Acta Agrobotanica

Article ID: 7325
DOI: 10.5586/aa.7325

Publication History
Received: 2019-12-09
Accepted: 2020-05-05
Published: 2020-06-30

Handling Editor
Joanna Kaczmarek; Institute of Plant Genetics, Polish Academy of Sciences, Poland

Authors' Contributions
GRD: carried out all experiments, collected the data and wrote the first draft of manuscript; MRH: supervised and designed the research; DH: supervised the research, helped in the experiments, and wrote the final draft of manuscript; AM: analyzed and interpreted the data

Funding
We thank Dr Davoud Hassanpanah, the manager of Zare-Ghostare-Arta Company, for the facilities and financial assistance.

Competing Interests
No competing interests have been declared.

ORIGINAL RESEARCH PAPER in GENETICS

Diallel Cross in Potato Cultivars (*Solanum tuberosum* L.) and Evaluation of Their Progenies Under Deficit Water Stress

Ghasem Rahimi Darabad[1], Mohammad Reza Hassandokht[2*], Davoud Hassanpanah[3], Amir Mousavi[4]

[1]Department of Horticulture Science and Agronomy, Science and Research Branch, Islamic Azad University, Tehran, Iran
[2]Department of Horticultural Sciences, Faculty of Agricultural Sciences, College of Agriculture and Natural Resources, University of Tehran, Karaj, Iran
[3]Horticulture Crops Research Department, Ardabil Agricultural and Natural Resources Research Center, AREEO, Ardabil, Iran
[4]National Institute of Genetic Engineering and Biotechnology, Tehran, Iran

*To whom correspondence should be addressed. Email: mrhassan@ut.ac.ir

Abstract

This study was performed to assess superior potato clones for agronomic traits and water deficit stress tolerance in laboratory and greenhouse settings over 3 years (2016–2018). Four cultivars, 'Satina,' 'Caesar,' Savalan,' and 'Agria' were used as parents and crossed by mutual hybridization based on a diallel cross using the Griffing III method. Of 279 successful crosses, 7,980 true potato seeds from 12 breeding populations were obtained, from which 2,313 seeds germinated and 244 hybrids were selected. The selected hybrids were cultured in triplicate in a split-plot based on a randomized complete block design. The main factor consisted of three levels of irrigation (100%, 80%, and 60% of available water) and a subfactor of 12 populations (♀'Agria' × 'Satina'♂, ♀'Agria' × 'Caesar'♂, ♀'Agria' × 'Savalan'♂, ♀'Satina' × 'Agria'♂, ♀'Satina' × 'Caesar'♂, ♀'Satina' × 'Savalan'♂, ♀'Caesar' × 'Satina'♂, ♀'Caesar' × 'Agria'♂, ♀'Caesar' × 'Savalan'♂, ♀'Savalan' × 'Satina'♂, ♀'Savalan' × 'Agria'♂, and ♀'Savalan' × 'Caesar'♂). In all three environmental conditions, the highest tuber yield and tuber weight per plant were related to ♀'Agria' × 'Caesar'♂. The most general combining ability that produced positive and significant tuber yield in mild and severe stress conditions was in 'Agria' and 'Caesar' cultivars. Therefore, these cultivars can easily transfer these traits to offspring and increase the expression of these traits. The specific combining ability between potato cultivars had positive and significant effects on tuber yield under the growth conditions tested. These crosses can be used for the production of drought resistant potato clones.

Keywords
breeding population; clone; general combine ability (GCA); specific combine ability (SCA); *Solanum tuberosum*

1. Introduction

Potato (*Solanum tuberosum* L.) is the fourth most important food crop produced after wheat, rice, and corn. Despite the limited genetic diversity of commercial varieties, potatoes are highly related species (Jansky, 2006).

The most important goal in breeding programs is to increase yield, but the quantitative and polygenic aspects of this trait make it difficult to study (Heidari Roodbali et al., 2016). Little progress in the selection for tuber yield has encouraged breeders to focus on the selection of secondary traits (Landjeva et al., 2008) that have high heritability and are highly correlated with tuber yield (Sadeghi, 2014).

