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Combining ability analysis of tuber yield and related traits and bacterial wilt (*Ralstonia solanacearum*) resistance in potato

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Abstract

In potatoes (*Solanum tuberosum* L. 2n=4x=48) both the general combining ability (GCA) effects of parents and specific combining ability (SCA) effects of crosses are important in conditioning traits of economic importance. The objective of this study was to determine the combining abilities for tuber yield, its components and bacterial wilt resistance on selected potato varieties and clones. Fourteen parents [eight male varieties that are commonly grown in Kenya and six female clones with moderate tolerance to bacterial wilt from the International Potato Center (CIP)] were crossed using the North Carolina II mating design. The resultant 48 families were evaluated for yield and yield components and bacterial wilt resistance in inoculated fields at Kenya Agricultural Research Institute, National Agricultural Research Laboratories (KARI-NARL) and at a farmer's field at Kinale using a 6 × 8 alpha lattice experimental design with three replications. Generally, crosses tested at Kinale took a longer time to start wilting, had lower values for the area under the disease progress curve (AUDPC), percentage of symptomatic tubers based on tuber numbers (PSTTN) and percentage of symptomatic tubers based on weight (PSTTW) than at KARI-NARL. Significant ($P \leq 0.001$) GCA effects were observed for males for total tuber weight (TTW) and days to maturity (DTM) while the GCA effects for females were significant ($P \leq 0.001$) for TTW and total tuber numbers ha^{-1}(TTN)($P<0.01$) at KARI-NARL.

Keywords: Bacterial wilt, Gene action, General combining ability, Potato, Specific combining ability.
Abbreviations: GCA=General Combining Ability, SCA=Specific Combining Ability, CIP=International Potato Center.

Introduction

Understanding gene action and its inheritance helps in selecting suitable parents and their crosses to use in a breeding programme, to choose proper mating design or to identify the subsequent selection procedure to follow. Gene action reflects gene differences that provide the basis for the selection of desirable genotypes in plant breeding (Rasmusson and Gengenbach, 1983; Sleper and Poehlman, 2006). In potatoes (*Solanum tuberosum* L., 2n=4x=48) both the general combining ability (GCA) effects of parents and specific combining ability (SCA) effects of their crosses are important in conditioning economic traits. In this crop all genetic effects are fixed at the F_1 stage, as with clonal propagation, there is no further segregation. The GCA seems to be significantly larger than the SCA for tuber yield and quality traits in crosses between non-related parents; however, SCA appears to be more important among related parents (Ortiz and Golmirzaie, 2004). Tuber yield components do show low GCA but this may vary according to mating designs and locations (Bradshaw and Mackay, 1994; Ortiz and Golmirzaie, 2002). Accordingly, past studies showed that SCA was more important than GCA for total tuber yield, marketable tuber yields, average tuber weight, number number/plant and plant vigour (Gopal and Minocha 1998; Kumar and Kang, 2005). However, other studies (Iqbal and Khan, 2003; Haydar et al., 2009) found both GCA and SCA to be significant in controlling potato tuber yields; the GCA variance was double that of SCA indicating the predominance of additive gene action in controlling this trait (Haydar et al., 2009). In controlling tuber number/plant and the tuber % dry matter content, the SCA was found to be greater than GCA (Haydar et al., 2009). Resistance to bacterial wilt of potatoes is caused by *Ralstonia solanacearum* (Smith 1896). Yabuuchi et al., (1995) was reported to be controlled by a few genes (Martin, and French, 1985) and by three independent and dominant major genes (Buddenhagen, 1986). In addition, it was reported that both additive and non-additive gene actions are important in the inheritance of the resistance (Rowe and Sequeira, 1970). Later, it was reported that resistance is controlled by at least four major genes (French et al., 1997; Grimsley and Hanson, 1998). Other studies indicated that the resistance is polygenic and quantitative in nature, and involves genes with major and minor effects (Tung et al., 1993; Cook and Sequeira, 1994). Tung et al. (1992) found that the SCA effect was more important than the GCA effect in conditioning resistance to bacterial wilt, and there was a strong genotype x environment interaction. In the contrary, it was found that both GCA and SCA effects were important in bacterial wilt resistance in tomatoes; GCA was found to be six times as large as SCA indicating the predominance of additive gene effects in bacterial wilt resistance (Osiru et al., 2001). There is also evidence that in the inheritance of resistance to bacterial wilt in potatoes, non-additive gene action is important, and is largely of the epistatic type (Tung et al., 1992a; Tung et al., 1992b; 1993). Therefore, breeding schemes designed to make use of both additive and non-additive gene actions seem most suitable in developing resistance. Moreover, the genetic background for adaptation is of crucial importance for expression of resistance (Tung, 1992; Tung et al 1993). Several studies have shown that the resistance to bacterial wilt in potatoes is very complex in nature; it is probably a function of environmental adaptation with genes for adaptation being involved (Tung et al., 1990; Tung et al., 1992a; Tung et al., 1992b). There is a large amount of interaction between genes for resistance and those for adaptation (Tung et al., 1992a; Tung et al., 1992b). Therefore, potato clones with a wide genetic background for both bacterial wilt resistance and adaptation tend to display a high level of resistance, which is stable over environments (Tung, et al., 1993). Good adaptation of the potential host to a particular environment is likely to strengthen expression of the resistance to wilt (Tung et al., 1990; Tung et al., 1992b). In order to develop a stable resistance in potato populations, a wide genetic base for resistance and adaptation to the environment where the pathogen occurs would therefore be necessary (Tung et al., 1993). Hayward (1991) reported that resistance of different crop plants to *R. solanacearum* is a polygenic phenomenon and depends upon environmental conditions. In Kenya, potato production has not achieved its full potential because of a number of constraints. These include low soil fertility, inadequate supply of certified seeds, use of low yielding varieties, and diseases (FAO, 2009). The most common diseases include late blight, viral infections and bacterial wilt (Kaguongo et al., 2008). Bacterial wilt has spread to all potato growing areas in Kenya, affecting over 70% of potato farms and causing yield losses of between 50% and 100% (Otipa et al., 2003; Muthoni et al., 2013). Because most measures to control the disease have largely failed or are impractical (Martin and French, 1985; Kaguongo et al., 2008; Champoiseau et al., 2010; Muthoni et al., 2010), breeding for host resistance could be the only viable option. In an attempt to develop improved potato clones with high yield and yield related traits and bacterial wilt resistance, the KARI-Tigoni potato research program in Kenya is constantly evaluating various locally grown varieties and clones from the International Potato Center (CIP) that are adapted to tropical highland environments. Consequently, detailed information on the combining ability of potato clones that are commonly grown by farmers and clones from the International Potato Center need to be determined as this information is essential for the breeding program. Therefore, the objective of this study was to determine the combining ability effects for yield and yield related traits and bacterial wilt resistance of selected potato clones and their crosses. Selected parental clones and promising families will be used for further breeding in Kenya and similar agro-ecologies.

