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Combining ability analysis of yield and resistance to late blight disease caused by *Phytophthora infestans* in Uganda

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Abstract

Breeding for resistance to late blight disease caused by *Phytophthora infestans* (Mont.) de Bary in potato is the most economically, effective and ecologically sustainable method to control the disease and boost productivity. The study estimated combining ability effects of yield, yield related traits, late blight resistance and gene action controlling resistance to *Phytophthora infestans*. Eighteen F^1 families generated from two sets of 12 parents, using a North Carolina Design II, were evaluated for relative area under disease progress curve (rAUDPC), yield and yield related traits in two late blight hotspot locations of Kachwekano and Kalengyere research stations. Trials were established using an alpha lattice design (6 x 5) with two replications. Both additive and non-additive genetic effects were important in controlling yield and late blight resistance. However, additive gene action was dominant. The general combining ability (GCA) to specific combining ability ratio (SCA); (GCA/SCA) for total tuber weight and late blight resistance was 0.53 and 0.62 respectively. Broad-sense heritability estimates were 0.78 for total tuber weight and 0.68 for relative area under disease progress curve (rAUDPC). This study showed some evidence of maternal effects for rAUDPC (1.45) and average tuber weight (ATW) (1.56), although these were not significant at $P<0.05$. Parents Kinigi, 392657.8, 396034.103, 396038.107, 395011.2, NKRK19.17, NKRN59.58 and 395017.14 had good GCA effects for both late blight resistance and yield related traits. Crosses of 392657.8 x 395017.14 and 396038.107 x NKRN59.58 had the highest SCA effects for yield related traits, while families Kinigi x NKRK19.17and 392657.8 x NKRN59.41 had the lowest SCA effects for rAUDPC. The relatively high heritability estimates and predominant additive genetic effects imply that genetic advances in resistance to Phytophthora infestans and tuber yield among these genotypes can be realized by selecting superior clones.

Key words: Heritability, *Solanum tuberosum,* gene action, rAUDPC, *Phytophthora infestans* resistance

Introduction

Late blight of potato caused by *Phytophthora infestans* (Mont.) de Bary is the most devastating disease in the tropical highlands of Uganda. The disease causes estimated yield losses between 30 and 100% in different parts of the country (Byarugaba et al., 2013). Late blight is the major reason for the use of fungicides on potatoes in Uganda (Low, 1997). As much as the disease can be managed through the use of fungicides, most small-scale farmers cannot afford them because both contact and systemic fungicides are expensive. Additionally, fungicide application is by hand. Farmers rarely use protective clothing, posing health risks and diverse environmental hazards (Kromann et al., 2009; Forbes, 2012). Consequently, there is poor disease management due to partial access to fungicides, high disease pressure and inadequate farmer knowledge of disease dynamics (Forbes, 2012). Breeding for host resistance is a sustainable approach to late blight control and management in Uganda. Though breeding for resistance to *Phytophthora infestans* has been a priority of the potato breeding program in Uganda over the past years. However,, previously released resistant varieties have quickly succumbed to virulent races of the pathogen (Mulema et al., 2004; Byarugaba et al., 2013).

Early efforts to breed for resistance against late blight focused on qualitative resistance controlled by major R genes. Even though R genes are greatly effective when compatible races are present, race-specific resistance controlled by major resistance (R) genes is not considered resilient due to interminable changes in the pathogen. As a result, the focus nowadays is on quantitative, race non-specific resistance through minor resistance genes. This is more durable and effective against various pathogenic strains of *Phytophthora infestans* (Kumar et al., 2007) Based on this concept, the International Potato Centre (CIP) developed, a population group (B3) with quantitative resistance to *Phytophthora* *infestans* with no known major (R) genes. Late blight resistance in this population was improved after several cycle of recombination (B3C0, B3C1 and B3C2) (Landeo et al., 2001; Kaila, 2015). In addition, population B3 genotypes have a wider genetic background for various economic traits. This germplasm is available to many developing countries for breeding purposes (Yao et al., 2011). As a result, the National Potato Program of Uganda obtained some of these clones together with the existing and adapted varieties for evaluation. The clones which were high yielding with resistance to *Phytophthora infestans* in the target environments were identified (Namugga et al., 2017). These were used as parents to generate new progenies with variable resistance to late blight.