Development of potato genotypes that have drought tolerance is also necessary (Coleman, 2008). The occurrence of drought stress at the end of the season will have less effect on these tolerant genotypes due to their evasion from drought stress and faster completion of the life cycle (Deshi et al., 2015). Potatoes are less sensitive to water shortage in the early vegetative period and maturity period, while water shortage during germination and tuber formation can cause serious damage to potato plants (Ayas & Korukçu, 2010). Nouri et al. (2016) identified the 'Satina' and 'Savalan' cultivars, which are tolerant to mild and severe water deficit stress. Hassanpanah et al. (2016) conducted hybridization of potato cultivars with a diallel cross using the Griffing III method and selected 397045-13, 397031-16, and 397067-6 as a promising clones. These clones had uniform tubers, yellow to dark yellow skin color, yellow to light yellow flesh color, round and oval round tubers, shallow to medium eye depth, late maturity, and are used for the consumption chips and frying.

This research was performed to create genetic diversity in potato crops and assess suitable hybrids for agronomic traits that are both marketable and adaptable to the climatic conditions of Iran. Our study was conducted in laboratories and greenhouses at Zare-Ghostare-Arta Company over 3 years (2016–2018).

2. Material and Methods

2.1. Generating Genetic Diversity (2016)

This experiment used four cultivars: 'Satina,' 'Caesar,' 'Savalan,' and 'Agria' as parents for the genetic crossings. From each stem, two flowers were selected for crossing and all other flowers were removed. The experimental design followed a diallel cross using the Griffing III method (Griffing, 1956; Pooni et al., 1984). The crosses were performed early in the morning or after the sunset when the air temperature was low. The true potato seed (TPS) produced from similar crosses were harvested together and were evaluated in 2017.

Out of 279 crosses between 'Agria,' 'Satina,' 'Caesar,' and 'Savalan' cultivars, 157 berries were harvested and 7,980 TPS were obtained from 12 breeding populations during 2016. Produced seeds included 1,322 seeds from cross-breeding ♀'Agria' × 'Satina'♂ (16.57%); 485 seeds from cross-breeding ♀'Agria' × 'Caesar'♂ (6.08%); 2,163 seeds from cross-breeding ♀'Agria' × 'Savalan'♂ (27.11%); 1,495 seeds from cross-breeding ♀'Satina' × 'Agria'♂ (18.73%); 1,224 seeds from cross-breeding ♀'Satina' × 'Caesar'♂ (15.34%); 175 seeds from cross-breeding ♀'Satina' × 'Savalan'♂ (2.19%); 106 seeds from cross-breeding ♀'Satina' × 'Caesar'♂ (1.33%); 75 seeds from cross-breeding ♂'Satina' × 'Caesar'♀ (0.94%); 101 seeds from cross-breeding ♂'Savalan' × 'Caesar'♀ (1.27%); 212 seeds from cross-breeding ♀'Savalan' × 'Satina'♂ (2.66%); 312 seeds from cross-breeding ♀'Savalan' × 'Agria'♂ (3.91%), and 101 seeds from cross-breeding ♀'Savalan' × 'Caesar'♂ (3.88%).

2.2. Evaluation of Clones in the Greenhouse (2017)

Breeding populations produced from the crosses were cultivated in plastic pots (10 × 10 cm) containing peat-moss and mineral pumice in a 1:1 volume ratio. During plant growth, irrigation and weeding were conducted on a regular basis. For pest control, Confidor poison (250 mL per 400 L water per ha) was used. For the control of fungal diseases, Mancozeb fungicide (1 g per 10 m^2) was used. After harvesting, clones were evaluated for tuber number and weight per plant, eye depth, skin color, and tuber shape.

2.3. Evaluation of Clones in the Field Under Water Deficit Stress Conditions (2018)

The selected clones were cultured in a split-plot using randomized complete block design in triplicate. The main factor consisted of three levels of irrigation (100%, 80%, and 60% of field capacity) and a secondary factor of 12 populations (♀'Agria' × 'Satina'♂, ♀'Agria' × 'Caesar'♂, ♀'Agria' × 'Savalan'♂, ♀'Satina' × 'Agria'♂, ♀'Satina' × 'Caesar'♂, ♀'Satina' × 'Savalan'♂, ♀'Caesar' × 'Satina'♂, ♀'Caesar' × 'Agria'♂, ♀'Caesar' × 'Savalan'♂, ♀'Savalan' × 'Satina'♂, ♀'Savalan' × 'Agria'♂, and ♀'Savalan'

× 'Caesar'♂). The rows were spaced 75 cm apart and the distance between the tubers was roughly 25 cm. The amount of water irrigation was determined at each stage of potato growth based on field capacity (FC), permanent wilting point (PWP), bulk density (Bd.D), available water (AW), and readily available water (RAW) (Rasoulzadeh & Raof, 2013). The soil moisture content was 21.147% at irrigation start time. The soil moisture content during the growth stages was determined using a portable soil moisture meter (model PMS-714, Taiwan). The amount of water consumed at different stages of potato growth is shown in Table 1.