Results

Analysis of variance for genotypes across sites

The combined analysis of variance showed significant differences among the crosses for TTW ($P \leq 0.001$), TTN ($P \leq 0.05$), PWTTW ($P \leq 0.001$), PSTTW ($P \leq 0.05$) and DTM ($P \leq 0.01$) (Table 3). The environmental (site) effect was significant ($P \leq 0.001$) for all the traits studied except PSTTN and AUDPC. The interaction between cross x site had significant ($P \leq 0.05$) effects for TTN and DTM.

There were significant differences ($P \leq 0.001$) among crosses for latent infection (Chi-square = 108.027; df=47) for Kinale and (Chi-square= 107.590; df=47) for the KARI-NARL site. In addition, the mean % LI was higher at KARI-NARL (56.4) than at Kinale (53.8).

Ranking of crosses for bacterial wilt resistance across sites

Generally, the crosses planted at Kinale took longer time to start wilting (53 days) and had lower values of AUDPC (1871.1), PSTTN (15.9) and PSTTW (18.0) than the crosses planted at KARI-NARL (Table 4). Potato crosses' resistance level to bacterial wilt as determined by ranking based on the mean value across sites for %LI, AUDPC, DTOW, PSTTW and PSTTN showed that the five most resistant crosses were 392278.19 x Ingabire, 394903.5 x Meru Mugaruro, 394903.5 x Bishop Gitonga, 394903.5 x Cangi and 392278.19 x Meru Mugaruro in that order (Table 4). Potato crosses' resistance to bacterial wilt as determined by ranking based on PTIT showed that the five most resistant crosses were 394903.5 x Ingabire, 394904.9 x Ingabire, 391919.3 x Ingabire, 394895.7 x Ingabire and 394905.8 x Ingabire in that order (Table 4). There was a significant ($P \leq 0.05$) and positive (r=0.318) correlation between the two ranking methods. However, no cross was resistant to bacterial wilt; crosses 394903.5 x Ingabire and 394904.9 x Ingabire were moderately resistant while crosses 391919.3 x Ingabire and 394895.7 x Ingabire were moderately susceptible. The other crosses ranged from susceptible to highly susceptible. General and specific combining ability estimates for selected tuber yield traits and bacterial wilt resistance at KARI-NARL.

Significant differences were found among the crosses for TTW ($P \leq 0.001$), TTN ($P \leq 0.05$), PWTTW ($P \leq 0.001$) and ($P \leq 0.001$) DTM at KARI-NARL (Table 5). Significant ($P \leq 0.001$) GCA effects were observed for males for TTW and DTM while GCA for females was significant for TTW ($P \leq 0.001$) and TTN ($P \leq 0.05$). In addition, male parents had far much higher GCA effect for TTW (812.65) than the female parents (480.60) while the opposite was true for TTN where males parents had GCA of (316230799728.1) and the females (4597865057068.8) (Table 5). The SCA effects were significant ($P \leq 0.05$) for TTN and ($P \leq 0.001$) for TTW, PWTTW and DTM (Table 5).The SCA was more important than GCA in the expression of all traits except PSTTW and AUDPC (Table 5).

Among the male parents, Kihoro had the highest GCA effects for TTW (7.96) followed by Bishop Gitonga (6.75) while Meru Mugaruro had the lowest (-10.51) (Table 5.6). Ingabire had the lowest GCA effects for AUDPC (-208.16) and PSTTW (-2.73) followed by Meru Mugaruro (200.10) and (-2.26) respectively (Table 6). Among the female parents, 391919.3 had the highest GCA for TTW (5.24) followed by 394903.5 (3.16) while 392278.19 had the lowest (-7.17) (Table 6). In addition, 391919.3 had the lowest GCA effects for AUDPC (-128.02) and PSTTW (-1.84) followed by 394895.7 (-53.02) and (-1.25) respectively (Table 6).