In potato, both the general combining ability (GCA) effects of parents and specific combining ability (SCA) effects of their crosses are important in determining economic traits, as all genetic effects are fixed at the F^1 stage and there is no further segregation. A combining ability analysis is the basis for identification of the best parents and their crosses (Mondal and Hossain, 2006). The objectives of this study were to estimate combining ability effects and gene action for yield, yield related traits and late blight resistance. Genotypes resistant to *Phytophthora infestans* with high yields will be evaluated further and eventually released as varieties in Uganda.

Results

Analysis of variance for crosses across sites

The combined analysis of variance and ratio of GCA/SCA for the relative area under the disease progress curve (rAUDPC), total tuber weight (TTW) and average tuber weight (ATW) among the families are summarized in Table 1. There were significant differences among crosses for all the traits. The environmental (site) effect was significant ($P \leq 0.01$) for TTW and ATW. The GCA mean squares for females (GCA_f) were significant for all traits. GCA mean squares for males (GCA_m) were significant for all traits except ATW. The SCA effects were significant for all the tested traits. The GCA_m x environment interaction was significant for the ATW. No significant interactions were observed between environment and sets of parents for all the traits assessed. The GCA_f effects were higher than the GCA_m effects for rAUDPC and ATW, while additive GCA_m effects were only dominant for TTW. For ATW, SCA effects were higher than the additive main effects of either male or female parents. However, the GCA was more important than the SCA in the expression of all the traits. The ratio of additive/ non-additive genetic effects ranged from 0.38 (ATW) to 0.62 (rAUDPC).

Heritability estimates and maternal effects

The estimates of broad (H^2) and narrow -sense heritability (h^2), maternal effects for rAUDPC and yield related traits across locations are presented in (Table 2). The broad sense heritability values ranged from 0.68 to 0.78. The narrow-sense heritability values ranged from 0.27 to 0.43, rAUDPC had the highest value. In general, this study showed some evidence of maternal effects for some traits (rAUDPC, F = 1.45 and ATW, F = 1.56), although these were not significant at $P \leq 0.05$.

General combining ability effects of parents

The GCA effects of potato parents at Kachwekano and Kalengyere are presented in Table 3. Significant GCA effects were observed among all the parents for ATW. Parents Kinigi, 392657.8, 396026.103, 395017.14, NKRN59.41and 395011.2 had significant GCA effects for TTW. GCA effects for rAUDPC were significant for Kinigi, 392657.8, 395017.14, NKRK19.17, 396026.103, 396038.107, NKRN59.48 and 395011.2. Among the female parents, 396038.107 had the lowest GCA effect for rAUDPC (-1.18) followed by 392657.8 (-0.82). Male parents NKRN59.48 (-1.9) and NKRK19.17 (-1.09) had the lowest GCA effects. For yield related traits, 392657.8 had the highest GCA effects for TTW (0.32) followed by 396026.103 TTW (0.27). For ATW, 396034.103 had the highest GCA of 0.06 followed by 396026.103 (0.03). Kinigi had the lowest GCA effect for all the yield related traits. For TTW, parent 395017.14 had the highest GCA effect for TTW (1.60) while NKRN59.41 had the lowest (-0.54)

Specific combining ability effects of families

The SCA effects of 18 potato F^1 families evaluated at Kachwekano and Kalengyere are presented in Table 4. All crosses showed significant SCA effects for ATW, except Kinigi x 395017.14 and 396026.103 x 395011.2. For TTW, SCA effects were significant for the crosses 396034.103 x 395017.14 and 393220.54 x NKRN59.58. Crosses 392657.8 x 395017.14 and 396038.107 x NKRN59.58 had the highest SCA effects for all the yield related traits (TTW and ATW). For rAUDPC, significant SCA effects were observed for crosses of 392657.8 x NKRK19.17 only. The lowest SCA effects for rAUDPC were -2.29 and -1.92 for crosses Kinigi x NKRK19.17and 392657.8 x NKRN59.41, respectively.