Table 1 Water consumed in different stages of potato growth provided by tape irrigation under normal conditions.

Stages of potato growth	Irrigation number	Water consumed amount (m^3 per ha)	Effective rain amount (m^3 per ha)	Applied water volume* (m^3 per ha)
Planting stage	1	159.06	102	261.06
Planting till tuberization	3	477.18	339	816.18
Tuberization till tuber maturity	9	6,435.0	121	6,556.0
Total	13	7,071.24	562	7,633.24

* Applied water volume = Water consumed amount + Effective rain amount.
The 100%, 80%, and 60% available water were 7,633.24, 6,106.59, and 4,579.94 m^3 per hectare, respectively.

After calculating the water requirement for irrigation at 100%, the values were determined for 80% and 60% irrigation, respectively. Analysis of variance was performed after confirmation of the normality of the data obtained from trait measurements. Mean comparisons of measured traits were done using a least significant difference (LSD) test at a 5% probability level. Statistical computation and table construction used SAS 9.1 and Excel software. The SAS ver. 9.1 statistical software with the SAS-Griffing-Method3 program was used to estimate the effects of general and specific combining abilities and genetic components of the clones. The effects of the general combining ability (GCA) and specific combining ability (SCA) (Moghadam & Amiri-Oghan, 2010), standard errors for the effects of general and specific combining (Kempthorne, 1957; Vasal et al., 1992), the variance of general and specific combinations in potato (Bradshaw, 2006; Thompson & Mendoza, 1984), degree of dominance (Dick et al., 1988), and general and specific inheritance (Teklewold & Becker, 2005) were estimated.

3. Results

In this experiment, 279 crosses between 'Agria,' 'Satina,' 'Caesar,' and 'Savalan' cultivars were conducted to produce 7,980 true potato seeds from 12 breeding populations in 2016. From 2,313 seeds, we selected 244 hybrids, which had a mean tuber weight per plant of approximately 975.5 g and 7.5 tubers per plant. The results of the analysis of variance showed different levels of water deficit stress significantly affected the genotypes and their interactions with respect to tuber number and weight per plant, tuber yield, main stem number per plant, main stem diameter, and stolon length at a probability of 1% and the trait tuber dry matter percent between genotypes at a 1% probability level (Table 2).

The highest tuber yields were observed in normal growth conditions (100% available water), in clones related to crosses of ♀'Satina' × 'Agria'♂, ♀'Agria' × 'Caesar'♂, ♀'Agria' × 'Savalan'♂, ♀'Satina' × 'Agria'♂, ♀'Caesar' × 'Agria'♂, ♀'Caesar' × 'Savalan'♂, ♀'Savalan' × 'Satina'♂, ♀'Savalan' × 'Agria'♂, and ♀'Savalan' × 'Caesar'♂. In mild stress conditions, (80% of available water) clones related to ♀'Agria' × 'Caesar'♂ and ♀'Caesar' × 'Savalan'♂ produced the highest tuber yields, and in severe stress conditions (60% available water), clones related to ♀'Agria' × 'Caesar'♂ produced the most tubers compared to the other clones tested. The highest tuber yield was reported in a clones of ♀'Agria' × 'Caesar'♂ and ♀'Caesar' × 'Savalan'♂ under normal, mild, and severe stress conditions.

The results of analysis of variance showed that the environmental condition, genotype, and their interactions had a significant effect on tuber yield at a 1% probability level. This result indicates the presence of sufficient genetic diversity

Table 2 Results from the variance analysis of the studied traits in the potato genotypes grown under water deficit stress.