Among the crosses, 394905.8 x Kihoro had the highest (31.94) SCA effect for TTW followed by 394903.5 x Kenya Karibu (31.46) (Table 7).

General and specific combining ability estimates for selected tuber yield traits and bacterial wilt resistance at Kinale

At Kinale site, significant ($P \leq 0.001$) differences were found among the crosses for TTW and PWTTW (Table 8). In addition, significant GCA effects were observed for males for TTW ($P \leq 0.001$) while for females, the GCA effects were

Table 1. Name, source, parentage, and reaction to bacterial wilt of the 14 potato parents.

Parent	Germplasm maintainer	Male/Female	Reaction to bacterial wilt
Cangi	KARI- Tigoni	Male	Susceptible
Kenya Karibu	KARI- Tigoni	Male	Susceptible
Tigoni	KARI- Tigoni	Male	Susceptible
Sherekea	KARI- Tigoni	Male	Susceptible
Meru Mugaruro	KARI- Tigoni	Male	Susceptible
Kihoro	KARI- Tigoni	Male	Susceptible
Ingabire	KARI- Tigoni	Male	Susceptible
Bishop Gitonga	KARI- Tigoni	Male	Susceptible
391919.3	CIP	Female	Tolerant
394904.9	CIP	Female	Tolerant
394905.8	CIP	Female	Tolerant
392278.19	CIP	Female	Tolerant
394895.7	CIP	Female	Tolerant
394903.5	CIP	Female	Tolerant

CIP= International Potato Center, KARI-Tigoni= Kenya Agricultural Research Institute, National Potato Research Centre, Tigoni

Table 2. Resistance levels of potatoes to bacterial wilt based on percentage of total infected tubers.

Resistance levels	PTIT
Highly resistant	0
Resistant	1<15
Moderately resistant	15- <30
Moderately susceptible	30- <45
Susceptible	45- <60
Highly susceptible	≥60

Modified from CIP(2007)

Table 3. Combined analysis of variance for bacterial wilt resistance and, tuber yields and related traits at KARI-NARL and Kinaleo.

Source of variation	df	Mean squares							
		TTW	TTN	PSTTN	PWTTW	PSTTW	AUDPC	DTOW	DTM
Sites	1	3541.17***	0.275422294E+16***	29639.23 ns	1950.47***	921.71***	1012.50 ns	975.35***	5210.50***
Rep(sites)	4	503.66***	508913253243.4***	21230.78 ns	45.49 ns	84.22 *	974801.00 ns	554.51***	39.93 ns
Crosses	47	1029.74***	1558531282495.7*	18950.26 ns	612.64***	41.33*	1462926.20 ns	98.22 ns	47.47*
Crosses x sites	47	65.75 ns	1525525137858.0*	18704.06 ns	16.67 ns	7.56 ns	936388.20 ns	42.01 ns	49.51*
Residual	188	124.71	1003526528920.5	18449.45	85.28	28.76	1143526.22	75.44	32.84

*= Significant at P≤ 0.05; **= Significant at P≤ 0.01; ***= Significant at P≤ 0.001; df=Degrees of freedom; TTW= Total tuber weight ($t\ ha^{-1}$); TTN=Total tuber number per hectare; PSTTN= Percentage of symptomatic tubers (% of total tuber number per hectare); PWTTW= Percentage of ware sized tubers (% of total tuber weight in $t\ ha^{-1}$); PSTTW= Percentage of symptomatic tubers (% of total tuber weight in $t\ ha^{-1}$); AUDPC= Area under the disease progress curve; DTOW= Days to onset of wilting; DTM=

significant for TTW (P≤ 0.01). Male parents had higher GCA for TTW (552.97) than female parents (496.37); the opposite was the case for PWTTW where male parents had lower GCA (91.73) than the female parents (156.39) (Table 8). The SCA effects were significant (P≤ 0.001) for TTW and PWTTW (Table 8). The SCA was more important than GCA in the expression of all traits except PSTTW and PSTTN (Table 5.8). For these two traits, GCA was almost equal to SCA (Table 8). Among the male parents, Meru Mugaruro had the lowest GCA for PSTTN (-1.18) and AUDPC (-315.52) (Table 9) followed by Ingabire PSTTN (-0.77) and AUDPC (-211.35). Kihoro had the highest GCA for TTW (8.34) followed by Bishop Gitonga (4.76). Among the female parents, 391919.3 had the lowest GCA for AUDPC (-212.81) followed by 394895.7 (-169.69). Among the crosses, 391919.3 x Ingabire had the lowest SCA effects for PSTTN (-2.46) while 394903.5 x Cangi had the lowest SCA effects for AUDPC (-1014.48) (Table 10). Furthermore, 394905.8 x Kihoro had the highest SCA effects for TTW (27.13) followed by 394903.5 x Kenya Karibu (24.37) (Table 10).