Family means across locations

Means and ranking of TTW, ATW and rAUDPC within and across locations are presented in

. The mean rAUDPC (= 100 max) across locations indicated that families 393220.54 x NKRN59.58 and Kinigi x NKRN59.41 with disease severity of 2.5% and 4.2%, respectively, were the most resistant. Families 392657.8 x 395017.14 and 396034.103 x NKRK19.17 were the best yielders with a TTW of 13.3 t ha^{-1} and 11.1 t ha^{-1} respectively. Families Kinigi x NKRN59.41 (3.8) and 393220.54xNKRN59.58 (2.3) were the lowest in TTW across locations. Additionally, families 392657.8 x 395017.14 (96.9) and 396026.103 x 395011.2 (75.8) had the highest ATW across locations. Ranking of the families revealed crosses 393220.54 x NKRN59.58, Kinigi x NKRN59.41, 396038.107 x NKRN59.48, 392657.8 x NKRN59.41 and 396026.103xNKRN59.48 as the most resistant. The highest yielding families were 392657.8 x 395017.14, 396034.103 x NKRK19.17, 396026.103 x 395011.2, 393220.54 x 395011.2 and 392657.8 x NKRK19.17.

Table 1: Combined analysis of variance of potato genotypes for late blight resistance, tuber yield and related traits tested at two locations in Uganda in 2017.

Means squares				
Source of variation	DF	TTW	ATW	rAUDPC
Set[1]	1	5.31	0.27	3.24
Site	1	49.37**	1.03**	16.22
Site*Set	4	7.40	0.17	11.8
Replication (Site)	2	68.94***	1.55***	86.34*
Female (Set)	4	20.22**	0.40**	63.12**
Male (Set)	4	32.11***	0.26	43.60*
Female*Male (Set)	8	29.12**	0.68***	40.95*
Site*Female (Set)	4	4.11	0.25	12.81
Site*Male (Set)	4	8.89	0.40**	10.01
Site*Female*Male (Set)	8	3.30	0.10	4.03
Error	32	6.15	0.14	20.16
R-Square		0.74	0.72	0.60
		0.53	0.38	0.62

[1] Set within an environment, DF = Degrees of freedom; *= significant at P≤0.05; **= significant at P≤0.01; ***= significant at P≤0.001; TTW = total tuber weight; ATW = average tuber weight; rAUDPC = relative area under the disease progress curve; GCA/SCA ratio calculated according to Baker (1978).

Table 2: Broad, narrow -sense heritability and maternal effects for yield related traits and rAUDPC across two locations in Uganda in 2017

Heritability/Traits	TTW	ATW	rAUDPC
H^2	0.78	0.77	0.68
h^2	0.31	0.27	0.43
MS_F/MS_M	0.63	1.56	1.45

GCA/SCA ratio calculated according to Baker (1978); H^2 = broad sense heritability; h^2 = narrow sense heritability; MS_F = mean square of the female parent; MS_M = mean square of the male parent; TTW = total tuber weight; ATW = average tuber weight; rAUDPC = relative area under the disease progress curve

Table 3: Estimates of general combining ability effects for, TTW, ATW and rAUDPC of 12 potato parents evaluated in two locations in Uganda in 2017.