Sources of variation	*Df*	*MS* Tuber number per plant	Tuber weight per plant	Tuber yield	Main stem number per plant	Main stem diameter	Dry matter percent	Stolon length
Replication	2	0.18 ns	44.4444 ns	12.48 ns	1.00 ns	1.56 ns	1.07 ns	1.00 ns
Water deficit stress (A)	2	10.63**	1,283,416.08**	3,604.33**	16.00**	100.77**	3.034 ns	4.088**
Error 1	6	2.031	4,444.44	12.48	1.00	0.86	1.067	1.00
Genotypes (B)	11	3.113**	83,877.72**	235.55**	2.909**	13.24**	9.994**	12.28**
A × B	22	1.15**	19,796.26**	55.59**	1.18**	6.99**	0.571 ns	2.82**
Error 2	66	0.5054	9,141.41	25.67	0.454	0.868	1.068	0.696
CV	-	13.27	12.62	12.60	18.38	9.48	5.009	9.98

Note: ns and ** indicate nonsignificant and significant differences at a 1% probability level, respectively.

Table 3 Analysis variance of general and specific combining ability of potato tuber yield in genotypes under three environmental conditions.

Sources of variation	*Df*	*MS* Normal condition (100% available water)	Mild stress condition (80% available water)	Severe stress condition (60% available water)
GCA	3	82.40**	61.41**	33.68*
SCA	4	18.14*	18.05*	27.84*
REC	6	25.26*	28.95**	49.82**
E	66	8.559	8.559	8.559

Significant differences at a 5% (*) and 1% (**) probability level.

in tuber yield between the crosses. The results of the variance analysis of general combining ability (GAC) and specific combining ability (SAC), and the reverse effects of tuber yield showed that in all three environmental conditions there was a significant difference at a probability level of 5% and 1% (Table 3).

Significant differences between clones indicated that there was also a significant difference between the general combining ability of the clones and the role of gene additive effects. The most significantly positive GCA effects were for tuber yield under normal growth conditions in 'Agria' and 'Savalan' cultivars, while under mild and severe stress conditions, these effects were most significantly positive in 'Agria' and 'Caesar' cultivars (Table 4). Therefore, these cultivars can easily transfer this trait to their offspring and increase the presence of this trait in future generations. The significance of the general combining ability effect indicates a role for additive effects in the control of trait expression.

According to the estimated GCA effects among the cultivars, the highest positive GCA for tuber yield was observed in 'Agria' and 'Caesar' cultivars under mild and severe water stress conditions and the lowest in 'Satina' and 'Savalan' cultivars (Table 4). In this study, two parents included 'Agria' and 'Caesar' cultivars with positive and significant GCA and two parents included 'Satina' and 'Savalan' cultivars with negative and significant GCA were.

In normal growth conditions, the highest SCA in the direct crosses for tuber yield was significantly positive in compounds of ♀'Agria' × 'Caesar'♂ and significantly negative in compounds of ♀'Agria' × 'Savalan'♂. In the reverse crosses, the SCA was significantly positive in compounds of ♀'Satina' × 'Caesar'♂ and ♀'Satina' × 'Savalan'♂ (Table 4).

In mild stress growth conditions, the highest SCA in the direct cross for tuber yield was in compounds of ♀'Agria' × 'Caesar'♂ in the positive direction and ♀'Agria' × 'Savalan'♂ in the negative direction. In the reverse cross, compounds of ♀'Caesar' × 'Agria'♂ in the negative direction and ♀'Savalan' × 'Caesar'♂ in the positive direction had the highest SCA for tuber yield (Table 4).

Table 4 Estimation of general combining ability (GCA), specific combine ability (SCA), and inverse (REC) potato tuber yield in normal, mild, and severe water stress conditions.

♀		♂ 'Agria'	'Satina'	'Caeser'	'Savalan'
GCA					
'Agria'	Normal	5.562**			
	Mild stress	2.0875**			
	Severe stress	2.838**			
'Satina'	Normal		−5.24**		
	Mild stress		−5.7875**		
	Severe stress		−5.213**		
'Caeser'	Normal			−1.463**	
	Mild stress			4.8125**	
	Severe stress			4.463**	
'Savalan'	Normal				1.1375**
	Mild stress				−1.1125**
	Severe stress				−2.08**
SCA					
'Agria'	Normal		2.28	74.53**	−200.41**
	Mild stress		−0.158	65.217**	−166.567**
	Severe stress		0.000	44.48**	−5.78**
'Satina'	Normal			−1.542	3.283
	Mild stress			−0.583	−0.158
	Severe stress			−3.33	−2.20
'Caeser'	Normal				2.283
	Mild stress				−0.158
	Severe stress				0.00
'Savalan'	Normal				
	Mild stress				
	Severe stress				
REC					
'Agria'	Normal				
	Mild stress				
	Severe stress				
'Satina'	Normal	−2.30			
	Mild stress	−2.350			
	Severe stress	0.150			
'Caeser'	Normal	−2.85	3.55*		
	Mild stress	−5.450**	1.550		
	Severe stress	2.650	−2.750		
'Savalan'	Normal	−0.05	6.75**	−2.050	
	Mild stress	2.000	4.650**	−5.050**	
	Severe stress	4.950**	1.250	−0.700	

