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Combining ability analysis of earliness and yield of potato (*Solanum tuberosum* L.) genotypes in Uganda

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Abstract Potato (*Solanum tuberosum* L.) is a major food and cash crop mainly grown by small-scale farmers in the highland regions of Uganda. Changing global weather patterns require varieties that are able to grow within the short rainfall cycles and yield optimally under the prevailing conditions. The objectives of this study were to estimate the combining ability effects for early maturity, yield and yield related traits in potato. Eighteen F^1 families generated from two sets of 12 parents using a North Carolina Design II were evaluated for days to 50% flowering, leaf senescence, yield and yield related traits in two different locations. Both additive and non-additive genetic effects influenced the expression of traits. However, additive genetic effects were predominant over the non-additive for most of the traits. The GCA/SCA ratios were 0.68 and 0.78 for days to 50% flowering and average tuber weight. Broad sense heritability estimates were 0.70 for total tuber weight and 0.78 for days to 50% flowering. The predominance of additive genetic effects imply that, genetic gains can be achieved through different selection methods and traits transferred to the respective progenies. Parents Rwangume, 396,038.107, 395,011.2, NKRK19.17, 393,077.54, Kimuri, and 392,657.8 had desirable GCA effects for the number of days to flowering and yield related traits. Families of Rwangume × NKRK19.17, 393,077.54 × 395,011.2, 396,038.107 × Rwangume and 396,038.107 × 395,011.2 had desirable SCA effects for yield and number of days to 50% flowering. The selected parents and families will be subjected to further clonal evaluation and selection.

Keywords Combining ability · Earliness · Gene action · Heritability · Maturity · *Solanum tuberosum*

Introduction

Potato (*Solanum tuberosum* L.) is a major food and cash crop, mainly grown by small-scale farmers in the highland regions of many African countries. Uganda is the ninth largest producer of potato in Africa with an annual production of 188,000 tons harvested from about 39,000 ha per year (FAOSTAT 2016). Potato yields in Uganda have remained low about 4.8 t ha^{-1} (FAOSTAT 2016) against a potential of about 25 t ha^{-1} which can be achieved under good

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management and when suitable varieties are deployed. These low yields have been attributed to a number of confounding factors that are biotic, abiotic, and socio-economic constraints, as well as poorly adapted and adopted varieties. The most preferred attributes by most potato farmers in Uganda were identified as high yields followed by marketability, resistance to blight and early maturity (Namugga et al. 2017a, b).

Crop maturity is an agronomic trait where crops undergo progressive growth stages from emergence to senescence, characterized by their reproductive capacity and phenology (Khan et al. 2013). Potato maturity is normally assessed by monitoring vine characteristics and change in colour of the potato plant leaves is an indicator of crop maturity (Haga et al. 2012; Iragaba 2013). Potato varieties are classified into maturity types based on the lengths of the season required to produce a harvestable product (Haga et al. 2012; Khan et al. 2013). Variability among varieties for the number of days from planting to maturity has led to designation of the potato varieties as early, medium, late and very late maturity classes (Ruzukas et al. 2009). Breeders normally evaluate maturity period while developing new varieties because it is a critical aspect in commercial potato production. Standard maturity measurements in potato are lacking because tubers are produced underground and monitoring their development presents many challenges. As a result, breeders commonly assess potato maturity classes based on physiological changes in the potato vine. Tuber production is associated with changes at the whole plant level, such as reduction in leaf development, flowering, fruit set and change of foliar colour (Haga et al. 2012).

