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Assessment of morphophysiological traits for selection of heat-tolerant potato genotypes

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Abstract: Since potato production has been expanded into warmer regions, breeding heat-tolerant potato varieties has also been considered among the top priorities in most breeding programs in recent years. Identification of traits related to heat tolerance in potato is crucial for selection of heat-tolerant genotypes. The objective of this study was to evaluate the responses of 17 potato genotypes to high temperature stress for identifying some candidate traits associated with heat tolerance. Haulm dry weight (HDW), leaf area index (LAI), photosynthetic rate (Pn), stomatal conductance (Gs), transpiration rate (Tr), SPAD value, and mean tuber weight (MTW) of potato genotypes at control conditions were significantly and positively correlated with tuber yield of genotypes grown under high temperature conditions, whereas canopy temperature (CT) was negatively associated with tuber yield. Classification of potato genotypes based on heat tolerance was done by principal component analysis with yield-correlated traits. The classification results showed high similarities with the yield performance of genotypes grown under high temperature conditions. The HDW, LAI, Pn, Gs, Tr, CT, and SPAD of potato genotypes grown under normal conditions might be useful traits to screen for heat-tolerant genotypes.

Key words: Potato, screening, heat tolerance

1. Introduction

Being a highly nutritious food, potato is considered as one of the most promising crops to reduce hunger, malnutrition, and poverty in the world due to its high yield potential as reflected by a very high harvesting index above 75% (Scott et al., 2000; Thiele et al., 2010). Although the global potato production increased in the last two decades, this was mainly due to an increase in the cultivated area, whereas the average yield rates remained nearly stable in developing countries (Walker et al., 2011). The majority of the annual world potato production is contributed by developing countries, where it is cultivated in marginal areas prone to environmental anomalies such as heat, drought, and salinity (Scott and Suarez, 2012). However, potato is a cool season crop with an optimal growth temperature between 17 and 21 °C (Struik and Ewing, 1995; Levy and Veilleux, 2007). Temperatures higher than optimum significantly affect several physiological traits related to yield and quality such as haulm growth, dry matter production and partitioning, tuber initiation and growth, photosynthetic rate, and the synthesis of hormones, enzymes, and other metabolites (Levy and Veilleux, 2007). Expansion of potato production into developing countries mainly in tropical and subtropical regions, where average temperatures are higher than optimal, brought heat stress phenomena onto agenda of potato producers. In addition to this expansion, global warming scenarios also give an alert for the sustainability of potato production in most regions including traditional production areas in Europe and North America (Hijmans, 2003; Holden et al., 2003; Haverkort and Verhagen, 2008; Van Oort et al., 2012). Hijmans (2003) estimated the effects of global warming on potato production in different regions of the world and concluded that the global potential yield of potato could decrease by 18%–32% without adaptation and by 9%–18% with adaptation. His estimation for potato yield decrease in Turkey was 36.7% without adaptation and 17.1% with adaptation. The development of heat-tolerant potato varieties is one of the most feasible approaches to cope with global warming. Apart from the global warming, breeding heat-tolerant potato varieties is also very important to get high yields in Mediterranean–type environments due

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to supraoptimal temperatures during the growing period (Frusciante et al., 1999, Çalışkan, 2001). In the last decades, potato breeding has concentrated on improving the yield of final product at lower production costs, reducing the use of chemicals in the field by enhancing resistance to pests and diseases, increasing cold hardiness of tubers, and extending postharvest storage duration. However, breeders have long paid little attention to developing heat-tolerant potato varieties or identifying the traits related to heat tolerance (Thiele et al., 2010; Monneveux et al., 2013). Breeding heat-tolerant potato varieties is now considered among the top priorities in most breeding programs to ensure sustainability of potato production under the aforementioned threats.

There are two prerequisites for success of a breeding program aimed to develop heat-tolerant cultivars: choosing the most appropriate parents and using a reliable screening method in early generations (Hijmans, 2003; Levy and Veilleux, 2007). Previous studies indicated that it is possible to find sources for heat tolerance among potato varieties, breeding lines, and wild *Solanum* species (Gautney and Haynes, 1983; Levy, 1986; Levy et al., 1991; Reynolds and Ewing, 1989; Midmore and Prange, 1991; Tai et al., 1994), and it is also possible to breed heat-tolerant potato varieties using conventional breeding (Susnoschi et al., 1987; Levy et al., 1991; Haynes et al., 1992; Veilleux et al., 1997; Levy et al., 2001) and mutations (Das et al., 2000). Using a reliable selection method is crucial for success in a breeding program aimed at developing heat-tolerant potato varieties (Sattelmacher, 1983; Nowak and Colborne, 1989; Reynolds and Ewing, 1989; Veilleux et al., 1997; Levy and Veilleux, 2007). Several screening methods were proposed to identify heat-tolerant lines in potato such as growth and yield evaluation under field conditions (Gautney and Haynes, 1983; Levy, 1986; Levy et al., 1991; Tai et al., 1994), controlled conditions (Sattelmacher, 1983; Reynolds and Ewing, 1989; Midmore and Prange, 1991) or both (Veilleux et al., 1997) by using in vitro techniques (Nowak and Colborne, 1989; Gopal and Minocha, 1998), chlorophyll fluorescence measurements (Hetherington et al., 1983; Greaves and Wilson, 1986; Sipos and Prange, 1986), and cell membrane stability (Nagarajan and Bansal, 1986; Ahn et al., 2004; Çalışkan and Nam, 2009).

Determination of morphological and physiological traits contributing to the heat tolerance of potato genotypes is crucial to improve efficiency of the selection process of tolerant varieties. The hypothesis of this study was that some vegetative growth and physiological traits could be used to easily determine the heat-tolerant potato genotypes having high yield under hot field conditions. To test the hypothesis, the responses of some traits of potato genotypes to high temperature were first assessed under optimal or supraoptimal growing temperatures in a Mediterranean-type environment. Afterwards, correlations between some traits and tuber yield were investigated. Finally, the heat tolerances of 17 potato genotypes were classified by principal component analysis (PCA) using yield-correlated morphophysiological traits.

2. Materials and methods

The field experiments were carried out at the Experimental Farm of Mustafa Kemal University in Hatay, in the Mediterranean region of Turkey (36°15′N, 36°30′E; 83 m elevation) in 2013 and 2014. Monthly mean, maximum, and minimum air temperature, relative humidity, and rainfall during the experimental period are represented in Figure 1. The soil of the experimental site, developed from alluvial deposits of river terraces, is classified as heavy clay (Vertisol) (IUSS Working Group WRB, 2015) with the predominant clay minerals being smectite and kaolinite. Soil texture is 62.92% clay, 27.68% silt, 9.40% sand, and 3.01% organic matter with a pH of 7.9. Seventeen potato genotypes including 11 Hungarian breeding lines and 6 standard varieties were evaluated to determine their heat tolerance levels under field conditions. The characteristics of the genotypes are summarized in Table 1. The potato genotypes were planted on two different dates (in January and April) to be able to create normal and heat-stressed conditions. The normal potato growing period is between January and mid-June in the Hatay region (Çalışkan et al., 2004). Delaying the planting of potato after March causes significant reduction in tuber yield due to heat stress throughout the tuber initiation and bulking stages (Çalışkan et al., 2004). While potato tubers were planted on 30 January for the normal growing period and 1 April for heat-stressed conditions in 2013, the next year genotypes were planted on 11 January for the normal growing period and 6 April to implement stressful conditions. Field experiments were laid out in a split plot design with four replications using planting dates as the main plots and potato genotypes as subplots. Each subplot consisted of two rows, 810 cm in length and with 70 cm between rows, according to field experimentation standards for potato cultivar evaluation in Turkey. Seed tubers were planted by hand with in-row spacing of 30 cm. The emergence of all genotypes at the normal growing period was completed between 1 and 8 March in 2013 and between 21 and 28 February in 2014. The emergence of late-planted plots was completed between 24 and 30 April in both years. Before planting, plots were fertilized with 60 kg ha^{-1} each of N, P_2O_5, and K_2O. For protection against soil-borne diseases, potato tubers were treated with Mancozeb at 0.8% (w/w) before planting. The experimental plots were irrigated with overhead sprinklers five times for the control treatment in both experimental years, and six and four times for the heat stress treatment in 2013 and 2014, respectively. The

Table 1. The characteristics of genotypes used in the study.

