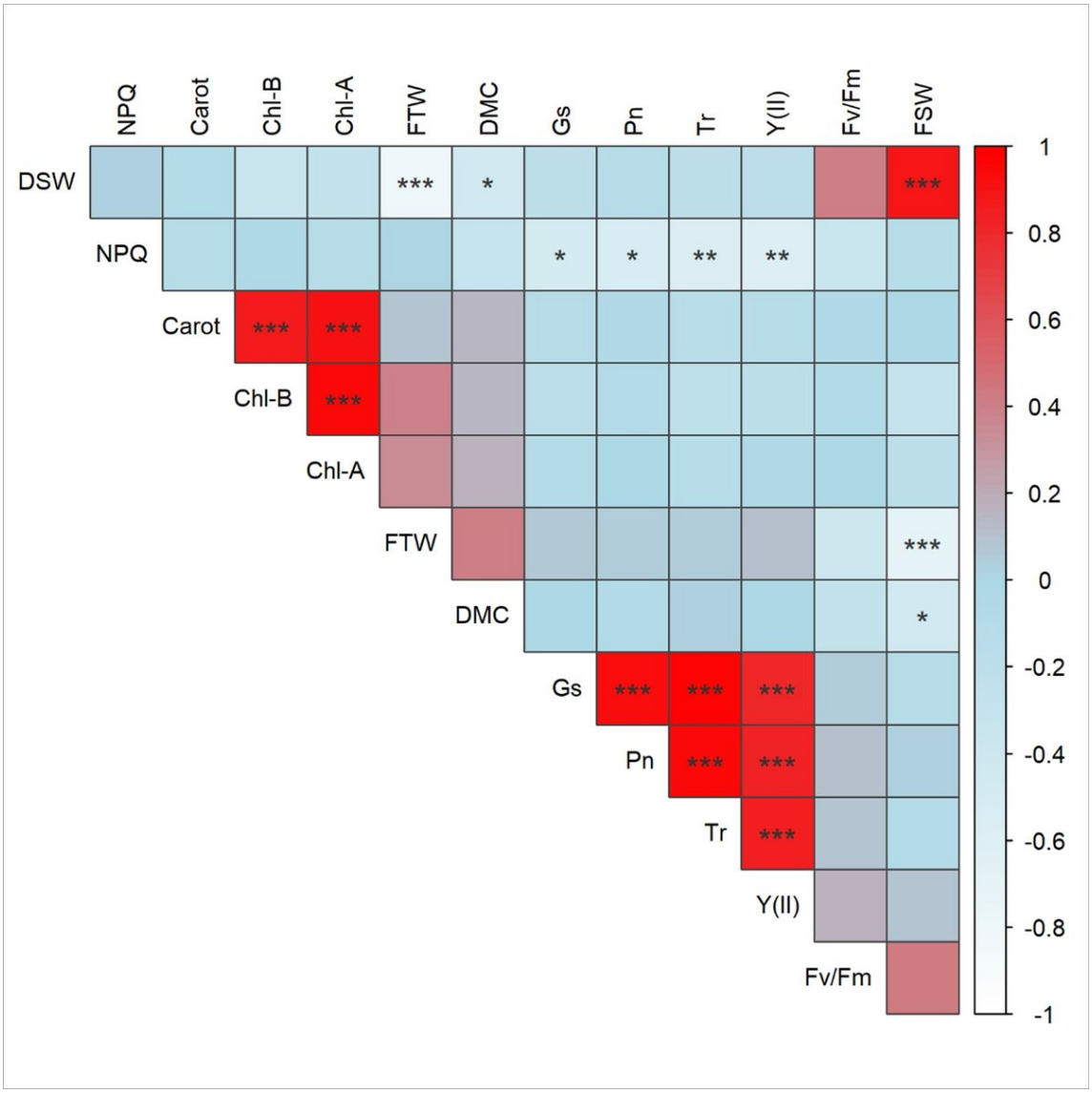

Figure 11

Figure 4: Correlation between variables net photosynthesis rate (Pn); stomatal conductance rate (Gs); transpiration rate (Tr); efficiency of PSII (YII); non-photochemical quenching (NPQ); maximum quantum efficiency of the PSII (Fv/Fm); chlorophyll-A (Chl-A); chlorophyll-B (Chl-B); total chlorophyll content (Total); carotenoid contents (Carot); fresh shoot weight (FSW); dry shoot weight (DSW); fresh tuber weight (FTW); dry matter content (DMC%) in potato (Solanum sect. Petota, Solanaceae) germplasm accessions from Embrapa Potato Genebank under CT and HS conditions.

Supplementary Files

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

- supplementaryfigure1.jpg