Traits			
	TTW	ATW	rAUDPC
Set one			
Females			
Kinigi	-0.502**	-0.073**	1.201**
396034.103	0.177	0.065**	-0.385
392657.8	0.324*	0.008**	-0.816*
Males			
395017.14	0.315*	-0.019**	1.473**
NKRN59.41	-0.538**	-0.017**	-0.387
NKRK19.17	0.233	0.037**	-1.086**
SE	0.120	0.010	0.420
Set two			
Females			
396026.103	0.271*	0.032**	0.833*
393220.54	-0.213	-0.021**	0.345
396038.107	-0.058	-0.011**	-1.177**
Males			
NKRN59.48	-0.150	-0.016**	-1.960**
NKRN59.58	-0.242	-0.023**	0.255
395011.2	0.392**	0.039**	1.704**
SE	0.260	0.003	0.430

SE = standard error; *, ** significantly different from zero at ≥ 1.96SE and 2.56SE respectively *= significant at P≤0.05; **= significant at P≤0.01; TTW = total tuber weight; ATW= average tuber weight; rAUDPC = relative area under the disease progress curve

Table 4: Estimates of specific combining ability (SCA) effects for TTW, ATW and rAUDPC, of 18 F^1 potato families evaluated in two locations in Uganda in 2017.

Traits	TTW	ATW	rAUDPC
Set one			
Kinigi x 395017.14	0.053	-0.003	1.185
Kinigi x NKRN59.41	-0.069	-0.017*	1.101
Kinigi x NKRK19.17	0.016	0.020*	-2.287
396034.103 x 395017.14	-0.690*	-0.122**	-0.627
396034.103 x NKRN59.41	0.386	0.059**	0.822
396034.103 x NKRK19.17	0.303	0.063**	-0.194
392657.8 x 395017.14	0.636	0.125**	-0.558
392657.8 x NKRN59.41	-0.317	-0.042**	-1.923
392657.8 x NKRK19.17	-0.319	-0.083**	2.481*
SE	0.660	0.020	1.260
Set two			
396026.103 x NKRN59.48	-0.418	0.026**	-0.498
396026.103 x NKRN59.58	0.255	-0.015*	-0.556
396026.103 x 395011.2	0.163	-0.010	1.054
393220.54 x NKRN59.48	0.711	0.031**	0.653
393220.54 x NKRN59.58	-0.915*	-0.101**	-0.858
393220.54 x 395011.2	0.204	0.070**	0.205
396038.107 x NKRN59.48	-0.294	-0.057**	-0.155
396038.107 x NKRN59.58	0.661	0.117**	1.414
396038.107 x 395011.2	-0.367	-0.060**	-1.259
SE	0.780	0.010	1.260

SE = standard error; *, ** significantly different from zero at ≥ 1.96SE and 2.56SE respectively *= significant at P≤0.05; **= significant at P≤0.01; TTW = total tuber weight; ATW= average tuber weight; rAUDPC = relative area under the disease progress curve

Table 5: Family and parent means of total tuber weight, average tuber weight and relative area under the disease progress curve of 18 potato families evaluated at two locations in Uganda in 2017