Genotype	Maturity/precocity	Utilization	Tuber shape	Flesh color	Origin
01-536	Intermediate to early	Processing	Round to oval	Cream	Hungary
02-173	Intermediate to early	Table	Oval	Yellow	Hungary
02-363	Intermediate to early	Processing	Round	Light yellow	Hungary
03-113	Intermediate to early	Processing	Round	Deep yellow	Hungary
04-123	İntermediate to late	Processing	Oval	Deep yellow	Hungary
06-62	Intermediate to early	Table/processing	Round to oval	Deep yellow	Hungary
07-258	Intermediate to early	Processing	Round	Yellow	Hungary
08-212	Intermediate to late	Table/processing	Oval	Yellow	Hungary
Balatoni Rozsa	Early	Table	Oval	Light yellow	Hungary
Arany Chipke	Intermediate to late	Processing	Round	Deep yellow	Hungary
Demon	Intermediate to early	Table	Oval	Yellow	Hungary
Agata	Very early	Table	Oval	Light yellow	Netherland
Agria	Intermediate to late	Table/processing	Oval to long	Yellow	Germany
Banba	Intermediate to late	Table/processing	Oval to long	Light yellow	Ireland
Marabel	Early	Table	Oval to long	Light yellow	Germany
Hermes	Intermediate to late	Processing	Oval to round	Yellow	Austria
Russet Burbank	Intermediate to early	Processing	Long to oval	White	USA

plots were fertilized with ammonium nitrate two times at 100 kg N ha^{-1} and 250 kg N ha^{-1} at emergence and the tuber bulking period, respectively, in both years. No fungicide or insecticide application was needed during the growing period in both years. Weed control was maintained by hand hoeing during the growing period in both years, while an additional herbicide, haloxyfob-R methyl ester, was also sprayed against grass weeds in the second year. The harvest dates were 15 June 2013 and 11 June 2014 for the normal growth period and 20 July for heat stress treatments in both years. While the vegetation of genotypes under control conditions ranged from 99 to 106 days in 2013 and from 103 to 109 days in 2014, it ranged from 81 to 87 days under higher temperature conditions in both years. Plant height (PH) and stem thickness (ST) were measured on 10 plants in each replicate at 59–66 days after emergence (DAE) based on the genotypes' emergence date in 2013 and 2014. Measurements of haulm dry weight (HDW) and leaf/stem ratio (LSR) were done on four plants at 59–66 DAE. Green leaf area was measured with a leaf area meter (LICOR, LAI 3100C, USA) on four plants at 59–66 DAE and then leaf area index (LAI) was calculated. Photosynthetic rate (Pn), stomatal conductance (Gs), and transpiration rate (Tr) were measured on fully expanded upper third or fourth leaves with a LICOR LI-6400XT portable photosynthesis system using a built-in light source set at 1500 µmol photons m^{-2} s^{-1} PAR and a built-in CO$_2$ injection system set at 400 µmol. Measurements of Pn, Gs, and Tr for each genotype were performed on two plants in each replicate, totally in 4 replicates (8 plants for each genotype), only in 2014. The average of two plants was regarded as the value of one replication for each genotype. The traits of Pn, Gs, and Tr were measured between 0930 and 1400 hours on 3 and 4 May 2014 (59–65 DAE based on genotypes) for the control treatment, whereas they were measured on 28 June and 29 June 2014 (59–66 DAE based on genotypes) for late planting. Canopy temperature (CT) using an infrared thermometer (Sinometer BM380, China) and chlorophyll content (SPAD) using a chlorophyll meter (Minolta SPAD 502, USA) were measured for upper leaves of 10 plants in each replicate at 59–66 DAE in 2014. Agronomical traits such as number of tubers per plant (TN), mean tuber weight (TW), and tuber yield per hectare were determined after harvest. Total tuber number per plot was divided by total plant number per plot for calculation of TN. Similarly, total tuber weight per plot was divided by total tuber number per plot for calculation of TW. In addition, the heat susceptibility index (HSI) (Fischer and Maurer, 1978) and heat tolerance index (HTI) (Fernandez, 1992) were calculated for each genotype using tuber yield values under normal and stressful environments as indicated below:

$$HSI = 1 - (Y_s / Y_p) / SI,$$

where SI is stress intensity and $SI = 1 - (\bar{Y}_s / \bar{Y}_p)$; and

$$HTI = (Y_s \times Y_p) / (\bar{Y}_p)^2,$$

where Y_s is the yield of the given genotype under hot field conditions, Y_p is the yield of the given genotype under control conditions, and $\bar{Y}_s$ and $\bar{Y}_p$ are the mean yields of overall genotypes under stress and control conditions, respectively.

Two-way analysis of variance (ANOVA) was performed using the PROC GLM procedure of the SAS statistical software (SAS Institute, 2002) to analyze the data set. The data presented are the mean values of morphological and agronomic measurements of 2 years. Differences between mean values were compared using Fisher's least significant difference (LSD) test at $P \leq 0.05$.

Correlation coefficients were run to identify significant associations between investigated traits using the SAS PROC CORR procedure (SAS Institute, 2002). Statistical significance for correlation between yield and other traits was reported at $P \leq 0.01$, $P \leq 0.05$, or $P \leq 0.07$ levels.

PCA using SAS PROC PRINCOM (SAS Institute, 2002) was performed to classify potato genotypes for heat tolerance according to Demirel et al. (2016). Values of only yield-correlated traits of 17 potato genotypes were included in the PCA. Eigenvectors generated by PCA were used to grade potato genotypes for their heat tolerance. The first two principal component (PC) scores, PC1 and PC2, accounted for maximum variability of the parameters tested and were used to classify the genotypes. Genotypes having +PC1 and +PC2 scores were classified as tolerant, those with +PC1 and –PC2 scores as moderately tolerant, those with –PC1 and +PC2 scores as moderately susceptible, and those with –PC1 and –PC2 scores as susceptible according to Kakani et al. (2005).

3. Results

3.1. Climatic conditions

The monthly average air temperature during the normal growing period varied between 9.1 and 24.2 °C in 2013 and between 11.8 and 23.3 °C in 2014 (Figure 1). However, it ranged from 17.8 to 27.1 °C during the late growing period in 2013 and from 18.8 to 27.4 °C in 2014. From emergence to harvest, the average maximum air temperature was 25.0 °C and 24.5 °C under normal growing conditions in 2013 and 2014, respectively (Figure 1). Under late growing conditions, the average maximum air temperature from emergence to harvest was 29.7 °C and 28.8 °C in 2013 and 2014, respectively (Figure 1). While the average maximum air temperature from tuberization to harvest was 26.8 and 25.8 °C under normal growing conditions in 2013 and 2014, respectively, it was 30.0 °C under late growing conditions in both years. In addition, from tuberization to harvest under control conditions, the number of days with daily maximum temperature of ≥30 °C was 18 in 2013 and 12 in 2014, whereas it was 36 days and 32 days under late growing conditions in 2013 and 2014, respectively.