In potato, both the general combining ability (GCA) effects of parents and specific combining ability (SCA) effects of their progeny are important in determining economic traits. This is due to the fact all genetic effects are fixed at the F^1 generation through the development of clones without further segregation (Muthoni et al. 2012). Earliness in potato has not received sufficient attention in Uganda and elsewhere as there seems to be limited information regarding the subject. However, some findings suggest that both additive and non-additive genetic effects control earliness in potato, though additive genetic effects were found to be more important (Iragaba 2013). However, detailed information regarding inheritance of this trait and combining ability of parents is still limited. This is accompanied by the growing need for early maturing and high yielding varieties to counteract the effects of changing weather patterns. Earliness is a quantitative trait that is affected by genetic and physiological factors of a plant besides environmental conditions (Basbag et al. 2007). Earliness is reported to contribute to disease escape especially to infection pressures that appear late in the season. Earliness is also beneficial in areas with multiple cropping systems, limited land or short favourable growing seasons. In Uganda, potato is a smallholder farmer crop so early maturing varieties would allow favourable rotation patterns and contribute greatly to food security. This study was undertaken to determine the combining ability effects for early maturity, yield and yield related traits in potato in order to develop potato clones that are early maturing with high yield potential.

Materials and methods

Parental materials and crosses

Twelve genetically diverse clones were selected and used as parents. Six clones were obtained from the National Potato Program of Uganda and four were advanced clones from the International Potato Centre (CIP) belonging to population B3C2 with variable resistance to late blight. These materials were selected based on their flowering abilities, number of days to flowering, flowering duration and medium to high yields (Namugga et al. 2017a, b). Parents were assembled into two sets of six parents each based on their flowering abilities, yield and resistance to late blight. Crosses were made using a North Carolina Design II (NCD II) to generate 18 families (Table 1). In the first set three female clones (Rwangume, 396,026.103 and 396,038.107) were crossed with three males (Kimuri, 391,046.14 and NKRK19.17). In the second set, three female parents; 392,657.8, 393,220.54 and 396,038.107 were crossed with three males; NKRN59.48, Rwangume and 395,011.2. Parents Rwangume and 396,038.107 were used in both sets. Controlled hand pollination was performed at flowering following emasculation (Acquaah 2007). At maturity, berries of the same cross were harvested and bulked. In total, 18 families were generated (two sets of nine families each).

Table 1 Description of potato parents used in the crossing block. *Source*: Namugga et al. (2017a, b)

Set	Parent	Parent type	Yield (t ha^{-1})	Days to flowering
1	Rwangume	Female	25.2	59
1	396,026.103	Female	33.1	54
1	396,038.107	Female	42.8	61
1	Kimuri	Male	17.1	52
1	391,046.14	Male	34.6	52
1	NKRK19.17	Male	37.0	61
2	392,657.8	Female	43.7	55
2	393,077.54	Female	43.2	59
2	396,038.107	Female	42.8	61
2	Rwangume	Male	25.2	59
2	395,011.2	Male	25.5	54
2	NKRN59.48	Male	30.0	61

Planting sites

The field trials were established at Kachwekano research station and on a farm in Nyabumba. Both sites are located in South-western Uganda; Kachwekano is located in, 01°16′S 29°57′E at 2200 meters above sea level while Nyabumba at 2230 meters above sea level. Both sites have a bi-modal rainfall pattern separated by a dry spell ranging from 30 to 60 days. Planting was done in March and harvesting in July 2017.

Experimental design and trial establishment

Experiments were established during the planting season between March and June 2017 using a 7 × 4 alpha lattice design with two replications at both locations. Parents Rwangume and 396,038.107 were used in both set. The 18 F^1 families were planted in two row plots of 20 tubers each at 75 cm between rows and 30 cm between plants. Planting was done by hand and N:P:K: 17:17:17% fertilizer was applied at 100 kg ha^{-1}. Pest and disease control was done using recommended insecticides and fungicides. Crop hand weeding and ridging were carried out as recommended.

Data collection

Data were collected on days to flowering and leaf senescence. Days to flowering was recorded as number of days from planting to 50% flowering of all the plants in a plot. Leaf senescence was measured as the number of days from flowering to 100% of the leaves dying off. At harvest, yield related data was taken in a plot for, total weight of all the tubers harvested in a plot (TTW) and expressed in t ha^{-1}. Average tuber weight (ATW) was calculated as the total tuber weight per plant divided by the total tuber number of tubers per plant.