Standard error (*SE*) (GCA) = 0.317; critical difference (*CD*) = *SE* × *t*0.05 = 0.808; *CD* = *SE* × *t*0.01 = 0.994.
SE (SCA)= 1.423; *CD* = *SE* × *t*0.05 = 3.730; *CD* = *SE* × *t*0.01 = 4.593.
SE (REC)= 1.267; *CD* = *SE* × *t*0.05 = 3.231; *CD* = *SE* × *t*0.01 = 3.978.
Significant differences at a 5% (*) and 1% (**) probability level.

In severe water stress conditions, the highest SCA observed in the direct cross for tuber yield was in compounds of ♀'Agria' × 'Caesar'♂ in the positive direction and ♀'Agria' × 'Savalan'♀ in the negative direction; while in the reverse cross, compounds of ♀'Savalan' × 'Agria'♂ in the positive direction had the highest SCA (Table 4). These crosses can, therefore, be used to produce hybrids with increased tuber yield under drought stress. In this study, the 'Agria' and 'Caesar' cultivars had a good composition for tuber yield that resulted in Additive × Additive and Additive × Dominance interactions when used as parents.

The direct cross of ♀'Agria' × 'Caesar'♂ had the highest tuber yield. Among the studied genotypes, when 'Agria' and 'Caesar' cultivars were grown under mild and severe stress conditions, they had a significantly positive general combining ability for tuber yield, indicating that they are suitable parents for breeding programs. Indeed, the use of cultivars with significantly positive specific combining for tuber yield is emphasized. For example, crossing 'Agria' and 'Caesar' cultivars with 'Satina' and 'Savalan' cultivars had a significantly positive specific combining ability. Therefore, selection among the offspring resulting from these crosses, in addition to increased additive effects of genes, also increased the genetic efficiency of the selection (Table 4).

In Table 5, the general and specific heritability values are presented. The general heredity of tuber yield in 100%, 80%, and 60% available water was 93.88%, 93.32%, and 87.07%, respectively (Table 5). The specific heredity of tuber yield in 100%, 80%, and 60% available water was 71.94%, 80.16%, and 64.36%, respectively (Table 5). The dominance degree for tuber yield in these growth conditions was positive (Table 5). The positive sign indicates incomplete dominance in order to increase the relevant trait. The ratio of the variance of general combining ability to the variance of the specific combining ability for tuber yield in in 100%, 80%, and 60% available water was estimated to be more than one (Table 5).

Table 5 Genetic components of tuber yield in genotypes grown under three environmental stress conditions.

Combining ability*	In 100% available water	In 80% available water	In 60% available water
GCA	59.66579	43.92079	23.12579
SCA	12.00117	31.82117	11.40117
REC	71.50283	82.58283	145.1828
GCA/SCA	4.971666	1.380238	2.028371
$\delta^2 a = 2\delta^2 g$	119.3316	87.84158	46.25158
$\delta^2 d = \delta^2 s$	12.00117	31.82117	11.40117
$\delta^2 g/\delta^2 s$	9.943332	2.760477	4.056741
Degree of dominance	0.317	0.601	0.496
General heritability	93.88	93.32	87.07
Specific heritability	71.94	80.16	64.36

* $\delta^2 a$ – dditive variance; $\delta^2 g$ – variance of general combining ability; $\delta^2 d$ – dominance variance; $\delta^2 s$ – variance of the specific combining ability.