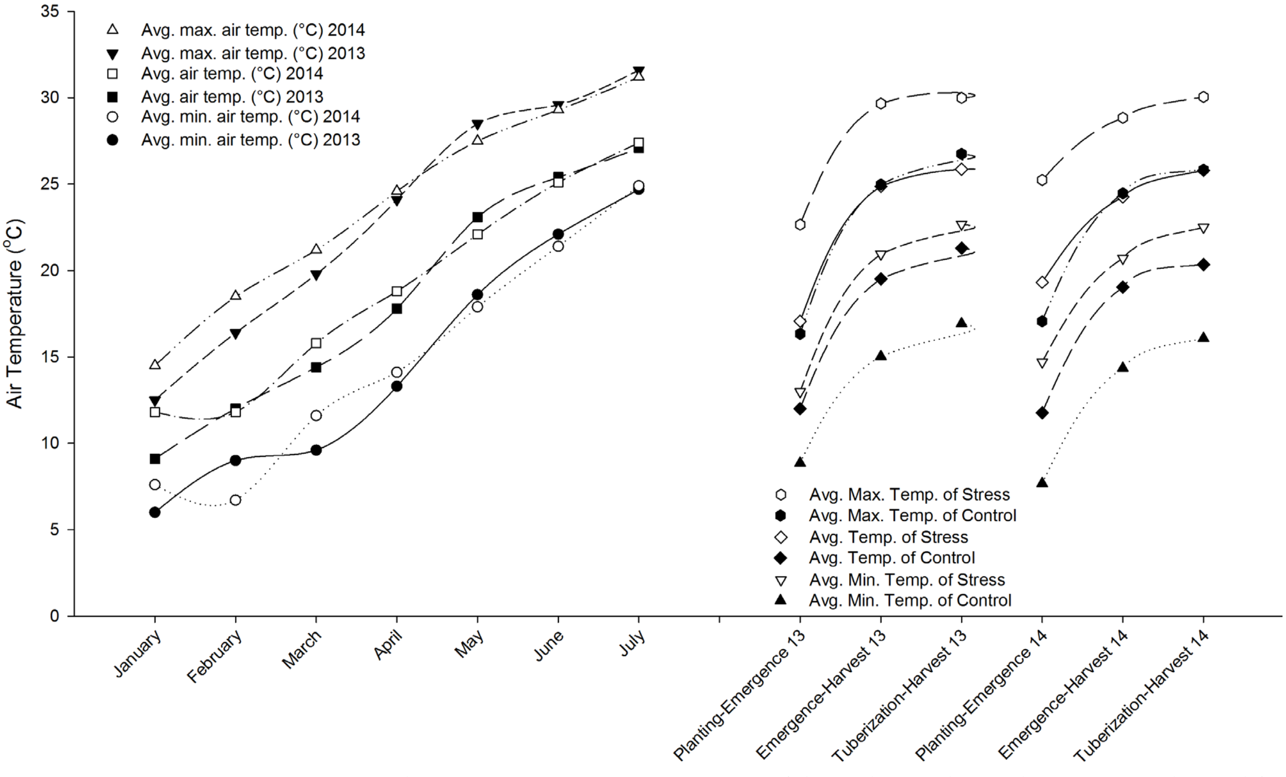

Figure 1. Average, average minimum, and average maximum air temperatures of the study area during the experimental period for different growing stages of potato in 2013 and 2014.

3.2. Vegetative growth traits

In terms of genotype × environment interaction, aboveground vegetative growth traits such as PH, HDW, ST, LAI, and LSR were significantly affected by high temperatures in both years (Table 2). The PH of potato genotypes increased under high temperature conditions. Under control conditions, PH values of the genotypes ranged from 34.39 to 53.15 cm (mean: 44.63 cm), whereas PH values varied between 40.92 and 70.52 cm (mean: 59.03 cm) under high temperature conditions (Table 3). High temperature enhanced the haulm dry weight of genotypes and the average value of all potato genotypes for HDW was 53.36 and 83.71 g plant^{-1} under control and higher temperature conditions, respectively (Table 3). However, HDW values ranged from 30.19 g plant^{-1} (02-173) to 76.36 g plant^{-1} (01-536) and from 42.66 g plant^{-1} (Agata) to 124.69 g plant^{-1} (03-113) under control and higher temperature conditions, respectively. All potato genotypes responded with a decrease in stem thickness of around 24% under high temperature conditions (Table 3). Two-year average values of all potato genotypes for LAI were 2.49 and 2.63 under control and high temperature conditions (Table 3). The mean LAI values of all genotypes were slightly higher under high temperature conditions, but the response of genotypes to growing environment in respect to LAI was more distinct (Table 3). The LAIs of Demon, Agata, Agria, Hermes, 02-173, 02-363, 03-113, and 04-123 increased under warmer field conditions, while LAI values decreased in genotypes such as Arany Chipke, Banba, Russet Burbank, 01-536, and 06-62 due to heat stress. High growth temperature also resulted in lower leaf/stem ratio (LSR) in all genotypes, except 06-62 (Table 3).

3.3. Physiological traits

The Pn of genotypes was significantly lower under high temperature in comparison with the normal growing environment (Table 4). Although Pn of most genotypes decreased under heat stress, some genotypes (02-363, 04-123, and Marabel) had higher Pn in the stressful environment. The Gs of genotypes was significantly affected by growing environment (Table 4). Higher Gs values were obtained from the stressful environment, although lower Gs values were recorded for some genotypes (03-113, Balatoni Rozsa, and Banba). An increase was observed in transpiration rate for all genotypes at high temperature conditions compared to the control. The average value of all potato genotypes for Tr was 8.61 and 13.37 mmol m^{-2} s^{-1} under control and higher temperature conditions, respectively (Table 4). Tr of genotypes ranged from 6.44 (Marabel) to 10.46 mmol m^{-2} s^{-1} (Banba) under control conditions and from 11.14 (02-173) to 15.69 mmol m^{-2} s^{-1} (04-123) under higher temperature conditions.

CT values of potato genotypes were significantly ($P \leq 0.01$) affected by growing environment (Table 2). While the average value of all genotypes for CT was 20.96 °C under control conditions, it was 25.85 °C at higher temperature conditions (Table 4). The value of CT ranged from 19.06 °C (07-258) to 23.06 °C (02-173) under control conditions, whereas it varied between 24.62 (06-62) and 27.36 °C (Russet Burbank) under higher temperature conditions.

Table 2. ANOVA for investigated traits of 17 potato genotypes grown in 2013 and 2014 or as 2-year average.

	Source	d.f.	PH	HDW	ST	LAI	LSR	TN	TW	TY	HSI	HTI	SPAD	Pn	Gs	Tr	CT
			Mean squares														
2013	Genotype (G)	16	266.0**	3377.1**	1.1**	3.4**	0.4**	12.7**	2012.7**	174.2**	0.218**	0.206**					
	Environment (E)	1	6035.6**	20,362.0**	567.5**	0.7 ns[a]	4.8**	43.1**	64,763.5**	7386.8**							
	G × E	16	60.1**	1222.9**	0.9**	1.2**	0.2**	2.4**	302.6**	73.7**							
	CV (%)		7.4	7.1	3.0	7.4	7.2	5.0	3.9	4.4	4.7	5.4					
2014	Genotype (G)	16	415.6**	2599.3**	11.81**	3.08**	0.41**	9.95**	2770.2**	325.37**	0.156**	0.474**	71.1**	35.02**	0.051**	6.89**	5.85**
	Environment (E)	1	8137.5**	44,623.8**	138.41**	0.65*	4.24**	55.78**	45,471.9**	7109.40**			1334.4**	189.18**	0.407**	768.36**	814.87**
	G × E	16	47.0**	746.6**	1.15**	0.21**	0.06**	2.12**	823.7**	51.00 ns			7.0**	12.06**	0.034**	5.06**	1.76**
	CV (%)		7.2	4.7	4.7	6.8	10.0	4.9	4.3	4.7	6.7	6.2	3.6	4.5	10.9	4.6	3.0
Two-year average	Genotype (G)	16	259.8**	2547.4**	4.4**	2.8**	0.4**	9.6**	2060.2**	194.3**	0.151**	0.250**					
	Environment (E)	1	7044.3**	31317.4**	317.5**	0.7**	4.5**	49.7**	54,693.9**	7249.9**							
	G × E	16	27.3**	738.1**	0.5**	0.5**	0.1**	1.1**	497.7**	53.5**							
	CV (%)		5.5	4.6	2.9	5.2	6.0	3.2	2.8	3.4	4.1	4.2					

[a] Nonsignificant, $P > 0.05$; * significant at $P \leq 0.05$; ** significant at $P \leq 0.01$; PH, plant height (cm); HDW, haulm dry weight (g plant^{-1}); ST, stem thickness (mm); LAI, leaf area index; LSR, leaf/stem weight ratio; TN, number of tubers per plant (number plant^{-1}); TW, mean tuber weight (g); TY, tuber yield (t ha^{-1}); HSI, heat susceptibility index; HTI, heat tolerance index; SPAD, chlorophyll index; Pn, photosynthetic rate (µmol CO_2 m^{-2} s^{-1}); Gs, stomatal conductance (mol H_2O m^{-2} s^{-1}); Tr, transpiration rate (mmol H_2O m^{-2} s^{-1}); CT, canopy temperature (°C).