Data analyses

Analysis of variance

Data for the different traits over two sets and across environments were subjected to the standard analysis of variance using the using general linear model (GLM) procedure of SAS 9.3 (SAS 2011) statistical program. Analyses of variance of NCD II pooled over sets and across environments (Hallauer and Miranda 1988) were conducted for all the traits. Main effects due to female and male effects within sets are independent estimates of GCA while male × female interaction effects represent SCA variance within sets. Spearman correlation coefficients were calculated for the studied traits to determine their association.

Estimation of general and specific combining ability effects

Data were analysed over sets and across environment. Parents were considered as fixed effects in the test of significance. The GCA and SCA values for each trait were calculated following the NCII mating design across sites (Hallauer et al. 1988). General and specific combining abilities (GCA and SCA respectively) for the parents and progenies were determined; and their significance tested (Singh and Chaudhary 1979). The relative importance of GCA and SCA in influencing the performance of the crosses were estimated using the general predicted ratio (GPR) for all the traits (Baker 1978).

Estimating heritability

Heritability estimates were calculated using the female additive variance for both narrow and broad sense heritability (Dabholkar 1999) as follows: narrow sense heritability; $h_f^2 = 4\sigma_f^2/(\sigma_e^2/r + 4\sigma_{mf}^2 + 4\sigma_f^2) = V_{Af}/V_P$; broad sense heritability; $h_f^2 = 4\sigma_f^2 + 4\sigma_{mf}^2/(\sigma_e^2/r + 4\sigma_{mf}^2 + 4\sigma_f^2) = V_{Gf}/V_P$. Where r = number of replication; σ_e^2 = environmental variance = MS_e; σ_f^2 = variance of female parents = GCA_f variance = MS_f; σ_{fm}^2 = variance due to interaction between females and males = SCA variance = MS_{mf}; V_{Af} = additive genetic variance due to female parents; V_P = phenotypic variance; V_{Gf} = total genetic variance.

Results

Analysis of variance for crosses across sites

The combined analysis of variance and ratio of GCA/SCA for days to flowering (DAF), leaf senescence (LS), total tuber weight (TTW) per hectare and average tuber weight (ATW) per hectare among the families is presented in Table 2. Significant differences within sets observed for ATW ($P \leq 0.05$). The environmental effect was highly significant ($P \leq 0.001$) for all the traits except for number of days to 50% flowering. The GCA mean squares for females (GCA_f) were significantly different for DAF, and TTW at $P \leq 0.001$, and $P \leq 0.05$, respectively. The GCA mean square for males (GCA_m) were significantly different for DAF ($P \leq 0.001$) and TTW ($P \leq 0.05$). The SCA effects for the crosses were significant for all the tested traits except ATW. The environmental interactions with families were only significant for TTW. The GCA_f effects were higher than male GCA effects for LS, TTW and ATW, while the additive male effects were slightly more for DAF. Overall, the GCA was more important than the SCA in the expression of all the traits (Table 2). The additive/non-additive genetic effects using Baker's ratio was highest for ATW (0.78) and lowest for LS (0.41).

Heritability estimates

The broad sense heritability values were highest for DAF (0.78) and lowest for ATW (0.39) (Table 3). The narrow sense heritability estimates were highest for DAF (0.40) and the lowest for LS (0.09).

General combining ability effects of parents

Significant GCA effects were observed among all the parents for ATW (Table 4). Female parents 392,657.8 and 396,038.107 had significant GCA effects for DAF, while male parents Rwangume and NKRN59.48 had GCA effects significant for TTW (Table 4). Among the female parents, 396,038.107 had the lowest GCA effects for DAF (− 1.44) followed by Rwangume (− 0.42), while 392,657.8 had the highest (1.14). Male parents 395,011.2 and NKK 19.17 had the lowest GCA effects for DAF (− 0.59 and − 0.38), respectively (Table 4). For yield and related traits, Rwangume had the highest GCA effects for TTW (0.41) followed by NKRK19.17 (0.28), while the lowest GCA effect was for NKRN59.48 (− 0.20). Additionally, the GCA effects for ATW were highest for 393,077.54 (0.02).