Discussion

This study aimed at determining the combining abilities for bacterial wilt resistance as well as tuber yield and its components in selected potato cultivars currently grown by farmers in Kenya as well as other advanced clones from the International Potato Center. Potato crosses planted at Kinale took longer time to start wilting and had lower values of %LI, AUDPC, PSTTN and PSTTW than the crosses planted at KARI-NARL possibly due to the low temperatures experienced at Kinale compared to KARI NARL. Kinale site is in Upper Highland (UH_1) agro-ecological zone as opposed to KARI-NARL which is at Lower Midland (LM_3)(Jaetzold et al., 2006c). It has been previously reported that high temperature promote survival, reproduction, infectivity, and spread of *R. solanacearum* and hence disease development (Harris, 1976; Martin and French, 1985).

The current study found that for all tuber yields related traits (TTN, TTW, PWTTW and DTM), SCA was greater than GCA. This is due to the fact that potato is naturally highly heterozygous and families could have dominant genetic effects for these traits. Most of the parents used in this study were bred at CIP (except Kihoro, Bishop Gitonga, Cangi and Meru Mugaruro) and are closely related. It was previously reported that GCA is significantly larger than SCA for tuber yields and quality traits in crosses between non-related parents while SCA appears to be more important among related parents (Neele et al., 1991; Ortiz and Golmirzaie, 2004). This is because in closely related breeding material, the number of different alleles at a locus is likely to be limited. Consequently, variation in additive gene action is limited while non-additive gene action, like dominance or epistasis, can result in a relatively large variation between

Table 4. Ranking of the potato crosses' resistance to bacterial wilt at Kinale and KARI-NARL.

Cross	AUDPC		DTOW		PSTTW		PSTTN		% LI		Overall Rank (a)	PTIT	Overall Rank (b)
	Kinale	KARI-NARL	Kinale	KARI-NARL	Kinale	KARI-NARL	Kinale	KARI-NARL	Kinale	KARI-NARL			
391919.3 x Bishop Gitonga	1815	1928	57	57	17.1	20.1	18.1	22.3	53.3	60.0	19.0	65.4	26.5
391919.3 x Cangi	1413	1832	57	47	13.8	18.7	15.0	18.6	40.0	73.3	6.0	63.7	24.0
391919.3 x Kenya Karibu	1775	1847	57	50	18.0	20.9	15.1	18.5	53.3	53.3	8.0	61.2	18.0
391919.3 x Kihoro	1720	1870	60	57	17.8	19.7	18.6	22.0	53.3	53.3	14.0	62.8	23.0
391919.3 x Meru Mugaruro	1745	1790	50	50	16.4	19.1	17.4	18.2	80.0	66.7	25.0	78.1	43.0
391919.3 x Tigoni	1845	1908	57	47	17.8	21.5	16.8	18.7	53.3	53.3	16.0	61.6	20.0
391919.3 x Sherekea	1788	1882	57	50	16.3	19.0	18.1	22.2	60.0	80.0	22.0	75.8	40.0
391919.3 x Ingabire	2053	1747	53	53	19.7	19.2	13.3	26.0	13.3	20.0	15.0	32.8	**3.0**
394904.9 x Bishop Gitonga	2140	2183	50	47	18.9	22.2	18.9	23.0	60.0	60.0	43.0	68.4	32.0
394904.9 x Cangi	1837	1912	53	50	19.1	21.6	17.7	23.0	80.0	80.0	31.0	84.1	47.0
394904.9 x Kenya Karibu	2502	2650	53	43	20.0	31.0	18.8	29.7	66.7	73.3	48.0	77.1	41.0
394904.9 x Kihoro	1880	2267	47	43	21.6	23.0	17.1	25.0	73.3	80.0	47.0	81.5	45.0
394904.9 x Meru Mugaruro	2010	2097	53	47	18.6	24.6	17.0	17.8	60.0	26.7	26.0	53.3	6.5
394904.9 x Tigoni	1787	2400	50	53	18.1	28.6	16.6	26.3	53.3	40.0	32.5	58.4	13.0
394904.9 x Sherekea	2297	2453	53	50	20.6	25.0	19.4	22.4	66.7	66.7	44.0	73.6	38.0
394904.9 x Ingabire	1750	1817	53	50	16.0	19.3	17.2	21.9	13.3	13.3	10.0	30.3	**2.0**
394905.8 x Bishop Gitonga	2090	2133	47	43	21.3	25.0	16.4	22.2	60.0	46.7	39.0	62.5	22.0
394905.8 x Cangi	2213	1993	53	47	18.9	21.7	17.6	21.7	46.7	93.3	37.0	75.4	39.0
394905.8 x Kenya Karibu	1875	1945	53	53	19.2	20.8	17.0	21.9	66.7	46.7	23.0	65.4	26.5
394905.8 x Kihoro	1827	1970	50	47	20.0	22.2	16.5	20.4	86.7	80.0	34.0	86.5	48.0
394905.8 x Meru Mugaruro	1580	1715	50	50	15.7	18.7	14.2	19.8	46.7	60.0	12.0	61.1	17.0
394905.8 x Tigoni	1895	1933	57	47	17.7	22.7	16.1	18.4	60.0	46.7	21.0	61.5	19.0
394905.8 x Sherekea	2255	2198	53	43	19.2	24.5	20.5	23.1	53.3	26.7	40.0	53.26	6.5
394905.8 x Ingabire	1648	1667	53	47	17.9	16.9	19.7	24.0	20.0	40.0	20.0	45.1	**5.0**
392278.19 x Bishop Gitonga	1955	2077	50	47	21.1	23.0	14.4	22.1	66.7	80.0	38.0	78.0	42.0
392278.19 x Cangi	2073	2200	50	40	19.2	23.6	19.0	24.5	40.0	60.0	41.5	60.6	16.0
392278.19 x Kenya Karibu	2037	2190	53	50	19.2	23.2	14.1	18.8	66.7	66.7	29.0	72.2	36.0
392278.19 x Kihoro	2217	2397	57	47	22.7	27.5	18.5	24.9	66.7	26.7	36.0	58.9	14.0
392278.19 x Meru Mugaruro	1440	1588	57	57	14.9	16.2	14.2	16.2	80.0	80.7	**5.0**	83.0	46.0
392278.19 x Tigoni	2185	2218	47	40	20.3	26.0	16.9	24.4	60.0	26.7	41.5	55.7	10.0
392278.19 x Sherekea	1618	1735	53	60	17.4	19.5	18.5	21.4	60.0	73.3	18.0	73.2	37.0
392278.19 x Ingabire	1253	1362	50	60	12.2	17.1	13.8	15.2	46.7	46.7	**1.0**	54.4	9.0
394895.7 x Bishop Gitonga	1785	1860	50	60	15.2	20.2	15.4	18.0	53.3	66.7	9.0	66.6	29.0
394895.7 x Cangi	1815	2172	57	47	18.9	24.1	16.9	20.9	66.7	80.0	30.0	78.2	44.0
394895.7 x Kenya Karibu	1735	1853	57	47	15.7	18.5	14.1	16.0	73.3	60.0	11.0	71.8	35.0
394895.7 x Kihoro	1802	1878	57	53	17.1	20.6	17.4	20.9	86.7	26.7	17.0	65.5	28.0
394895.7 x Meru Mugaruro	1928	2028	50	47	18.7	21.5	17.8	23.2	53.3	73.3	35.0	70.6	34.0
394895.7 x Tigoni	1677	1812	60	60	16.4	17.7	16.8	19.2	73.3	46.7	7.0	67.4	30.0
394895.7 x Sherekea	1910	1887	53	47	18.7	20.4	17.2	20.8	46.7	66.7	27.0	64.7	25.0
394895.7 x Ingabire	1848	1913	53	47	15.3	20.0	18.6	17.1	13.3	46.7	13.0	42.6	**4.0**
394903.5 x Bishop Gitonga	1573	1632	53	63	16.1	17.5	17.4	23.3	20.0	66.7	**3.0**	54.2	8.0
394903.5 x Cangi	1293	1395	53	50	14.1	17.9	17.7	18.4	46.7	46.7	**4.0**	56.3	12.0
394903.5 x Kenya Karibu	1980	2133	53	50	19.6	25.0	16.8	19.1	20.0	73.3	28.0	55.9	11.0
394903.5 x Kihoro	7412	2130	47	40	19.9	24.3	19.2	26.2	66.7	33.3	45.0	61.9	21.0