4. Discussion

The importance of specific combining ability effects is the presence of a nonadditive effect on the control of traits. Both general and specific combining ability effects are important in controlling traits and additive and nonadditive effects. Therefore, in these cultivars, the frequency of genes with additive effects was high, which indicated that they can be used for breeding programs based on their selection (Ahmad et al., 2009). When the general combining ability (GCA) was negative for tuber yield in 'Satina' and 'Savalan' cultivars in mild and severe stress conditions, they could not efficiently transfer this trait to offspring. The cultivars that have a significant GCA for specific traits could easily transfer the desired traits to their offspring; in other words, these are suitable cultivars for breeding programs for the desired traits (Fathi et al., 2007). Therefore, depending on the direction and purpose of the breeding program, the parents could be selected (Dehghanpour, 2013). Finally, based on our results, 'Agria' and 'Caesar' cultivars are the best combination for improving tuber yield in mild and severe water stress conditions, indicating that these parents may be used to improve different cross-combinations. Accordingly, 'Agria' and 'Caesar' varieties with a positive GCA and an ability to transfer the improved tuber yield trait to future generations can participate as one of the parents in breeding programs for tuber yield optimization. However, 'Satina' and

'Savalan' cultivars had negative GCA for tuber yield and should not be considered for breeding programs aimed to improve tuber yields. Given that GCA is based on additive gene effects, lines that have a relatively high GCA will also have high additive gene effects and can be used to produce synthetic varieties of potatoes (Sharma & Madhu, 2013). These results are consistent with reports by Sharma & Madhu (2013) and Gopal (1996). Rowel et al. (1986) showed that for the production of hybrid plants with high SCA, parents with high GCA are not needed, but parental composition with low GCA usually produce hybrids with better SCA. Akhtar and Chowdhry (2006) reported that combining ability and gene effects have importance roles in breeding of genetic materials. Selection of a breeding method that exploits the genetic potential of different crop characteristics of a plant depends on the type of genes controlling a trait and their inheritance. The estimation of general and specific combining ability helps breeders determine what the breeding program and genotype selection strategies they use (de la Vega & Chapman, 2006). Rather et al. (2007) conducted growth experiments in more than two environments and reported that variance due to the general and specific combining abilities indicates an importance for additive and nonadditive effects of inherited genes in all studied traits. Sanford (1960). further concluded that specific combining ability was relatively more important than the general combining ability for tuber yield. However, Mohammed (2009) reported that the effects of general combining ability are more important than those of specific combining ability in the grain yield traits in sorghum. The specific combining ability expresses the nonadditive contribution of genetic variance (Hosana et al., 2015), and the ratio of GCA to SCA + GCA can be used as a criterion for determining the importance of additive genetic effects (Baker, 1978). If this ratio is close to one, it indicates the importance of additive effects in determining a trait (Fan et al., 2008).

The general heritability of the tuber yield in all three water stress environments ranged from 83% to 94%. Estimation of general heritability of traits indicates more of a role for genetic effects in controlling these traits and suggests that the additive effect of genes is approximately equal to the nonadditive effect on genetic control of all traits studied (Golparvar et al., 2004). The specific heritability of tuber yield in all three environments ranged from 64% to 80%. The low specific heritability is shown in the genetic control of the studied traits, while the role of nonadditive effects of genes (i.e., dominance and epistemic) had more of an impact than the additive effect of the genes. Yield is a quantitative trait that is controlled by a number of genes and therefore, selection based on yield is not useful for its improvement (Richards, 1996). Morphological and phenological traits can be easily and precisely measured and have relatively high heritability, so selection based on these traits is a consistent and fast way to improve tuber yield (Yap & Harvey, 1972). If the degree of dominance is more than one, it indicates the action of the genes controlling this trait is super dominant or false dominant (Sharifi et al., 2010).

5. Conclusion

In this study, we produced 279 crosses between 'Agria,' 'Satina,' 'Caesar,' and 'Savalan' cultivars and collected 7,980 true potato seeds from 12 breeding populations. Of these, 2,313 seeds were used to select 244 hybrids. The selected clones had a mean tuber weight per plant of about 975.5 g and 7.5 tubers per plant. In all three environmental conditions, the hybrids that produced the highest tuber yield and tuber weight per plant were related to ♀'Agria' × 'Caesar'♂. The most significantly positive general combining ability for tuber yield in mild and severe water stress conditions were the 'Agria' and 'Caesar' cultivars. Therefore, these cultivars can easily transfer this trait to offspring and increase this trait within the crop population. The specific combining ability for tuber yield in normal, mild and severe stress conditions were significantly positive in the direct cross for the compounds of ♀'Agria' × 'Caesar'♂, and in the reverse cross for the compounds of ♀'Satina' × 'Caesar'♂, and ♀'Satina' × 'Savalan'♂ in under normal conditions. Under mild stress conditions, compounds of ♀'Savalan' × 'Caesar'♂ had significantly positive specific combining ability, while in severe stress conditions, the compounds of ♀'Savalan' × 'Agria'♂ in the positive direction had the highest tuber yield. These crosses are suitable for producing clones with high tuber yield and drought stress tolerance.