Specific combining ability effects of families

Crosses largely showed significant SCA effects for ATW while no significant SCA effects were observed for other traits (Table 5). The highest SCA effects for TTW were among the crosses of Rwangume × NKRK19.17 (0.36) followed by 393,077.54 × 395,011.2 (0.25). Crosses of 396,038.107 × Rwangume had highest SCA effects for ATW (0.021). For number of days to 50% flowering, families of Rwangume × NKRK19.17 (− 1.38) and 396,038.107 × 395,011.2 (− 0.75) had the lowest SCA effects (Table 5).

Family means across locations

The mean number of days to flowering was 54, while total tuber weight was 9.3 t ha^{-1}. Average tuber weight was 0.5 (Table 6). The number of days to flowering ranged from 44.1 to 62 days. Families with

Table 2 Combined analysis of variance for days to 50% flowering, leaf senescence, and tuber yield and related traits evaluated at two locations in Uganda in 2017

Source of variation	*df*	Mean square			
		DAF	LS	TTW	ATW
Set[a]	1	29.73	13.91	6.63	0.12*
Site	1	39.15	1702.85***	1387.66***	1.64***
Replication (site)	2	71.49*	76.15	28.96*	0.00
Female (set)	10	81.68***	40.4	22.26*	0.05
Male (set)	10	87.31***	21.93	20.60*	0.02
Female × male (set)	20	79.45***	89.75*	31.46**	0.02
Site × set	1	57.18	25.54	7.27	0.08
Site × female (set)	10	11.63	18.82	8.66	0.04
Site × male (set)	10	20.16	59.23	11.26	0.03
Site × female × male (set)	20	18.69	52.85	19.42*	0.02
Error		20.09	29.03	9.65	0.03
R-square		0.84	0.78	0.92	0.82
GCA/SCA ratio		0.68	0.41	0.58	0.78

[a]*Set* set within an environment, *df* degrees of freedom, *DAF* days to 50% flowering, *LS* days to leaf senescence, *TTW* total tuber weight, *ATW* average tuber weight, *GCA/SCA* ratio calculated according to Baker (1978)

*Significant at $P \leq 0.05$; **significant at $P \leq 0.01$; ***significant at $P \leq 0.001$

Table 3 Broad and narrow-sense heritability (H^2 and h^2) for days to 50% flowering, leaf senescence, and tuber yield and related traits evaluated at two locations in Uganda in 2017

Heritability/traits	DAF	LS	TTW	ATW
H^2	0.78	0.45	0.70	0.39
h^2	0.40	0.09	0.28	0.34

H^2 broad sense heritability, h^2 narrow sense heritability, *DAF* days to 50% flowering, *LS* days to leaf senescence, *TTW* total tuber weight, *ATW* average tuber weight

less days to flowering were 396,038.107 × 395,011.2 (44.1) and 396,038.107 × NKRN59.48 (47.5). The average total tuber yield was 9.3 t ha^{-1} and families 393,077.54 × Rwangume (14.7 t ha^{-1}) and (Rwangume × NKRK19.17 (13.0 t ha^{-1}) were the best yielders Average tuber weight ranged from 0.3 to 0.6 (Table 6).

Correlation between traits

The correlations between the four traits across locations are presented in Table 7. Correlations were positive and significant between LS and TTW ($P \leq 0.001$); LS and ATW ($P \leq 0.01$).

Discussion

The significant mean squares of families for days to flowering and total tuber weight indicated the presence of genetic variation among parents and their crosses. This implies that genotypes that are early maturing with high yields can be selected for. The significant GCA and SCA mean squares of the traits observed shows that both additive and non-additive gene action were involved in the expression of the traits.

The Baker's ratio for number of days to 50% flowering and leaf senescence were 0.68 and 0.41 respectively. These results signify the predominance of additive genetic effects in controlling the number of days to flowering and non-additive effects for leaf senescence. These findings differ from what has been reported in other studies. For instance, Iragaba (2013) found both additive and non-additive gene action control earliness in potato, though additive genetic effects were more important. Buso et al. (2000) reported both additive and non-additive effects to

Table 4 Estimates of general combining ability (GCA) effects for days to 50% flowering, leaf senescence, total tuber weight and average tuber weight of 12 potato parents evaluated at two locations in 2017