Table 3. Two-year average values of vegetative growth-related traits of 17 potato genotypes grown under control or high temperature conditions.

Genotypes	cPH	hPH	cHDW	hHDW	cST	hST	cLAI	hLAI	cLSR	hLSR
01-536	44.58 c*	59.99 d	76.36 a	78.99 f	12.85 d	9.70 f	3.26 a	2.84 c	2.10 b	1.66 a
02-173	37.41 f	55.62 h	30.19 j	53.76 i	11.83 f	8.15 h	1.57 e	1.67 g	1.85 c	1.20 h
02-363	37.29 g	53.17 j	37.45 i	66.96 g	11.69 g	8.92 g	1.67 e	2.10 f	1.64 f	1.40 e
03-113	53.82 a	61.59 c	69.45 c	124.69 a	13.19 b	10.35 c	3.21 a	3.74 a	1.47 g	1.32 f
04-123	44.71 c	59.32 f	49.30 f	103.79 c	11.71 g	8.97 g	2.44 c	3.10 b	1.81 d	1.52 b
06-62	47.72 b	64.92 b	74.76 a	78.56 f	13.50 a	9.73 f	3.34 a	2.84 c	1.33 g	1.44 d
07-258	45.74 c	63.79 b	60.07 e	104.57 c	13.31 a	10.21 d	3.12 b	3.22 b	1.71 d	1.29 g
08-212	47.13 c	59.71 e	51.28 f	80.97 e	13.28 a	10.30 d	2.52 c	2.60 d	1.86 c	1.39 e
Balatoni Rozsa	40.55 e	54.62 i	42.33 h	54.63 i	13.28 a	10.84 a	2.04 d	2.09 f	2.41 a	1.67 a
Arany Chipke	44.20 c	57.35 f	64.10 d	83.74 e	13.22 b	9.60 f	3.19 a	2.71 c	2.12 b	1.43 e
Demon	51.19 a	62.68 c	64.77 d	126.26 a	13.52 a	10.45 b	2.58 c	3.65 a	1.64 f	1.26 g
Agata	34.39 h	40.92 k	32.51 j	42.66 j	12.22 f	8.09 h	1.54 e	1.75 g	2.00 b	1.53 b
Agria	46.26 c	67.01 a	51.55 f	111.42 b	13.41 a	10.47 b	2.05 d	3.15 b	1.14 h	1.03 i
Banba	53.15 a	70.52 a	71.89 b	94.06 d	13.66 a	11.02 a	3.32 a	2.86 c	1.76 d	1.48 c
Hermes	45.11 c	56.48 f	47.13 g	83.84 e	13.38 a	10.77 a	2.06 d	2.35 e	1.79 d	1.55 b
Marabel	40.97 d	55.97 g	36.85 i	69.98 g	12.66 e	9.82 e	1.96 d	2.02 f	1.97 b	1.60 a
Russet Burbank	44.42 c	59.78 e	47.08 g	64.11 h	12.92 c	10.31 c	2.39 c	1.97 f	1.68 e	1.29 g
Mean	44.63	59.03	53.36	83.71	12.92	9.86	2.49	2.63	1.78	1.42

cPH, Plant height (cm) at control temperature; hPH, plant height (cm) at high temperature; cHDW, haulm dry weight (g plant^{-1}) at control; hHDW, haulm dry weight (g plant^{-1}) at high temperature; cST, stem thickness (mm) at control; hST, stem thickness (mm) at high temperature; cLAI, leaf area index at control; hLAI, leaf area index at high temperature; cLSR, leaf/stem weight ratio at control; hLSR, leaf/stem weight ratio at high temperature.
* Different letters next to mean values in the each column of the table indicate significant differences between genotypes ($P \leq 0.05$) based on LSD test.

Chlorophyll content of genotypes was compared by in-field SPAD readings under both control and heat conditions in 2014. High temperature conditions resulted in significant ($P \leq 0.01$) declines in the average values of all genotypes for SPAD from 42.70 to 36.44 (Tables 2 and 4). The chlorophyll content of each genotype was also reduced by high temperature. SPAD values of genotypes ranged from 39.04 (Russet Burbank) to 48.82 (Demon) under control conditions and from 31.70 (Hermes) to 43.53 (Demon) under higher temperature conditions.

3.4. Agricultural traits

The genotypes, growing environments, and their interactions were significantly effective on all agricultural traits such as TN, TW, and TY (Table 2). High temperatures resulted in significant decreases in TN in all genotypes except for Agata (Table 5). Agata produced even slightly more tubers under the stress condition. The highest TN was obtained from 03-113 (9.24 tubers plant^{-1}) under normal growing conditions while Banba (7.25 tubers plant^{-1}) produced the highest TN in the warmer growth environment. Heat stress also significantly reduced the TW of genotypes (Table 5). The 2-year average value of all potato genotypes for TW was 102.56 g under control conditions, and it was reduced to 62.45 g at higher temperature conditions. As a consequence, total tuber yield of genotypes was also dramatically decreased (51%) due to heat stress during the growing period. The experimental mean of tuber yield under normal growth conditions was 28.56 t ha^{-1}, whereas it was only 13.96 t ha^{-1} under warmer growth conditions (Table 5). Tuber yields of potato genotypes ranged from 17.85 t ha^{-1} (02-363) to 46.00 t ha^{-1} (Banba) under control conditions and from 9.50 t ha^{-1} (Russet Burbank) to 22.26 t ha^{-1} (Banba) under higher temperature conditions (Table 5). The HSI and HTI of each genotype were calculated based on tuber yields under control and high temperature conditions. The HSI of 17 potato genotypes varied between 0.424 (02-363) and 1.254 (08-212) based on 2-year average data (Table 5). The HTI of the genotypes ranged from 0.256 (02-173) to 1.253 (Banba) based on 2-year average data (Table 5). Differences between genotypes for both HSI and HTI were significant at $P \leq 0.01$ in 2013 and 2014 or as a 2-year average (Table 2).

While some traits were correlated with tuber yield under control conditions, some other traits were associated with tuber yield under high temperature conditions (Table

Table 4. Mean values of physiological traits of 17 potato genotypes grown under control or high temperature conditions in 2014.

Genotypes	cPn	hPn	cGs	hGs	cTr	hTr	cCT	hCT	cSPAD	hSPAD
01-536	25.88 b*	22.68 a	0.573 b	0.638 b	9.69 b	13.96 d	19.65 h	25.28 d	40.17 f	34.98 d
02-173	19.31 g	17.62 i	0.388 e	0.455 e	7.33 h	11.14 j	23.06 a	26.97 a	41.51 e	32.03 e
02-363	17.89 i	18.75 f	0.368 e	0.518 d	6.93 i	12.16 h	22.96 a	26.58 a	41.60 e	37.35 c
03-113	25.23 b	18.30 g	0.574 b	0.474 e	10.15 a	12.17 h	20.46 f	25.60 c	44.03 c	38.43 b
04-123	19.81 g	21.32 a	0.423 e	0.819 a	8.27 f	15.69 a	21.76 c	26.25 a	43.94 c	38.03 b
06-62	24.53 c	21.81 a	0.423 e	0.604 b	9.02 d	13.81 d	20.87 e	24.62 f	48.44 a	39.40 b
07-258	22.23 f	20.77 b	0.488 c	0.586 b	8.35 f	13.11 e	19.06 j	25.27 d	41.15 e	35.10 d
08-212	20.18 g	19.67 d	0.372 e	0.626 b	7.68 g	13.41 d	21.05 d	25.88 b	39.10 g	31.90 f
Balatoni Rozsa	25.23 b	19.23 e	0.612 a	0.544 c	9.80 b	12.63 g	21.15 d	26.87 a	42.81 d	37.30 c
Arany Chipke	22.70 e	21.69 a	0.587 b	0.609 b	9.25 c	14.08 d	20.81 e	25.56 c	41.95 d	37.48 c
Demon	26.00 b	22.13 a	0.568 b	0.602 b	9.68 b	13.65 d	19.65 h	25.53 c	48.82 a	43.53 a
Agata	22.71 e	19.35 e	0.456 c	0.640 b	8.44 e	13.85 d	21.59 c	25.39 d	39.97 f	37.50 c
Agria	25.95 b	21.23 a	0.480 c	0.539 c	8.62 e	12.85 f	22.20 b	26.00 b	46.62 a	38.98 b
Banba	27.47 a	22.31 a	0.645 a	0.638 b	10.46 a	13.56 d	19.56 i	24.83 e	45.17 b	38.63 b
Hermes	23.63 d	22.50	0.592 a	0.684 b	9.30 c	14.79 b	20.19 g	25.50 c	40.98 e	31.70 g
Marabel	19.05 h	20.02 c	0.328 f	0.660 b	6.44 j	15.07 a	21.42 c	25.89 b	40.54 e	33.60 d
Russet Burbank	19.67 g	18.01 i	0.304 g	0.404 f	7.04 i	11.37 i	20.82 e	27.36 a	39.04 g	33.48 d
Mean	22.79	20.43	0.481	0.591	8.61	13.37	20.96	25.85	42.70	36.44