Acknowledgments

The study was conducted in the laboratories and greenhouses of Zare-Ghostare-Arta Company. We thank the technical assistance of Eng. Mohsen Abed and Hosein Hassanpanah.

References

Ahmad, S., Quamruzzaman, A. K. M., & Uddin, M. N. (2009). Combining ability estimates of tomato (*Solanum lycopersicum*) in late summer. *SAARC Journal of Agriculture*, *7*(1), 43–56.

Akhtar, N., & Chowdhry, M. A. (2006). Genetic analysis of yield and some other quantitive traits inbread wheat. *International Journal of Agriculture and Biology*, *4*, 523–527. https://doi.org/10.1007/BF02853538

Ayas, S., & Korukçu, A. (2010). Water yield relationships in deficit irrigated potato. *Journal of Agriculture Faculty of Uludag University*, *224*, 23–36.

Baker, R. J. (1978). Issues in diallel analysis. *Crop Science*, *18*, 533–536. https://doi.org/10.2135/cropsci1978.0011183X001800040001x

Bradshaw, J. E. (2006). Genetics of agrihorticultural traits. In J. Gopal & S. M. P. Khurana (Eds.), *Handbook of potato production, improvement and postharvest management* (pp. 41–75). The Haworth Press.

Coleman, W. K. (2008). Evaluation of wild *Solanum* species for drought resistance 1. *Solanum gandarillasii* Cardenas. *Environmental and Experimental Botany*, *62*, 221–230. https://doi.org/10.1016/j.envexpbot.2007.08.007

Dehghanpour, Z. (2013). Diallel analysis of grain yield, number of kernel rows per ear and number of kernels per row in early maturity maize hybrids. *Iranian Journal of Crop Sciences*, *15*(4), 355–366.

de la Vega, A., & Chapman, S. C. (2006). Multivariate analyses to display interactions between environment and general or specific combining ability in hybrid crops. *Crop Science*, *46*, 957–967. https://doi.org/10.2135/cropsci2005.08-0287

Deshi, K. E., Obasi, M. O., Odiaka, N. I., Kalu, B. A., & Ifenkwe, O. P. (2015). Leaf area index values of potato *Solanum tuberosum* L. stored for different periods in different kinds of stores. *IOSR Journal of Agriculture and Veterinary Science*, *81*, 9–19.

Dick, J. A., Shattuck, V. I., & Christie, B. R. (1988). *The diallel cross, its analysis and interpretation*. University of Guelph, Office for Educational Practice.

Fan, X. M., Chen, H. M., Tan, J., Xu, C. X., Zhang, Y. M., Huang, Y. X., & Kang, M. S. (2008). A new maize heterotic pattern between temperate and tropical germplasms. *Agronomy Journal*, *100*, 917–923. https://doi.org/10.2134/agronj2007.0298

Fathi, M. R., Mesbah, M., Ranji, Z., Vazan, S., & Farokhi, A. (2007). Evaluation of general and specific combining ability of sugar beet diploid pollinators. *Journal of Sugar Beet*, *23*(2), 151–162.

Golparvar, A. R., Darvishi, F., Rezaei, A., & Balouti, A. G. P. (2004). Genetic assessment of some morpho-physiological traits in bread wheat under drought stress conditions. *Pajouhesh va Sazandegi*, *62*, 90–95.

Gopal, J. (1996). *In vitro selection, genetic, divergence and cross prediction in potato* [Unpublished doctoral dissertation]. Punjab Agricultural University.

Griffing, B. (1956). Concept of general and specific combining ability in relation to diallel crossing systems. *Australian Journal of Biological Sciences*, *9*(4), 463–493. https://doi.org/10.1071/BI9560463

Hassanpanah, D., Hassanabadi, H., Hoseinzadeh, A. A., Soheli, B., & Mohammadi, R. (2016). Factor analysis, AMMI stability value (ASV) parameter and GGE BI-plot graphical method of quantitative and qualitative traits in potato genotypes. *Journal of Crop Ecophysiology*, *10*(3), 731–748.

Hosana, G. C., Alamerew, S., & Tadesse, B. (2015). Test cross performance and combining ability of maize (*Zea mays* L.) inbred lines at Bako, Western Ethiopia. *Global Journal of Science Frontier Research*, *15*(4), 1–24.