Traits	DAF	LS	TTW	ATW
Set one				
Females				
Rwangume	− 0.421	− 0.403	− 0.238	− 0.002**
396,026.103	0.319	− 0.045	0.188	0.002**
396,038.107	0.102	0.448	0.049	0.000
Males				
Kimuri	0.298	− 0.602	− 0.031	0.003**
391,046.14	0.078	0.239	− 0.253	− 0.012**
NKRK19.17	− 0.376	0.362	0.284	0.009**
SE	0.900	1.680	0.270	0.001
Set two				
Females				
392,657.8	1.144**	− 0.124	0.025	− 0.004**
393,077.54	0.299	− 0.382	− 0.008	0.018**
396,038.107	− 1.443**	0.506	− 0.016	− 0.014**
Males				
Rwangume	0.561	0.209	0.411*	0.002
395,011.2	− 0.589	0.277	− 0.207	− 0.010
NKRN59.48	0.028	− 0.486	− 0.200**	0.008
SE	0.800	2.710	0.460	0.002

SE standard error, *DAF* days to 50% flowering, *LS* days to leaf senescence, *TTW* total tuber weight, *ATW* average tuber weight

*, **Significantly different from zero at ≥ 1.96 SE and 2.56 SE respectively *significant at $P \leq 0.05$; **significant at $P \leq 0.01$

Table 5 Estimates of specific combining ability (SCA) effects for days to 50% flowering, leaf senescence, total tuber weight and average tuber weight of 18 F^1 potato families evaluated at two locations in 2017

Traits	DAF	LS	TTW	ATW
Set one				
Rwangume × Kimuri	0.296	0.215	− 0.040	− 0.003
Rwangume × 391,046.14	1.079	0.249	− 0.318	0.007**
Rwangume × NKRK19.17	− 1.375	− 0.465	0.359	− 0.004*
396,026.103 × Kimuri	− 0.507	0.295	0.190	0.002
396,026.103 × 391,046.14	− 0.635	− 1.211	0.298	− 0.007**
396,026.103 × NKRK19.17	1.142	0.916	− 0.488	0.004*
396,038.107 × Kimuri	0.210	− 0.510	− 0.150	0.001
396,038.107 × 391,046.14	− 0.444	0.961	0.020	0.000
396,038.107 × NKRK19.17	0.234	− 0.451	0.130	0.000
SE	2.670	5.030	0.800	0.002
Set two				
392,657.8 × Rwangume	− 0.790	1.060	0.063	− 0.002
392,657.8 × 395,011.2	1.240	− 1.260	− 0.136	− 0.006**
392,657.8 × NKRN59.48	− 0.450	0.210	0.073	0.008**
393,077.54 × Rwangume	− 0.480	0.420	0.185	− 0.019
393,077.54 × 395,011.2	− 0.490	0.450	0.254	0.017**
393,077.54 × NKRN59.48	0.970	− 0.870	− 0.439	0.001
396,038.107 × Rwangume	1.260	− 1.470	− 0.249	0.021**
396,038.107 × 395,011.2	− 0.750	0.810	− 0.118	− 0.011**
396,038.107 × NKRN59.48	− 0.520	0.660	0.366	− 0.009**
SE	2.410	8.140	0.060	0.007

SE standard error, *DAF* days to 50% flowering, *LS* days to leaf senescence, *TTW* total tuber weight, *ATW* average tuber weight

*, **Significantly different from zero at ≥ 1.96 SE and 2.56 SE respectively *significant at $P \leq 0.05$; **significant at $P \leq 0.01$

Table 6 Family and parent means of days to 50% flowering, leaf senescence, tuber weight and average tuber weight of 18 potato families evaluated at two locations in 2017