	TTW (t ha^{-1})		ATW (g)		rAUDPC	
Families	Mean	Rank	Mean	Rank	Mean	Rank
Kinigi x 395017.14	7.7	14	40.0	18	8.5	18
Kinigi x NKRN59.41	3.8	31	16.6	31	4.2	2
Kinigi x NKRK19.17	7.2	18	45.6	14	8.0	15
396034.103 x 395017.14	7.4	16	37.6	21	8.2	17
396034.103 x NKRN59.41	8.4	13	45.7	13	9.3	20
396034.103 x NKRK19.17	11.1	2	45.4	16	12.3	30
392657.8 x 395017.14	13.3	1	96.9	1	14.8	32
392657.8 x NKRN59.41	6.1	24	45.5	15	6.8	9
392657.8 x NKRK19.17	9.2	8	57.7	5	10.2	23
396026.103 x NKRN59.48	6.6	20	33.4	25	7.3	13
396026.103 x NKRN59.58	8.9	12	54.9	8	9.9	21
396026.103 x 395011.2	11.1	3	75.8	2	12.3	31
393220.54 x NKRN59.48	9.2	9	52.4	10	10.2	24
393220.54 x NKRN59.58	2.3	32	13.9	32	2.5	1
393220.54 x 395011.2	9.3	7	49.3	11	10.3	26
396038.107 x NKRN59.48	5.8	26	31.5	26	6.4	7
396038.107 x NKRN59.58	9.2	10	56.9	6	10.2	25
396038.107 x 395011.2	7.6	15	43.3	17	8.5	19
Parents						
Kinigi	9.1	11	55.7	7	10.1	22
396034.103	7.3	17	48.7	12	8.1	16
392657.8	4.8	27	27.8	27	5.3	5
395017.14	9.9	6	53.7	9	11.0	27
NKRN59.41	3.9	30	24.0	29	4.4	3
NKRK19.17	4.8	28	27.0	28	5.3	6
396026.103	4.1	29	23.8	30	4.6	4
393220.54	10.3	5	67.4	3	11.4	28
396038.107	6.9	19	39.6	20	7.7	14
NKRN59.48	6.3	22	39.8	19	7.0	11
NKRN59.58	6.5	21	36.7	23	7.2	12
395011.2	6.2	23	37.5	22	6.9	10
Mean	7.5		44.0		8.4	
CV (%)	26.5		27.0		30.3	

TTW = total tuber weight; ATW = average tuber weight; rAUDPC = relative area under the disease progress curve

Table 6: Correlation coefficients of yield parameters and rAUDPC in 18 F^1 potato families tested at two locations in Uganda in 2017

Trait	ATW	TTW	rAUDPC
Average tuber weight	-		
Total tuber weight	0.86***	-	
rAUDPC	-0.86***	-0.99***	-

*= significant at P≤0.05; **= significant at P≤0.01; ***= significant at P≤0.001; TTW = total tuber weight; ATW= average tuber weight rAUDPC = relative area under the disease progress curve

Table 7: Description of parents used in the study: CIP = International Potato Center, NARO = National Agriculture Research Organisation

Set	Parent	Parent type	Source	Yield (t ha-^{1})	Reaction to late blight (% rAUDPC)
1	Kinigi	Female	NARO	32	32.9
1	396034.103	Female	CIP	35.4	27.5
1	392657.8	Female	CIP	43.7	14.1
1	395017.14	Male	CIP	18.9	27.1
1	NKR59.41	Male	NARO	24.1	22.9
1	NKRK19.17	Male	NARO	37.8	34.1
2	396026.103	Female	CIP	33.1	42
2	393220.54	Female	CIP	40.3	15.9
2	396038.107	Female	CIP	37.7	36.5
2	NKRN59.48	Male	NARO	30	26.1
2	NKRN59.58	Male	NARO	30	27.7
2	395011.2	Male	CIP	25.5	22.9

Source: Namugga et al. (2017)

Correlation among traits

Correlations between the three traits are presented in Table 6. Significant ($P < 0.001$) and positive correlation was found between TTW and ATW. Correlation between rAUDPC and all yield related traits were negative and significant ($P < 0.001$) for TTW and ATW.

Discussion

There was differential performance of parents and their families for the different traits between sites. The significant mean squares for families on rAUDPC and yield related traits at the two sites indicated the presence of genetic variation among parents and their crosses. This suggests that clones that are high yielding and resistant to late blight may be selected. Both additive and non-additive gene action were significant in inheritance of the traits measured. However, GCA effects were more important than SCA effects for all the traits except ATW. This implies that inheritance of these traits, except ATW, is due to additive genetic effects, hence further genetic gains can be realized by selecting superior clones.