Jansky, J. (2006). Overcoming hybridization barriers in potato. *Plant Breeding*, *125*, 1–12. https://doi.org/10.1111/j.1439-0523.2006.01178.x

Kempthorne, O. (1957). *An introduction to genetic statistics*. John Wiley and Sons.

Landjeva, S., Neumann, K., Lohwasser, U., & Börner, A. (2008). Molecular mapping of genomic regions associated with wheat seedling growth under osmotic stress. *Biologia Plantarum*, *52*, 259–266. https://doi.org/10.1007/s10535-008-0056-x

Moghadam, M., & Amiri-Oghan, H. (2010). *Biometric methods in quantitative genetic analysis*. Parivar.

Mohammed, M. I. (2009). Line × tester analysis across locations and years in Sudanese × exotic lines of forage sorghum. *Journal Plant Breeding and Crop Science*, *1*(9), 311–319.

Nouri, A. R., Nezami, A., Kafo, M., & Hassanpanah, D. (2016). Evaluation of water deficit tolerance of 10 potato cultivars (*Solanum tuberosum* L.) based on some physiological traits and tuber yield in Ardabil region. *Journal of Crop Ecophysiology*, *10-1(37*, 243–268.

Pooni, H. S., Jinks, J. L., & Singh, R. K. (1984). Methods of analysis and the estimation of the genetic parameters from a diallel set of crosses. *Heredity*, *52*(2), 243–253. https://doi.org/10.1038/hdy.1984.26

Rasoulzadeh, A., & Raof, M. (2013). *Principles and methods of irrigation*. Amidi.

Rather, A. G., Najeeb, S., Sheikh, F. A., Shikari, A. B., & Dar, Z. A. (2007). Combining ability analysis in maize (*Zea mays* L.) under high altitude temperate conditions of Kashmir. *The Maize Genetics Cooperation Newsletter*, *81*, 202–216.

Richards, R. A. (1996). Defining selection criteria to improve yield under drought. *Plant Growth Regulation*, *20*, 157–166. https://doi.org/10.1007/BF00024012

Roodbali, M. H., Abdolshahi, R., Baghizadeh, A., & Ghaderi, M. (2016). Genetic analysis of yield and yield related traits in bread wheat *Triticum aestivum* L. under drought stress condition. *Journal of Crop Breeding*, *18*, 1–6. https://doi.org/10.29252/jcb.8.18.1

Rowel, A. B., Ewing, E. E., & Plaisted, R. L. (1986). General combining ability of neotuberosum for potato production from true seed. *American Potato Journal*, *63*, 141–153. https://doi.org/10.1007/BF02853538

Sadeghi, F. (2014). Estimation of genetic structure of yield and yield components in bread wheat *Triticum aestivum* L. using diallel method. *Journal of Crop Breeding*, *13*, 101–113.

Sanford, L. L. (1960). *Comparative evaluation of clones as testers for yield, specific gravity and tuber appearance in the Potato* [Doctoral dissertation, Iowa State University]. https://doi.org/10.31274/rtd-180813-721

Sharifi, P., Dehghani, H., Momeni, A., & Moghadam, M. (2010). Diallel analysis for heterosis study and estimation of genetic parameters for some morphological traits in rice. *Seed and Plant Improvment Journal*, *26-1(1*, 77–104.

Sharma, M., & Madhu, B. (2013). Gene action and heterosis studies involving gynoecious lines in cucumber. *Indian Journal Genetics and Plant Breeding*, *792*, 131–136.

Teklewold, A., & Becker, H. C. (2005). Heterosis and combining ability in a diallel cross of Ethiopian mustard inbred lines. *Crop Science*, *45*, 2629–2635. https://doi.org/10.2135/cropsci2005.0085

Thompson, P. G., & Mendoza, H. A. (1984). Genetic variance estimates in a heterogeneous potato population propagated from true seed TPS. *American Journal of Potato Research*, *61*, 697–702. https://doi.org/10.1007/BF02852933

Vasal, S. K., Srinivasan, G., Pandey, S., Cordova, H., Han, C. C., & F, G. (1992). Heterotic pattern of ninety two white tropical CIMMYT maize lines. *Maydica*, *37*, 259–270.

Yap, T. C., & Harvey, B. L. (1972). Inheritance of yield components and morpho-physiological traits in barley. *Crop Science*, *12*, 283–286. https://doi.org/10.2135/cropsci1972.0011183X001200030008x