Crosses	DAF (days)	LS (%)	TTW (t ha^{-1})	ATW (kg)
Trait and mean performance across sites				
Rwangume × Kimuri	56.3	28.5	11.8	0.4
Rwangume × 391,046.14	58.5	32.0	9.8	0.4
Rwangume × NKRK19.17	46.9	29.6	14.6	0.5
396,026.103 × Kimuri	56.0	30.3	14.4	0.5
396,026.103 × 391,046.14	54.6	32.4	14.0	0.4
396,026.103 × NKRK19.17	59.9	36.6	13.0	0.5
396,038.107 × Kimuri	58.0	29.0	12.5	0.5
396,038.107 × 391,046.14	54.5	38.3	12.3	0.4
396,038.107 × NKRK19.17	55.4	33.9	14.9	0.5
392,657.8 × Rwangume	58.9	35.1	14.4	0.5
392,657.8 × 395,011.2	62.4	26.1	11.1	0.4
392,657.8 × NKRN59.48	58.1	28.9	12.0	0.5
393,077.54 × Rwangume	56.8	31.5	14.7	0.5
393,077.54 × 395,011.2	52.1	31.9	12.5	0.6
393,077.54 × NKRN59.48	60.4	23.6	9.8	0.6
396,038.107 × Rwangume	56.8	27.5	13.0	0.5
396,038.107 × 395,011.2	44.1	36.9	11.0	0.3
396,038.107 × NKRN59.48	47.5	33.3	8.7	0.4
Parents				
Rwangume	55.0	34.8	16.1	0.6
396,026.103	45.3	24.5	7.9	0.3
396,038.107	56.4	31.6	7.1	0.5
Kimuri	53.5	37.3	7.3	0.3
391,046.14	57.5	32.0	6.1	0.5
NKRK19.17	45.8	25.3	6.1	0.4
392,657.8	46.5	20.3	9.4	0.5
393,077.54	54.0	30.0	12.8	0.6
395,011.2	56.8	20.5	14.4	0.8
NKRN59.48	58.3	35.3	8.5	0.5
Mean	54.0	30.6	9.3	0.5
CV (%)	8.0	23.0	33.4	32.3

DAF days to 50% flowering, *LS* days to leaf senescence, *TTW* total tuber weight, *ATW* average tuber weight

influence maturity and total tuber yields. However, because traits are fixed in the F^1 generation when clones are developed, both genetic effects are of great importance in potato breeding (Muthoni et al. 2012). According to Singh and Chaudhary (2007), parents with significant GCA and SCA effects in the right direction would be desired for the trait of interest. For early maturity, the desirable gene action is negative, while for yield, is positive. In this study, both desirable and non-desirable GCA effects were passed on to the respective progenies. Parents Rwangume (− 0.42), 396,038.107 (− 1.44) and NKRK 19.17 (− 0.38) had desirable GCA effects for days to flowering and passed these on to their progenies. Crosses of female parent 393,077.54 displayed significant and negative SCA effects for days to flowering and leaf senescence. The best parents were 396,037.108, 393,077.54, Rwangume and NKRK19.17.

The current study found that the GCA effects for tuber yield related traits were more important than SCA effects. For example, the Baker's ratio for total tuber weight was 0.58 and average tuber weight was (0.78). This implies that additive genes largely influenced the expression of these traits. The predominance

Table 7 Phenotypic correlation between four traits of 18 potato families

Trait	LS	TTW	DAF	ATW
Leaf senescence	–			
Total tuber weight	0.343***	–		
Days to flowering	0.139	0.131	–	
Average tuber weight	0.278**	0.639***	0.122	

*Significant at $P \leq 0.05$; **significant at $P \leq 0.01$; ***significant at $P \leq 0.001$

DAF days to 50% flowering, *LS* days to leaf senescence, *TTW* total tuber weight, *ATW* average tuber weight