394903.5 x Meru Mugaruro	1297	1452	53	53	15.5	16.1	13.6	14.9	33.3	73.3	**2.0**	59.9	15.0
394903.5 x Tigoni	2522	2690	43	37	21.4	28.4	16.6	23.4	53.3	73.3	46.0	70.3	33.0
394903.5 x Sherekea	1978	2110	50	47	18.0	22.4	18.0	22.4	53.3	66.67	32.5	67.9	31.0
394903.5 x Ingabire	2072	2117	57	47	18.6	20.9	14.0	15.0	13.3	6.7	24.0	23.1	**1.0**
Mean	1871	1978	53	49	18.0	21.6	16.9	21.1	53.8	56.4		63.6	
% CV	28.0	27.4	6.9	11.7	12.4	15.6	11.8	14.2					
SE	524.47	541.73	3.67	5.75	2.23	3.37	2.00	3.00					

% LI= % Latent infection; DTOW= Days to onset of wilting; PSTTW= Percentage of symptomatic tubers (% of total tuber weight in t ha^{-1}); PSTTN= Percentage of symptomatic tubers (% of total tuber number per hectare); AUDPC= Area under the disease progress curve. PTIT= Percentage of total infected tubers.Overall rank (a) =ranking of crosses based on the means of AUDPC, DTOW, PSTTW, PSTTN and % LI. Overall rank (b) =ranking of crosses based on their mean PTIT

Table 5 . Analysis of variance of general and specific combining abilities for selected potato tuber traits at KARI-NARL