The GCA to SCA ratio for total tuber yield was 0.53, indicating the preponderance of additive genetic effects. Predominance of additive genetic effects observed for this trait has also been reported in previous studies (Killick, 1997; Gopal, 1998; Hirut, 2015; Muhinyuza et al., 2016). However, other studies reported both GCA and SCA to be significant for potato yield, with GCA being less important in magnitude than SCA (Ortiz and Golmirzaie, 2004; Ruiz de Galarreta et al., 2006; Haydar et al., 2009). On the other hand, some studies only reported significant SCA effects for yield (Gopal, 1998; Muthoni et al., 2015). The differences in the importance of GCA and SCA effects observed in many studies could be attributed to differences in genetic material used. For example Neele et al., (1991) and Ortiz and Golmirzaie (2004) reported GCA to be significantly greater than SCA for tuber yields and yield related traits while Muthoni et al. (2015) reported SCA effects to be greater than GCA.

The GCA/SCA ratio for rAUDPC was 0.62. This gives an indication that the additive effect was important in the expression of late blight resistance among the potato clones used. This agrees with previous reports on the relative importance of GCA and SCA for potato late blight resistance (Hirut, 2015; Muhinyuza et al., 2016). Landeo et al. (2001) reported large additive genetic variance for late blight resistance in a random sample of the B3C1 population, using three different mating designs. In other studies, the SCA variances were greater than the GCA variances for late blight resistance (Kaushik et al., 2000) while Landeo et al. (2000) found both additive and non-additive genetic effects to be equally important for horizontal resistance. The dominance of additive genetic effects for late blight resistance in this study confirms the absence of major R genes among the parents and showed that minor genes were responsible for the resistance.

All traits were highly heritable as revealed by the heritability estimates. The broad sense heritability value for rAUDPC (0.68) was similar to that reported in other studies (Christ and Hynes, 2001; Visker et al., 2004). Conversely, both broad and narrow sense (0.43) heritability values were lower compared to the 0.79 and 0.78 respectively, obtained by Hynes and Christ, (1999) in a diploid hybrid potato population. Broad sense heritability values for total tuber weight (0.78) and average tuber weight (0.77) were high, suggesting that genetic advances in resistance to *Phytophthora infestans* and tuber yield among these genotypes can be realized. Also with such large heritability estimates, it could be suggested that relatively few genes are involved. The narrow sense heritability estimates obtained differed from other findings, for example, Ortiz et al., (1997) obtained 0.54 and 0.27 for average tuber weight and marketable tuber weight, respectively. The presence of maternal effects for rAUDPC (1.45) and ATW (1.56) points to cytoplasmic inheritance, where DNA in the chloroplasts is not subject to Mendelian inheritance (Acquaah, 2012). Although these were not significant at $P \leq 0.05$, their presence would influence the choice of parents in a crossing scheme. Parents for improvement of these traits would be used as females.

The highly significant negative correlation between rAUDPC, and average tuber weight and total tuber weight observed in this study, shows the negative effect late blight imposes on tuber yield through the reduction of photosynthetic capacity of the foliage destruction. Several authors (Dowley et al., 2008; Mantecón, 2009; Muhinyuza et al., 2015; Hirut, 2015) have reported comparable results. Total tuber weight and average tuber weight were significantly and positively correlated (0.86). Hirut (2015) found a slightly higher correlation coefficient between total tuber weight and average tuber weight of 0.88 in combining ability studies of potato clones in Ethiopia. Mehdi et al., (2008) found total tuber yield to be largely influenced by higher number of tubers per plant and tuber size. This implies that total tuber weight can be selected for indirectly using average tuber weight.