cPn, Photosynthetic rate (μmol CO_2 m^{-2} s^{-1}) at control temperature; hPn, photosynthetic rate (μmol CO_2 m^{-2} s^{-1}) at high temperature; cGs, stomatal conductance (mol H_2O m^{-2} s^{-1}) at control; hGs, stomatal conductance (mol H_2O m^{-2} s^{-1}) at high temperature; cTr, transpiration rate (mmol H_2O m^{-2} s^{-1}) at control; hTr, transpiration rate (mmol H_2O m^{-2} s^{-1}) at high temperature; cCT, canopy temperature (°C) at control; hCT, canopy temperature (°C) at high temperature; cSPAD, chlorophyll index at control; hSPAD, chlorophyll index at high temperature. * Different letters next to mean values in the each column of the table indicate significant differences between genotypes ($P \leq 0.05$) based on LSD test.

6). Some morphological and agronomic traits under control conditions such as cPH ($r^2 = 0.65$), cHDW ($r^2 = 0.73$), cST ($r^2 = 0.77$), cLAI ($r^2 = 0.71$), and cTW ($r^2 = 0.69$) were positively correlated with the tuber yield of genotypes grown under control conditions. Some physiological traits under control conditions such as cSPAD ($r^2 = 0.50$), cPn ($r^2 = 0.82$), cGs ($r^2 = 0.62$), and cTr ($r^2 = 0.70$) were positively associated with tuber yield genotypes grown under control conditions, whereas cCT was negatively correlated ($r^2 = -0.63$) with tuber yield genotypes grown under control conditions.

The traits of cHDW ($r^2 = 0.57$), cLAI ($r^2 = 0.50$), and cTW ($r^2 = 0.45$) under control conditions were significantly and positively associated with tuber yield of genotypes grown under higher temperature. Moreover, cCT was negatively correlated ($r^2 = -0.56$) with tuber yield at higher temperature conditions whereas physiological traits such as cSPAD ($r^2 = 0.47$), cPn ($r^2 = 0.77$), cGs ($r^2 = 0.63$), and cTr ($r^2 = 0.68$) were positively correlated with tuber yield at high temperatures.

The number of tubers per plant (hTN) and mean tuber weight (hTW) under high temperature conditions were positively associated ($r^2 = 0.62$ and $r^2 = 0.55$, respectively) with tuber yield of genotypes grown under high temperature conditions. While physiological traits at high temperatures such as hSPAD ($r^2 = 0.48$) and hPn ($r^2 = 0.54$) were positively correlated with tuber yield of genotypes grown under hot field conditions, hCT was negatively associated ($r^2 = -0.62$). However, hGs and hTr were not correlated with tuber yield of genotypes grown under high temperature conditions.

HTI showed a positive correlation ($P \leq 0.01$) with tuber yield of genotypes grown under the control conditions ($r^2 = 0.92$) and higher temperature conditions ($r^2 = 0.85$) in 2013 (data not shown). Similarly, the HTI in 2014 was highly correlated ($P \leq 0.01$) with tuber yield under the control ($r^2 = 0.93$) and higher temperature ($r^2 = 0.96$) conditions (data not shown). For 2-year average data, the HTI also exhibited significant ($P \leq 0.01$) positive correlations with tuber yield under control conditions ($r^2 = 0.94$) or high temperature conditions ($r^2 = 0.93$) (Table 6). On the other hand, no significant correlation was observed between HSI and tuber yield of genotypes grown under high temperature conditions.

Table 5. Two-year average values of tuber yield, yield components, and susceptibility and tolerance indexes of 17 potato genotypes grown under control or high temperature conditions.

Genotypes	cTN	hTN	cTW	hTW	cTY	hTY	HSI	HTI
01-536	6.89 e*	5.68 f	107.34 e	70.81 b	31.48 e	16.59 b	0.888 i	0.634 d
02-173	5.87 g	4.32 j	81.32 i	55.21 h	20.22 k	9.96 h	0.960 f	0.256 m
02-363	5.39 i	4.87 i	79.56 i	67.73 d	17.85 l	13.75 e	0.424 l	0.307 k
03-113	9.24 a	6.98 b	73.59 j	47.56 j	28.47 g	13.70 e	0.992 e	0.477 e
04-123	7.72 c	6.52 c	62.67 k	44.11 k	20.87 k	12.12 f	0.798 j	0.321 j
06-62	8.59 b	6.43 c	89.79 h	56.36 g	32.67 d	15.35 d	1.022 e	0.610 d
07-258	6.93 e	5.08 g	95.33 f	63.44 e	28.64 g	13.63 e	0.993 e	0.473 e
08-212	6.55 f	4.55 j	108.00 e	54.20 i	30.06 f	10.26 h	1.254 a	0.378 g
Balatoni Rozsa	5.63 g	4.31 k	137.27 b	94.39 a	33.22 d	16.72 b	0.940 g	0.685 c
Arany Chipke	7.87 c	6.10 e	111.24 d	64.02 e	37.68 b	16.11 c	1.082 c	0.778 b
Demon	7.41 d	5.61 f	113.25 c	69.74 c	35.53 c	16.36 b	1.029 d	0.712 c
Agata	5.80 g	6.28 d	93.28 g	54.68 h	22.80 i	13.99 e	0.706 k	0.387 g
Agria	4.96 j	4.09 k	134.90 b	69.00 c	28.71 g	12.09 g	1.129 c	0.435 f
Banba	7.41 d	7.25 a	142.97 a	72.74 b	46.00 a	22.26 a	1.003 e	1.253 a
Hermes	5.71 g	4.87 h	98.69 f	59.60 f	23.76 i	12.25 f	0.928 h	0.356 h
Marabel	5.49 h	5.11 g	97.06 f	59.82 f	22.30 j	12.70 f	0.815 j	0.347 i
Russet Burbank	5.10 j	3.96 l	117.24 c	58.25 f	25.32 h	9.50 i	1.196 b	0.290 l
Mean	6.62	5.41	102.56	62.45	28.56	13.96	0.951	0.528

cTN, Number of tubers per plant (number plant^{-1}) at control temperature; hTN, number of tubers per plant (number plant^{-1}) at high temperature; cTW, mean tuber weight (g) at control; hTW, mean tuber weight (g) at high temperature; cTY, tuber yield (t ha^{-1}) at control; hTY, tuber yield (t ha^{-1}) at high temperature; HSI, heat susceptibility index; HTI, heat tolerance index. * Different letters next to mean values in the each column of the table indicate significant differences between genotypes ($P \leq 0.05$) based on LSD test.