Source of variation	df	Mean squares							
		TTW	TTN	PSTTN	PWTTW	PSTTW	AUDPC	DTOW	DTM
Replications	2	0.05*	18265738589182**	42410.90 ns	3.637 ns	135.31 *	476441.15 ns	544.44 ***	9.90 ns
Crosses	47	645.64***	24765618979.7*	37644.73 ns	336.688 ***	34.03 ns	242465.39 ns	101.05 ns	56.56 ***
GCA Males	7	812.65 ***	316230799728.1 ns	38557.07 ns	88.891 ns	60.29 ns	389677.75 ns	74.50 ns	96.03 ***
GCA Females	5	480.60 ***	4597865057068.8*	36448.06 ns	130.849 ns	62.17 ns	385586.98 ns	69.03 ns	42.08 ns
SCA	35	635.81 ***	2941744091674.5*	37633.21 ns	415.653 ***	24.76 ns	192576.98 ns	110.93 ns	50.73 ***
GCA/SCA		0.40	0.36	0.40	0.15	0.62	0.57	0.30	0.46
Residual	94	132.81	1871410119854.1	36884.75	91.65	38.42	315083.70	95.51	23.37

* = Significant at P≤ 0.05; **= Significant at P≤ 0.01; ***= Significant at P≤ 0.001; df=Degrees of freedom; TTW= Total tuber weight (t ha^{-1}); TTN=Total tuber number per hectare; PSTTN= Percentage of symptomatic tubers (% of total tuber number per hectare); PWTTW= Percentage of ware sized tubers (% of total tuber weight in t ha^{-1}); PSTTW= Percentage of symptomatic tubers (% of total tuber weight in ton ha^{-1}); AUDPC= Area under the disease progress curve; DTOW= Days to onset of wilting; DTM= Days to maturity.

Table 6 . General combining ability effects of parents for different traits at KARI-NARL

Males	TTN	PSTTN	TTW	PWTTW	PSTTW	AUDPC	DTOW	DTM
Bishop Gitonga	486110.64	-15.36	6.75	2.49	0.28	-9.55	3.54	4.31
Cangi	202160.19	-15.99	-2.05	2.60	-0.35	-61.22	-2.57	0.42
Kenya Karibu	-81790.03	-16.50	-2.37	-0.45	1.63	124.62	-0.35	0.14
Kihoro	239197.31	114.50	7.96	0.68	1.27	106.84	-0.35	-0.14
Meru Mugaruro	-699073.36	-18.83	-10.51	-0.99	-2.26	-200.10	1.32	-3.47
Tigoni	66357.97	-15.44	5.58	1.36	2.53	181.84	-2.01	0.97
Sherekea	41666.64	-15.10	1.86	-1.87	0.19	65.73	0.21	-2.36
Ingabire	-254629.36	-17.30	-7.23	-3.82	-2.73	-208.16	0.21	0.14
SE(males' GCA)	322439.50	45.27	2.72	2.26	1.46	132.31	2.30	1.14
Females								
391919.3	54012.31	-16.35	5.24	-0.62	-1.84	-128.02	2.01	1.04
394904.9	-205246.69	-13.54	-0.90	-3.59	2.80	243.85	-1.32	1.67
394905.8	405863.81	-15.73	2.12	3.52	-0.07	-34.06	-2.15	-1.25
392278.19	-566357.53	-16.23	-7.17	0.64	0.39	-7.60	0.76	-1.67
394895.7	-279320.69	-17.66	-2.45	0.81	-1.25	-53.02	1.60	-0.42
394903.5	591048.81	79.50	3.16	-0.76	-0.04	-21.15	-0.90	0.63
SE (females' GCA)	279240.80	39.20	2.35	1.95	1.27	114.58	1.99	0.99

TTN=Total tuber number per hectare; PSTTN= Percentage of symptomatic tubers (% of total tuber number per hectare); TTW= Total tuber weight (t ha^{-1}); PWTTW= Percentage of ware sized tubers (% of total tuber weight in t ha^{-1}); PSTTW= Percentage of symptomatic tubers (% of total tuber weight in ton ha^{-1}); AUDPC= Area under the disease progress curve; DTOW= Days to onset of wilting; DTM= Days to maturity.

progenies. Plaisted et al. (1962) speculated that informal previous selection which narrowed the genetic base of the tested genotypes may be one of the possible causes for obtaining greater estimates of SCA variance for various characters. Killick and Malcolmson (1973), using a concept developed in evolutionary population genetics suggested that traits subjected to directional selection would be expected to show little additive genetic variance, but a large degree of dominance and epitasis, whereas the reverse would be true for traits subjected to stabilising selection.

Previous studies (Johansen et al., 1967; Killick, 1977; Maris, 1989) found the GCA to be more important than SCA for maturity; this is in agreement with the findings of the current study. Tai (1976) reported that variation between progenies for tuber yields and number of tubers per plant was dominated by SCA effect while for average tuber weight and specific gravity the GCA effect was more important.

The current study also found that GCA was more important than SCA in the expression of PSTTW and AUDPC (at KARI-NARL) and PSTTW and PSTTN at Kinale. For DTOW, the GCA and SCA effects were almost equal. This is in agreement with previous studies which reported that both major and minor genes are involved in the expression of resistance to bacterial wilt; and inheritance of this resistance involves both additive and non-additive gene actions (Tung et al., 1993; Tung and Schmiediche, 1995). Furthermore, epistasis was found to be important in the inheritance of this resistance (Tung et al., 1992a; Tung et al., 1993). Other reports showed significant GCA and SCA effects for bacterial wilt resistance indicating that both additive and non-additive gene actions are important in conditioning resistance expression (Chakrabarti et al., 1994). Additionally, it was found that the non-additive variance component for disease severity was 4.5 times more than additive component and a large proportion of non-additive variance was due to dominance or epistatic genetic effects (Tung, 1992). Given these contradictory results, selection of a resistant parent or cross should be done cautiously. This could be due to the strong host-pathogen-environment interaction that affects the expression of resistance (French and Lindo, 1982; Tung et al., 1990; Tung, 1992; Tung et al., 1992b).