Materials and methods

Parental materials and crosses

Twelve genetically diverse clones were selected and used as parents. Seven clones were obtained from the National Potato Program of Uganda and five were from the International Potato Centre (CIP) belonging to population B3C2 with variable resistance to late blight. These parents were selected based on their flowering abilities, high to medium yields and acceptable level of resistance to *Phytophthora infestans* (Namugga et al., 2017). The parents were grouped into two sets of six parents based on their flowering abilities, yield and resistance to late blight. Both males and females were high yielding, resistant to late blight and good flowering abilities. Crosses were made using a North Carolina Design II (NCD II) to generate 18 families. In the first set three female clones (Kinigi, 396034.103 and 392657.8) were crossed with three males (395017.14, NKR59.41 and NKRK19.17). In the second set three female parents (396026.103, 393220.54 and 396038.107) were crossed with three males (NKRN59.48, NKRN59.58 and 395011.2). 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).

Study sites

Crosses to generate potato seed and the generation of seedlings were conducted at the Kachwekano research station, located in South-western Uganda, 01º 16'S 29º 57'E at 2200 meters above sea level. The clonal evaluations to determine combining abilities for late blight and tuber yield and its components were conducted at Kachwekano and Kalengyere research stations. Kalengyere is located at an altitude of 2450 masl, 01°13.2' S, 29° 47.8 'E. The two sites have volcanic (Andosols) soils with a bi-modal rainfall pattern separated by a dry spell ranging from 30-60 days. These locations have the same pathogen population (Njoroge et al., 2016) and are known to experience severe late blight disease pressure during the rainy season. Consequently, clones were evaluated under natural disease infestation.

Experimental design and trial establishment

Experiments were established during the main planting season of 2017A (March-June). Planting was done on the 14th and 16th of March 2017 at Kalengyere and Kachwekano, respectively. To increase the disease inoculum, a susceptible variety (Victoria) was planted adjacent to each row and around each replication as spreader rows. No control measure was taken against late blight. Trials were established using an alpha lattice design (6 x 5) with two replications. Each entry was represented by an experimental unit consisting of 40 plants assigned in a plot size of two rows of 4.5 m long at spacing of 0.75 m x 0.3 m. All the necessary agronomic practices were carried out as recommended.

Data collection

Data were collected on reaction to late blight infection and yield related traits. Late blight assessment started with the first appearance of the symptoms. Plants were visually rated at seven day intervals for percentage leaf and stem area with late blight lesions. This was done visually by comparing the green and non-green leaf portions affected by the disease using a 1 to 9 scale designed by the International Potato Centre, that is, 1=0%, 2=2.5%, 3=10%, 4=25%, 5=50%, 6=75%, 7=90%, 8=97.5% and 9=100% leaf area showing disease symptoms (Henfling, 1987). The mean percentage blighted foliar area per plot was calculated. Evaluations continued until the susceptible genotype reached 90-100% of leaf blight assessments and the area under the disease progress curve (AUDPC) was calculated (Campbell and Madden, 1990). The relative area under the disease progress curve (rAUDPC) was used in the analysis of variance. The rAUDPC was calculated using the following formula:

$$rAUDPC = \sum \frac{(T_{i+1} - T_i) * (\frac{D_{i+1} + D_i}{2})}{T_{Total} * 100} \qquad \text{(Equation 1)}$$

In equation 1, T_i = is the i^{th} day when an estimation of percentage foliar late blight is made and D_i = is the estimated percentage of area with blighted foliage at T_i. The total is the number of days at which the final assessment was recorded. At harvest, yield related data was taken 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 the two sets and across environments were subjected to the standard analysis of variance using the GLM procedure of SAS 9.3 (SAS Institute Inc, 2011) statistical program. Analyses of variance of NCD II pooled over sets and across environments were conducted for rAUDPC and yield. Spearman correlation coefficients were calculated for the studied traits to determine their association.

Estimation of general and specific combining ability effects

GCA and SCA effects were estimated using the following linear model (Hallauer and Miranda, 1988).