of additive genetic effects observed for these traits has been reported in previous studies (Killick 1977; Gopal 1998; Hirut 2015; Muhinyuza et al. 2016). These studies reported GCA to be more important in magnitude than SCA in affecting potato yield. However, some authors found both GCA and SCA to be significant for potato yield with GCA being less important in magnitude than SCA (Bradshaw and Mackay 1994; Ortiz and Golmirzaie 2004; Ruiz de Galarreta et al. 2006; Haydar et al. 2009). In other studies, significant SCA effects for yield have been reported (Gopal 1998; Ruiz de Galarreta et al. 2006; Muthoni et al. 2015). Differences between progenies for tuber yields and number of tubers per plant were found to be dominated by SCA effects, while for average tuber weight and specific gravity the GCA effect was more important (Tai 1976). The variations in the significance of GCA and SCA observed in several studies might be due to differences in genetic material used (Neele et al. 1991; Ortiz and Golmirzaie, 2004; Muthoni et al. 2015). The broad sense heritability estimates revealed number of days to 50% flowering (0.78) and total tuber weight (0.70) to be highly heritable traits. The narrow sense heritability estimates obtained in this study were varying and relatively low. This could be due to the genetic differences among the materials used and the environmental variations. Several authors (Ortiz et al. 1997; Bradshaw et al. 2000; Iragaba, 2013) found comparatively higher values for leaf senescence, days to flowering, total tuber yield, marketable and average tuber yield among different populations.

The significant positive correlations between yield related traits observed have been reported in other studies (Muhinyuza et al. 2016; Hirut 2015). Similarly, Mehdi et al. (2008) found total tuber yield to be largely influenced by higher number of tubers per plant and tuber size. This denotes that improving one trait would subsequently improve the other. The significant positive association between leaf senescence and days to 50% flowering, total tuber weight and average tuber weight obtained in this study, may be attributed to the fact that crop maturity is an agronomic trait, where a plant undergoes progressive growth stages from emergence to senescence, characterized by their reproductive capacity and phenology (Struik, 2010; Khan et al. 2013). This could also be due to the differences in environmental conditions as plant senescence takes place faster at higher temperatures (Kooman and Haverkort 1995).

Conclusion

The significant differences observed among general combining ability (GCA_f, and GCA_m), and specific combining ability (SCA) effects for the genotypes points to the presence of sufficient genetic variation, which can be exploited for crop improvement. Both additive genetic effects were important in inheritance of the traits measured. For traits where additive genetic effects were predominant, improvement can be made by selection and traits transferred to the respective progenies. For characters that were largely influenced by SCA and non-additive genetic action, further genetic gains can be achieved through hybridization of the desirable parents. Parents 393,077.54, 396,038.107, Rwangume and NKRK 19.17 had desirable GCA effects for days to flowering, total and average tuber weight, indicating that these had desirable attributes for high yield and early maturity. Families of Rwangume × NKRK19.17, 393,077.54 × 395,011.2, 396,038.107 × Rwangume and 396,038.107 × 395,011.2 had desirable SCA effects for yield and number of days to 50% flowering. The selected parents and families will be subjected to further clonal evaluation and selection.

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Compliance with ethical standards

Conflict of interest The authors declared that they have no conflict of interest.

References

Acquaah G (2007) Principles of plant genetics and breeding. Blackwell, Maden

Baker RJ (1978) Issues in diallel analysis. Crop Sci 18:533–536

Basbag S, Ekinci R, Gencer O (2007) Combining ability and heterosis for earliness characters in line × tester population of *Gossypium hirsutum* L. Hereditas 144:185–190

Bradshaw JE, Mackay GR (1994) Breeding strategies for clonally propagated potatoes. In: Bradshaw JE, Mackay GR (eds) Potato genetics. CAB International, Wallingford, pp 467–497

Bradshaw JE, Todd D, Wilson RN (2000) Use of tuber progeny tests for genetical studies as part of a potato (*Solanum tuberosum* subsp. *tuberosum*) breeding program. Theor Appl Genet 100:772–781

Buso J, Boiteux L, Peloquin S (2000) Heterotic effects for yield and tuber solids and type of gene action for five traits in 4× potato families derived from interploid (4×–2×) crosses. Plant Breed 119:111–117

Dabholkar AR (1999) Elements of biometrical genetics. Concept Publishing Company, New Delhi

FAOSTAT (2016) Production statistics. Food and Agriculture Organization of the United Nations

Gopal J (1998) General combining ability and its repeatability in early generations of potato breeding programs. Potato Res 41:21–28

Haga E, Weber B, Jansky S (2012) Examination of potential measures of vine maturity in potato. Am J Plant Sci 3:495–505