Materials and Methods

Study sites

The production of F_1 potato seeds and the seedling multiplication were done at the Kenya Agricultural Research Institute, National Potato Research Centre at Tigoni (KARI-Tigoni). The KARI-Tigoni station is located 40 km north-west of Nairobi city centre, at an altitude of 2051 meters above sea level (masl) latitude of 1^0 9' 7.22" South and longitude 36^0 41' 8.72" East (Jaetzold et al., 2006c). The average annual rainfall is 1096 mm with a bimodal distribution. The long rainy season occurs between March and May, while the short rainy season is between October and December (Jaetzold et al., 2006a). The mean annual air temperature is 18^0C and ranges between 12 and 24^0C. The soil type is humic-nitosol (alfisol) derived from quartz trachyte (Jaetzold et al., 2006a). The soil is very deep and well drained with a pH range of 5.5 to 6.5. The soil is of medium inherent fertility with organic carbon content of 1.65%. Exchangeable bases of potassium, calcium and magnesium are moderate to high with available potassium being about 21.2 ppm (Jaetzold et al., 2006c).

Determination of combining abilities for bacterial wilt resistance and tuber yield and its components was carried out at the Kenya Agricultural Research Institute, National Research Laboratories (KARI-NARL) and at a farmer's field at Kinale. The KARI-NARL station is located 7 km northwest of Nairobi at an altitude of 1795 masl, latitude of $1^0$15' 31.64" South and longitude $36^0$46' 17.96" East (Jaetzold et al. 2006c). The average annual rainfall is 1295 mm with a bimodal distribution. A long rainy season occurs between March and May while the short rainy season is between October and December (Jaetzold et al., 2006c). The mean air temperature ranges from 13.3 to 22.9^0C. The soil type is humic-nitosol (alfisol) derived from quartz trachyte (UNESCO, 1977) and is locally referred to as the Kikuyu Red Clay. The Kinale site is located 70 km northwest of Nairobi at an altitude of 2674 masl, latitude of $0^0$51' 30.43" South and longitude $36^0$36' 3.83" East (Jaetzold et al., 2006c). The average annual rainfall is 1276 mm with a bimodal distribution. A long rainy season occurs between March and May while the short rain season is between October and December (Jaetzold et al., 2006c). The mean air temperature ranges from 13.5 to 15.2^0C. The soil type is humic-andosol (Jaetzold et al., 2006c).

Plant materials and crosses

Eight potato clones selected previously in a bacterial wilt screening trial (Muthoni et al., 2014) were used as males for crossing using a North Carolina II mating design. The eight clones are high yielding and popular with Kenyan farmers, but highly susceptible to bacterial wilt (Muthoni et al., 2014). These clones were crossed to a set of six clones used as females, which were sourced from the International Potato Center (CIP) in Peru. These six clones are reported to have moderate tolerance to bacterial wilt (Priou, 2004). In the field, all the 14 parents (Table 1) were planted out in a crossing block. Each parent was planted in three rows; each row had about 100 plants. Plants spacing was 75 x 30 cm between and within rows respectively. During planting, (Diammonium phosphate (DAP) (18% N: 46% P_2O_5) was applied at the recommended rate of 500 kg ha^{-1}. Weeding, ridging, and pests and late blight control were carried out as per recommendations for potato production in Kenya (KARI, 2008). Planting was done on 13th September 2012.

Generation of true potato seed and F_1 seedlings

A few days after crossing, berries started forming on successful crosses and about 40 days later, they were harvested. The harvested berries were stored in khaki paper bags for three weeks to soften before processing. The ripened berries were processed by cutting them with a knife and emptying the seeds into a basin containing clean water. The seeds were washed and then spread on filter papers and placed on a table in the laboratory to air-dry overnight. The following day, all the seeds from each cross family were soaked in 1500 ppm GA_3 solution for 24 hours to break dormancy. Thereafter they were rinsed and immediately sown in plastic trays containing sterilized sand. Watering was done using a can and the seedlings were sprayed against pests and diseases as required. Four weeks later, all the seedlings were transplanted directly from the plastic trays into the field at KARI-Tigoni during the long rains season of 2013. Transplanting was done on 3rd April 2013.

Field management of F_1 seedlings

The seedlings were transplanted in rows at spacing of 75 x 30 cm. At transplanting, DAP (18% N: 46% P_2O_5) was applied

Table 7. Specific combining ability effects of crosses for different traits at KARI-NARL.