3.5. Principal component analysis

PCA was used to classify genotypes for their heat tolerance level and estimate favorable traits to be used in potato breeding programs for heat tolerance. With this aim, PCA was performed individually for i) the data of all traits at control or high temperatures (cHDW, cLAI, cPn, cGs, cTr, cCT, cSPAD, cTW, HTI, hTN, hTW, hSPAD, hPn, and hCT), which were correlated with tuber yield of genotypes grown under high temperature conditions; ii) the data of traits at control conditions (cHDW, cLAI, cPn, cGs, cTr, cCT, and cSPAD); which were correlated with tuber yield of genotypes grown under high temperature conditions; and iii) the data of traits at high temperature (hPn, hCT, and hSPAD), which were correlated with tuber yield of genotypes grown under higher temperature conditions.

As a result of PCA, genotypes were classified into four groups based on PC1 and PC2 values (Figure 2). Only the result of the PCA by using data for cHDW, cLAI, cPn, cGs, cTr, cCT, and cSPAD reflected the yield performance of genotypes grown under hot field conditions (Figures 2 and 3). As a result of the PCA, PC1 and PC2 accounted for 87.97% of total variation (Figure 2). Based on traits under control conditions, the genotypes of Banba, Balatoni Rozsa, Demon, Hermes, and Agria were classified as tolerant, whereas Arany Chipke, 01-536, 06-62, 03-113, and 07-258 were moderately tolerant (Figure 2). However, the genotypes of Agata, 02-173, 02-363, and 04-123 were graded as moderately susceptible and Russet Burbank, Marabel, and 08-212 as susceptible.

4. Discussion

In this study, the late-planted potato genotypes were exposed to higher temperatures during the whole growing period, particularly at the tuber bulking period (Figure 1).

Table 6. Correlation coefficients for investigated traits in 17 potato genotypes.

	cTY	hTY	cPH	hPH	cHDW	hHDW	cST	hST	cLAI	hLAI	cLSR	hLSR	cPn	hPn	cGs	hGs	cTr	hTr	cCT	hCT	cSPAD	hSPAD	cTN	hTN	cTW	hTW	HSI
hTY	0.777***																										
cPH	0.654***	0.363																									
hPH	0.582**	0.297	0.826***																								
cHDW	0.731***	0.573**	0.806***	0.700***																							
hHDW	0.342	0.179	0.822***	0.690***	0.617***																						
cST	0.770***	0.402	0.707***	0.599**	0.635***	0.430																					
hST	0.603**	0.328	0.712***	0.648***	0.485***	0.484**	0.848***																				
cLAI	0.707***	0.505**	0.767***	0.672***	0.950***	0.543**	0.594**	0.455*																			
hLAI	0.450*	0.309	0.827***	0.666***	0.760***	0.956***	0.472*	0.457*	0.685***																		
cLSR	0.041	0.190	−0.438	−0.531**	−0.288	−0.518**	−0.195	−0.114	−0.173	−0.448																	
hLSR	0.077	0.379	−0.210	−0.388	0.004	−0.428	−0.049	−0.033	0.042	−0.314	0.702***																
cPn	0.823***	0.770***	0.670***	0.488**	0.709***	0.495**	0.715***	0.565**	0.657***	0.693***	−0.065	0.102															
hPn	0.504**	0.540**	0.417	0.403	0.618***	0.468	0.438	0.333	0.483**	0.593**	−0.023	0.300	0.568**														
cGs	0.617***	0.633***	0.415	0.101	0.518**	0.292	0.503**	0.445	0.450	0.446*	0.300	0.375	0.832***	0.545**													
hGs	0.049	0.121	0.013	−0.008	0.111	0.147	−0.089	−0.045	0.022	0.171	0.290	0.516**	0.070	0.674***	0.193												
cTr	0.704***	0.676***	0.594**	0.294	0.677***	0.397	0.573**	0.430	0.640***	0.622***	0.142	0.271	0.907***	0.537**	0.937***	0.174											
hTr	0.100	0.142	0.047	0.050	0.177	0.232	0.031	0.010	0.096	0.240	0.264	0.535**	0.099	0.706***	0.182	0.950***	0.155										
cCT	−0.627***	−0.561**	−0.637***	−0.371	−0.774***	−0.526**	−0.710***	−0.506**	−0.741***	−0.687***	−0.072	−0.254	−0.591**	−0.575**	−0.565**	−0.210	−0.604**	−0.273									
hCT	−0.601**	−0.620***	−0.519**	−0.380	−0.667***	−0.419	−0.481	−0.140	−0.617***	−0.604**	0.211	−0.162	−0.582**	−0.726***	−0.470*	−0.500**	−0.555**	−0.540**	0.590**								
cSPAD	0.505**	0.475*	0.553**	0.583**	0.551**	0.556**	0.361	0.266	0.445	0.623***	−0.472	−0.278	0.576**	0.412	0.352	0.088	0.493**	0.094	−0.119	−0.405							
hSPAD	0.453	0.478*	0.437	0.346	0.455	0.361	0.215	0.150	0.359	0.514**	−0.234	−0.246	0.540**	0.318	0.392	0.094	0.507**	0.104	−0.161	−0.357	0.822***						
cTN	0.454*	0.400	0.639***	0.375	0.741***	0.545**	0.264	0.086	0.779***	0.674***	−0.160	0.052	0.372	0.301	0.398	0.226	0.582**	0.224	−0.431	−0.591**	0.459*	0.447					
hTN	0.406	0.615***	0.428	0.147	0.566**	0.339	0.077	−0.075	0.573**	0.450*	−0.062	0.288	0.399	0.385	0.430	0.441	0.560**	0.434	−0.362	−0.708***	0.370	0.500**	0.804***				
cTW	0.687***	0.452*	0.234	0.347	0.198	−0.019	0.658***	0.639***	0.132	−0.005	0.115	0.009	0.559**	0.275	0.404	−0.169	0.346	−0.127	−0.323	−0.036	0.138	0.138	−0.313	−0.244			
hTW	0.462*	0.548**	−0.060	0.105	0.064	−0.157	0.369	0.454*	−0.022	−0.088	0.372	0.231	0.445	0.185	0.473*	−0.173	0.331	−0.174	−0.179	0.096	0.141	0.220	−0.328	−0.294	0.752***		
HSI	0.514**	−0.125	0.565**	0.547**	0.391	0.309	0.693***	0.536**	0.440	0.300	−0.199	−0.360	0.322	0.111	0.112	−0.219	0.230	−0.167	−0.387	−0.050	0.121	−0.108	0.172	−0.178	0.475*	−0.017	
HTI	0.938***	0.931***	0.533**	0.486**	0.651***	0.257	0.584**	0.475*	0.613***	0.359	0.120	0.215	0.734***	0.545**	0.726***	0.154	0.741**	−0.145	−0.561**	−0.544**	0.448	0.494**	0.428	0.537**	0.610***	0.510**	0.214

Correlation coefficients were calculated using 2-year average data of traits, whereas coefficients of physiological traits were calculated using data from 2014. * Significant at $P < 0.07$; ** significant at $P \leq 0.05$; *** significant at $P \leq 0.01$.