$Y_{ijkpq} = \mu + S_p + g_i(S_p) + g_j(S_p) + h_{ij}(S_p) + E_q + r_k(SE)_{pq} + (ES)_{pq} + (Eg)_{iq}(S_p) + (Eg)_{jp}(S_p) + (Eh)_{ijq}(S_p) + (Eh)_{ijq}(S_p) + e_{ijkpq}$

Where: $i = 1, 2, 3$; $j = 1, 2, 3$; $k = 1, 2$; $p = 1, 2$; $q = 1, 2$; the terms for the model are defined as follows: Y_{ijkpq} denotes the value of a family from the mating between the i^{th} female parent, the j^{th} male parent, in the k^{th} block, within set p and in the q^{th} environment; μ = grand mean; S_p = the average effect of the p^{th} set; $g_i(S_p)$ = the GCA effect common to all F^1 families of the i^{th} female parent nested within p^{th} set; $g_j(S_p)$ = the GCA effect common to all F^1 families of the j^{th} male parent nested within p^{th} set; $h_{ij}(S_p)$ = the SCA effect specific to F^1 families of the i^{th} female and j^{th} male parent nested within p^{th} set; E_q= average effect of q^{th} environment; $r_k(SE)_{pq}$ = the effect of the k^{th} replication nested within the p^{th} set and q^{th} environment; $(ES)_{pq}$= the interaction between site and set effects; $(Eg)_{iq}(S_p)$ and $(Eg)_{jp}(S_p)$ = the interaction between site and GCA of the i^{th} female and j^{th} male parent, respectively nested within sets; $(Eh)_{ijq}(S_p)$ = the interaction between site and SCA, nested within sets; and e_{ijkpq} = the random experimental error.

The relative importance of GCA and SCA effects for each trait was determined according to the general predicted ratio (GPR) as follows: GCA/SCA = 2MSGCA/(2MSGCA+MSSCA) (Baker, 1978). When the GCA/SCA ratio is greater than 0.5, additive effects are more important than non-additive effects in the inheritance of the concerned trait, whereas if the ratio is smaller than 0.5, dominance effects are more important in the inheritance of the concerned character.

Estimating heritability and maternal effects

Heritability estimates were calculated using the female additive variance for both narrow and broad sense heritability (Dabholkar, 1999) as follows: Narrow sense heritability; $h_f^2 = 4\sigma^2_f / (\sigma^2_e/r + 4\sigma^2_{mf} + 4\sigma^2_f) = V_{Af} / V_P$; broad sense heritability; $h_f^2 = 4\sigma^2_f + 4\sigma^2_{mf} / (\sigma^2_e/r + 4\sigma^2_{mf} + 4\sigma^2_f) = V_{Gf} / V_P$. Where,

r = number of replication

σ^2_e = environmental variance = MS_e

σ^2_f = variance of female parents = GCA_f variance = MS_f

σ^2_{fm} = 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

Test for maternal effects: The ratio of MS_f: MS_m estimates the levels of maternal effects provided f = m in the design.

$F = MS_f / MS_m$, $F_{m,\ f}$ degrees of freedom at $P<0.05$. If the ratio is greater than 1 there is ample evidence to suggest presence of maternal effects.

Conclusions

The significant differences observed among general combining ability (GCA_f, and GCA_m), and specific combining ability (SCA) effects for the genotypes suggest the presence of sufficient genetic variation, which can be exploited for crop improvement. This study found additive gene action to be more important than non- additive genetic effects in the inheritance of yield related traits and resistance to late blight disease in potato. This signifies that improvement can be made by selection and traits transferred to the respective progenies. The best general combiners were 393220.54, Kinigi, 395011.2, 392657.8, 396026.103, NKRN59.48 and NKRN59.58. Families: 393220.54 x NKRN59.48, 396038.107 x NKRN59.58, 392657.8 x 395017.14, Kinigi x NKRK19.17 and 392657.8 x NKRN59.41 had desirable SCA effects for yield and resistance to *Phytophthora infestans*. The selected parents can be used for crop improvement purposes.

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Conflict of Interest Statement

"The authors declared that they have no conflict of interest”.

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