Hallauer AR, Miranda JB (1988) Quantitative genetics in maize breeding, 2nd edn. Iowa State University Press, Ames

Hallauer AR, Carena MJ, Filho JBM (1988) Hereditary variance: mating designs. In: Quantitative genetics in maize breeding. Iowa State University, Ames, pp 81–167

Haydar A, Alam MK, Khokan EH, Ara T, Khalequzzaman KM (2009) Combining ability and genetic variability studies in potato. J Soil Nat 3:1–3

Hirut GB (2015) Genetic analyses of drought tolerance and resistance to late blight among potato genotypes. PhD thesis, University of KwaZulu-Natal, South Africa

Iragaba P (2013) Inheritance and stability of earliness in potato. Masters thesis, Makerere University

Khan MS, Van Eck HJ, Struik PC (2013) Model-based evaluation of maturity type of potato using a diverse set of standard varieties and a segregating diploid population. Potato Res 56:127–146

Killick RJ (1977) Genetic analysis of several traits in potatoes by means of a diallel cross. Ann Appl Biol 86:279–289

Kooman PL, Haverkort AJ (1995) Modelling development and growth of the potato crop influenced by temperature and daylength LINTULPOTATO. In: Haverkort AJ, MacKerron DKL (eds) Potato ecology and modeling of crops under conditions limiting growth. Kluwer, Dordrecht, pp 41–60

Mehdi M, Saleem T, Rai HK, Mir MS, Rai G (2008) Effect of nitrogen and FYM interaction on yield and yield traits of potato genotypes under Ladakh condition. Potato J 35:126–129

Muhinyuza JB, Shimelis H, Melis R, Sibiya J, Gahakwa D, Nzaramba MN (2016) Combining ability analysis of yield and late blight [*Phytophthora infestans* (Mont.) de Bary] resistance of potato germplasm in Rwanda. Aust J Crop Sci 10:799–807

Muthoni J, Shimelis H, Melis R, Kabira J (2012) Reproductive biology and early generation's selection in conventional potato breeding. Aust J Crop Sci 6:488–497

Muthoni J, Shimelis H, Melis R (2015) Combining ability analysis of tuber yield and related traits and bacterial wilt (*Ralstonia solanacearum*) resistance in potato. Aust J Crop Sci 9:401–412

Namugga P, Sibiya J, Melis R, Barekye A (2017a) Phenotypic characterisation of potato (*Solanum tuberosum* L.) genotypes in Uganda. S Afr J Plant Soil. https://doi.org/10.1080/02571862.2017.1370561

Namugga P, Melis R, Sibiya J, Barekye A (2017b) Participatory assessment of potato farming systems, production constraints and cultivar preferences in Uganda. Aust J Crop Sci 11:932–940

Neele AEF, Nab HJ, Louwes KK (1991) Identification of superior parents in a potato breeding program. Theor Appl Genet 82:264–272

Ortiz R, Golmirzaie AM (2004) Combining ability analysis and correlation between breeding values in true potato seed. Plant Breed 123:564–567

Ortiz R, Iwanaga M, Peloquin SJ (1997) Evaluation of FDR diploid and tetraploid parents in potato under two different day-length environments. Plant Breed 116:353–358

Ruiz de Galarreta JJ, Ezpeleta B, Pascualena J, Ritter E (2006) Combining ability and correlations for yield components in early generations of potato breeding. Plant Breed 125:183–186

Ruzukas A, Jankauskiene Z, Jundulas J, Asakaviciute R (2009) Research of technical crops (potato and flax) genetic resources in Lithuania. Agron Res 7:59–72

SAS Institute (2011) SAS software release 9.1.3. SAS Institute Inc., Cary

Singh RK, Chaudhary BD (1979) Biometrical methods in quantitative genetic analysis. Kalyani Publishers, New Delhi

Singh RK, Chaudhary BD (2007) Biometrical methods in quantitative genetic analysis. Kalyani Publishers, New Delhi

Struik PC (2010) Can physiology help us to combat late blight in potato? Potato Res 53:277–287

Tai GCC (1976) Estimation of general and specific combing abilities in potato. Can J Genet Cytol 18:463–470