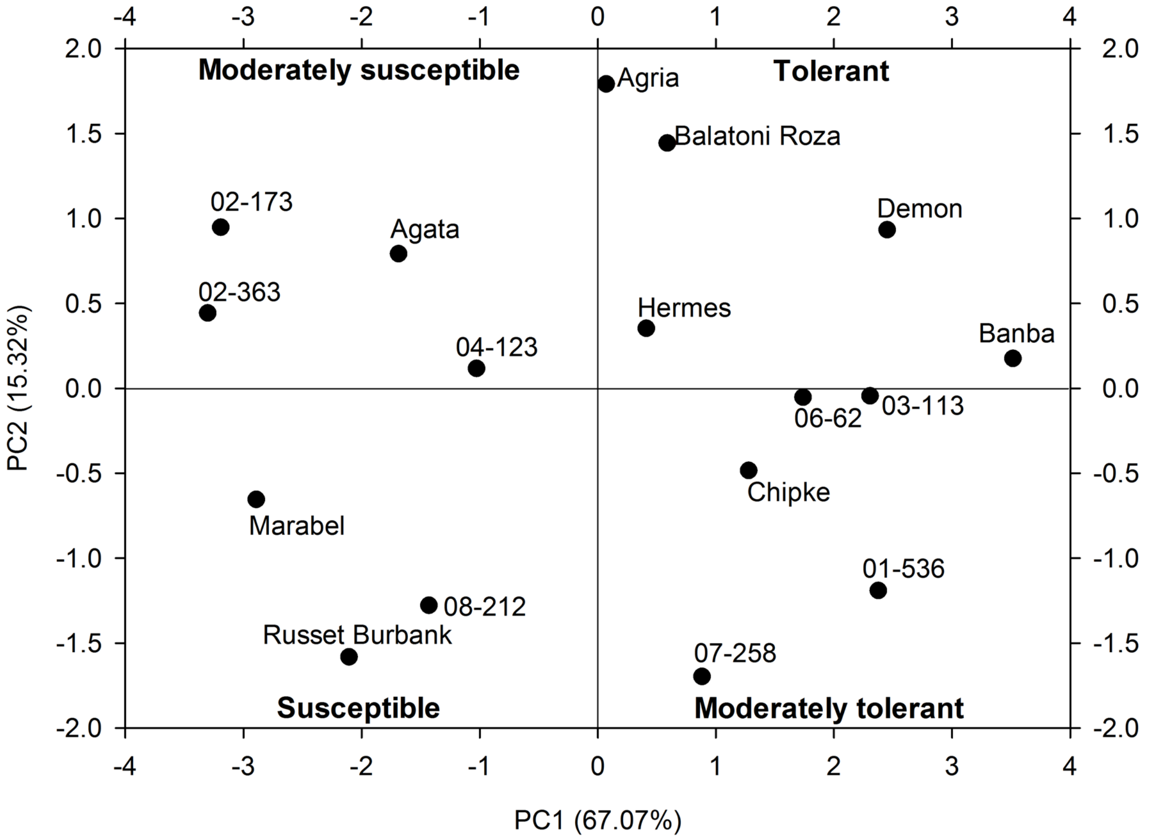

Figure 2. Classification of 17 genotypes for heat tolerance by PCA using data of cHDWm, cLAIm, cSPAD, cPn, cGs, cTr, and cCT.

Previous studies showed that high temperatures promoted internode elongation in potato and caused increases in the plant height of potato (Marinus and Bodlaender, 1975; Bennett et al., 1991; Rykaczewska, 2015). Similarly, the average PH of all genotypes increased by 32% under higher temperature conditions in this study (Table 3). HDW is one of the best indicators of potato vegetative growth. Based on 2-year averages, all potato genotypes enhanced their HDW by 57% under heat field conditions (Table 3), whereas the HDW of a few genotypes was lower at higher temperatures in the first year (data not shown). The results for PH and HDW indicated that aboveground vegetative growth of potato genotypes was significantly enhanced by high temperatures. cHDW was also significantly and positively correlated with tuber yields of genotypes grown under control or higher temperature conditions. This result proved that the genotypes with higher HDW under normal growing conditions produce higher tuber yield under normal or higher temperature conditions. However, the stem thickness of each genotype decreased under higher temperature conditions. Depending on the increase in PH, while the stem thickness of genotypes decreased, the node number of plants and internode length increased under higher temperature conditions (data not shown). These results showed that the height of potato genotypes increased by internode elongation with thinner stems under hot field conditions. Similarly, previous studies reported that high temperatures induced plant elongation and caused plant growth with thin stems (Ewing, 1981; Menzel, 1985; Nagarajan and Minhas, 1995). Although the LAI values of a few genotypes decreased at higher temperatures, the mean LAI of the overall genotypes was higher under heat field conditions (Table 3). However, the LAI of genotypes under heat field conditions increased significantly ($P \leq 0.05$) in 2014, whereas the increase in LAI was not significant in 2013. Since LAI is calculated by total leaf area ratio to a unit ground surface area, it is related to the number of leaves and the area of each leaf. Fleisher et al. (2006) reported that the widest leaf area in potato was observed at temperatures between 16.6 and 22.1 °C. On the other hand, individual leaf area of potato generally decreases under heat stress conditions (Khedher

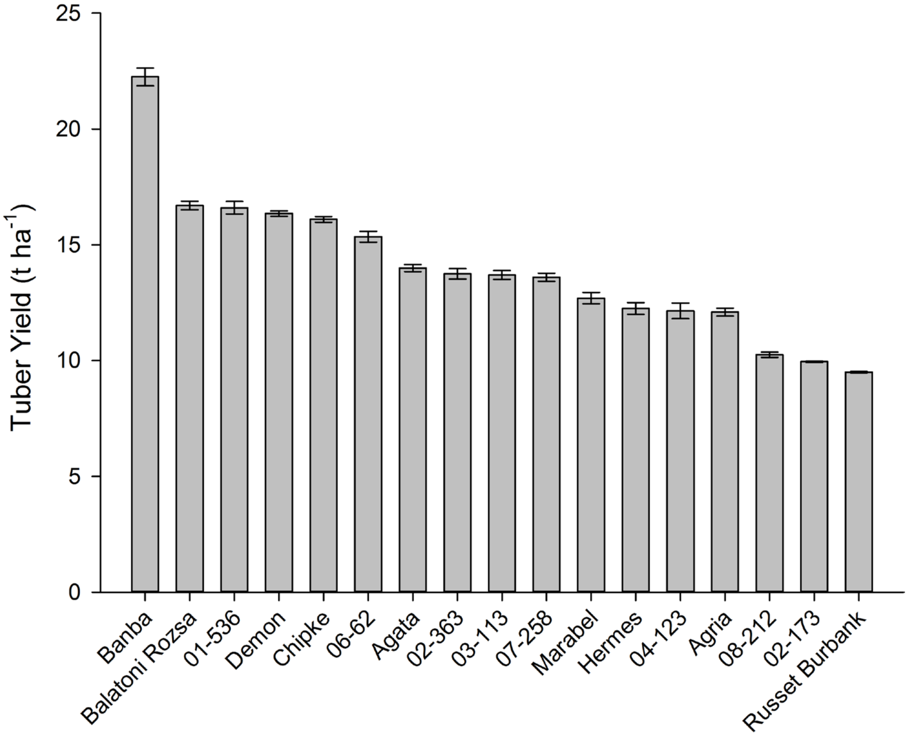

Figure 3. Two-year average tuber yield of 17 potato genotypes grown under higher temperatures. Bars represent 2-year average tuber yield with ±SE. The number of observations for 2-year average tuber yield of each genotype is eight, as four replications and 2 years of field trial.

and Ewing, 1985; Benoit et al., 1986; Lafta and Lorenzen, 1995). However, high temperatures increase plant height and number of leaves in potato (Marinus and Bodlaender, 1975; Timlin et al., 2006). Generally, individual leaf area, leaf weight, and leaf/stem ratio decrease in potato under high temperature conditions, since heat stress negatively affects dry matter production and allocation in potato plants (Marinus and Bodlaender, 1975; Ben Khedher and Ewing, 1985; Benoit et al., 1986; Lafta and Lorenzen, 1995). Although plant height of potato genotypes increased, leaf/stem ratio significantly decreased under hot field conditions. Because stems of tall potato genotypes were thicker than those of short genotypes, tall potato genotypes exhibited smaller leaf/stem ratios than short genotypes. It seems that the trait of leaf/stem ratio is more dependent on genetic factors in comparison to environmental factors.

While the optimum temperature range for the photosynthetic rate of potato is between 16 and 25 °C, higher temperatures decrease the photosynthetic rate by increasing photorespiration and respiration (Ku et al., 1977; Burton, 1981; Dwelle et al., 1981; Hammes and de Jager, 1990; Fleisher et al., 2006; Timlin et al., 2006). Similarly, high temperature negatively affected the photosynthetic rate of most potato genotypes in the study. Photosynthetic data of the study were consistent with the findings of Burton (1981) that the optimum temperature for European potato varieties was 20 °C, and each increase of 5 °C in temperature above the optimum caused about 25% decrease in the photosynthetic rate. In another study, the average photosynthetic rate of three different potato varieties was 37% less at 40 °C compared with the rate at 20 °C (Hammes and de Jager, 1990). Similarly, leaf photosynthesis of potato plants was reduced from 9.20 to 6.22 µmol m^{-2} s^{-1} at temperatures of 35 °C day/25 °C night compared to 20 °C day/15 °C night (Prange et al., 1990). Reynolds et al. (1990) reported that the CO_2 fixation rate of the heat-sensitive accession of *S. chacoense* was 45% lower than that of the heat-tolerant accession and, similarly, it was 27% less for the heat-sensitive accession of *S. stoloniferum* than the heat-tolerant accession after 2 to 3 days of heat treatment at 40 °C day/30 °C night. The photosynthetic rate of potato varieties are also decreased by high temperatures at the tuber initiation or bulking stages (Aien et al., 2011). In this study, while photosynthetic rates of potato genotypes declined under high temperature conditions, the stomatal conductance of almost all genotypes increased. The increase in stomatal conductance at high temperatures is similar to previous findings that the stomatal conductance rate remained constant at 35 °C (Dwelle et al., 1981) or increased at higher temperatures (Hancock et al., 2013). However, stomatal conductances of *S. chacoense* and *S. stoloniferum* were lower at 40 °C than those of controls at 25 °C, and they were lower in the heat-sensitive accessions than in the heat-tolerant accessions at 40 °C (Reynolds et al., 1990). Dwelle et al. (1981) concluded that the decline in carbon assimilation due to high temperature could not be attributed to changes in stomatal conductance, but the decrease must be due to direct high temperature inhibition of the photosynthetic rate. In this study, the transpiration rate of each genotype under high temperature conditions increased compared to control conditions. Under high temperature conditions, plants generally transpire more to cool off through higher stomatal conductance. Thus, the higher stomatal conductance under heat conditions could be due to high transpiration rates at higher temperature. Potato genotypes could increase their transpiration rates to prevent high temperatures arising in leaves by transpirational cooling mechanisms. Based on the correlation analysis, the traits of photosynthetic rate (cPn), stomatal conductance (cGs), and transpiration rate (cTr) of genotypes grown under control conditions were significantly and positively associated with tuber yield of genotypes grown under high temperature conditions. The results proved that the potato genotypes with higher photosynthetic rate, stomatal conductance, and transpiration rate under normal growing conditions produced more yield under high temperature conditions. Therefore, these physiological traits may be used in potato breeding programs for heat tolerance.

Generally, tuber numbers of early genotypes are affected less by heat stress due to their escape from stress through early initiation of tuberization. Agata is the earliest genotype in this experiment, and the number of tubers of this genotype did not decrease under high temperature conditions (Table 5). Similar findings were seen for Marabel, which is another early genotype. Unlike in other genotypes, mean stem numbers of Agata and Marabel did not decrease under high temperature conditions (data not shown). Temperatures exceeding 25 °C delay tuberization and cause decreases in tuber number (Borah and Milthorpe, 1962; Menzel, 1985; Struik et al., 1989; van Dam et al., 1996; Levy and Veilleux, 2007). Tuberization in potato is regulated by various hormones such as gibberellic acid (GA), cytokinin, jasmonic acid and related compounds, or abscisic acid (Menzel, 1983; Koda et al., 1991; Galis et al., 1995; Hannapel et al., 2004). Menzel (1983) reported that tuberization in potato was inhibited by increase in GA level under high temperature conditions. However, tuberization was initiated 10–20 days earlier compared to controls by exogenous applications of cytokinin either to an in vitro system or by direct application to stolons of developing potato plants (Galis et al., 1995). In this study, high temperature conditions resulted in inhibition for tuberization and gave rise to a decrease in the number of tubers. This could have been caused by an increase in GA level and decrease in cytokinin level. In this study, tuber growth and tuber weight were reduced under high temperature conditions. Tubers, being storage organs of the potato plant, are formed by accumulating photosynthetic products at stolon tips. Therefore, the continuity of photosynthetic production and the transported quantity of photosynthetic products into tubers are determiners for tuber growth. In this context, temperature as a factor affecting photosynthetic efficiency is very important for the growth of potato tubers. In this study, photosynthetic rate was decreased in genotypes under high temperature conditions and therefore tuber growth and tuber weight were reduced, probably due to decreases in transported quantities of photosynthetic products into the tubers (Marinus and Bodlaender, 1975; Menzel, 1985; Struik et al., 1989; van Dam et al., 1996; Levy and Veilleux, 2007).

In this study, tuber yield was decreased by reduction in the number of tubers and tuber weight under high temperature conditions. Previous studies suggested that high temperatures induced aboveground vegetative growth, delayed tuberization, and caused decreases in tuber growth due to a decline in photosynthesis and an increase in respiration and transpiration (Struik et al., 1989; Hammes and Jager, 1990; Levy and Veilleux, 2007). A decline in photosynthesis and an increase in both stomatal conductance and transpiration under high temperature conditions probably resulted in a decrease in tuber yield. The Arany Chipke variety was the highest-yielding cultivar at 41.7 and 16.8 t ha^{-1} under control and high temperature conditions, respectively, in the first year. However, in the second year, Banba produced the highest tuber yield at 53.6 and 30.3 t ha^{-1} under normal and higher temperature conditions, respectively. Based on 2-year averages, Banba, Balatoni Rozsa, 01-536, Demon, Arany Chipke, and 06-62, which produced higher yields than the average yield under high temperature conditions, were determined as promising potato genotypes for regions having higher temperatures than optimum.

Based on correlation analysis, cPH, cHDW, cST, cLAI, cPn, cGs, cTr, cSPAD, and cTW were positively correlated with tuber yield of genotypes grown under control conditions, whereas cCT was negatively associated with tuber yield under control conditions. Generally, tuber yield and yield components such as number of tubers or mean tuber weight are the most suitable traits for selection of candidate varieties under normal or higher temperature conditions. However, this study showed that, in addition to cTW, traits of cPH, cHDW, cST, cLAI, cPn, cTr, cCT, and cSPAD may be considered as promising traits for high-yielding potato genotypes under optimum temperature conditions. Traits under control conditions such as cHDW, cLAI, cPn, cGs, cTr, cSPAD, and cTW were also significantly and positively correlated with tuber yield under hot field conditions, whereas cCT was negatively associated. Therefore, the traits from control conditions, except cTW, were used for classification of genotypes for their heat tolerance by using PCA.

PCA is considered as a useful statistical tool for screening multivariate data that are highly correlated to each other (Johnson, 1998). In addition, PCA was used for classification of genotypes for heat tolerance in previous studies (Kakani et al., 2005; Liu et al., 2006; Demirel et al., 2016). The classification results of 17 genotypes for heat tolerance by using traits of cHDW, cLAI, cPn, cGs, cTr, cCT, and cSPAD exhibited a similarity to the yield performance of genotypes grown under higher temperature conditions (Figures 2 and 3). The PCA results proved that the traits of cHDW, cLAI, cPn, cGs, cTr, cCT, and cSPAD might be taken into account in potato breeding programs for selection of heat-tolerant genotypes. Since both tuber yield and heat tolerance are controlled by multiple traits, it is not logical to assume that only one yield-correlated trait is indicative of the tuber yield or heat tolerance of potato genotypes. Therefore, the yield-correlated traits identified in the study should be taken into account all together to estimate the tuber yield performance or heat tolerance of potato genotypes. The results demonstrated that the yield-correlated traits excluding tuber traits in this study could be helpful for potato breeders and may provide an opportunity for selection of heat-tolerant potato genotypes at an early stage in breeding programs under optimum environmental conditions. Performing PCA using yield-correlated traits allows for the classification of a large number of potato genotypes and might be a valuable tool for screening heat-tolerant potato genotypes.

The novelty of this study is the determination of some traits in potato grown under normal conditions, which were correlated with tuber yields of genotypes grown at higher temperatures. The reliability of those traits was confirmed by classification of genotypes for their heat tolerance performing PCA.

In conclusion, HDW, LAI, Pn, Gs, Tr, CT, and SPAD of potato genotypes grown under normal conditions might be useful traits to screen for heat-tolerant genotypes without growing them at high temperature conditions. Secondly, PCA can be performed for exploratory screening for heat-tolerant parents or advanced lines among a large number of genotypes. Therefore, these traits may be used to screen advanced potato breeding lines for high tuber productivity and heat tolerance.

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