Cross	TTN	PSTTN	TTW	PWTTW	PSTTW	AUDPC	DTOW	DTM
391919.3 x Bishop Gitonga	-449073.64	16.87	-10.99	8.84	0.57	87.47	1.88	-6.60
394904.9 x Bishop Gitonga	-1374998.64	14.70	-18.63	-12.34	-1.94	-29.41	-4.79	1.11
394905.8 x Bishop Gitonga	384258.86	16.15	-0.62	0.15	3.73	198.51	-7.29	2.36
392278.19 x Bishop Gitonga	-273147.81	16.49	7.34	-18.20	1.23	115.38	-6.88	4.44
394895.7 x Bishop Gitonga	328703.36	13.80	15.37	13.13	0.16	-55.87	5.63	3.19
394903.5 x Bishop Gitonga	1384257.86	-78.01	7.53	8.44	-3.76	-316.08	11.46	-4.51
391919.3 x Cangi	427468.81	13.75	-3.23	-2.39	-0.77	42.47	-2.01	2.29
394904.9 x Cangi	94135.81	15.33	-16.07	-15.62	-2.47	-249.41	4.65	-5.00
394905.8 x Cangi	-516974.69	16.27	13.06	7.38	0.55	110.17	2.15	-2.08
392278.19 x Cangi	-211420.03	19.53	-5.65	5.64	1.97	290.38	-7.43	-5.00
394895.7 x Cangi	20061.81	17.37	8.75	-6.54	4.04	307.47	-1.60	5.42
394903.5 x Cangi	186728.31	-82.24	3.14	11.53	-3.31	-501.08	4.24	4.38
391919.3 x Kenya Karibu	-1510800.97	14.15	5.08	-22.13	-0.48	-128.37	-0.90	-0.76
394904.9 x Kenya Karibu	970678.03	22.59	2.03	2.51	4.97	303.09	-4.24	-1.39
394905.8 x Kenya Karibu	-1121912.47	16.97	-20.25	4.40	-2.42	-123.99	6.60	-1.81
392278.19 x Kenya Karibu	1628084.86	14.33	1.94	1.14	-0.41	94.55	0.35	1.94
394895.7 x Kenya Karibu	155864.03	13.03	-20.26	10.06	-3.48	-196.70	-3.82	-2.64
394903.5 x Kenya Karibu	-121913.47	-81.07	31.46	4.02	1.83	51.42	2.01	4.65
391919.3 x Kihoro	-794752.31	-113.30	3.35	11.99	-1.34	-87.26	6.88	-0.49
394904.9 x Kihoro	-979937.31	-113.18	-7.55	-5.24	-2.66	-62.47	-3.13	-4.44
394905.8 x Kihoro	1520060.19	-115.51	31.94	-0.19	-0.66	-81.22	1.04	3.47
392278.19 x Kihoro	-26234.47	-110.52	-14.13	2.88	4.20	318.99	-1.88	-1.11
394895.7 x Kihoro	-165123.31	-113.11	-12.51	5.56	-1.06	-153.92	3.96	2.64
394903.5 x Kihoro	445987.19	565.61	-1.09	-14.99	1.51	65.87	-6.88	-0.07
391919.3 x Meru Mugaruro	-152777.64	16.23	3.49	-5.62	1.58	139.69	-2.57	-3.82
394904.9 x Meru Mugaruro	995369.36	13.04	25.73	14.30	2.41	74.48	-2.57	2.22
394905.8 x Meru Mugaruro	976850.86	17.14	-13.29	-3.69	-0.62	-29.27	1.60	-1.53
392278.19 x Meru Mugaruro	319444.19	14.10	4.89	8.44	-3.56	-182.40	5.35	2.22
394895.7 x Meru Mugaruro	-412036.64	22.47	0.32	-15.46	3.36	303.02	-5.49	-2.36
394903.5 x Meru Mugaruro	-1726850.14	-82.98	-21.14	2.04	-3.16	-305.52	3.68	3.26
391919.3 x Tigoni	1896603.03	13.33	10.32	2.99	-0.77	-123.92	-2.57	3.40
394904.9 x Tigoni	-66357.97	18.10	-4.88	16.20	1.63	-4.13	7.43	1.11
394905.8 x Tigoni	-825616.47	12.37	-6.86	-14.51	-1.39	-192.88	1.60	-2.64
392278.19 x Tigoni	-1927467.14	18.89	-0.98	-9.79	1.49	65.66	-7.99	-2.22
394895.7 x Tigoni	-140431.97	15.10	12.23	11.43	-5.21	-295.59	11.18	-3.47
394903.5 x Tigoni	1063270.53	-77.79	-9.82	-6.31	4.25	550.87	-9.65	3.82
391919.3 x Sherekea	291666.36	16.46	-2.70	5.85	-0.94	-34.48	-1.46	-1.60
394904.9 x Sherekea	-782406.64	13.87	11.44	-4.92	0.44	165.31	1.88	1.11
394905.8 x Sherekea	-60185.14	16.77	-0.32	-8.68	2.77	188.23	-3.96	0.69
392278.19 x Sherekea	467592.19	15.61	-2.14	19.13	-2.73	-301.56	9.79	4.44
394895.7 x Sherekea	624999.36	16.43	10.92	-14.82	-0.18	-104.48	-4.38	-0.14
394903.5 x Sherekea	-541666.14	-79.13	-17.21	3.45	0.63	86.98	-1.88	-4.51
391919.3 x Ingabire	291666.36	22.51	-5.31	0.48	2.15	104.41	0.76	7.57
394904.9 x Ingabire	1143517.36	15.56	7.94	5.11	-2.37	-197.47	0.76	5.28
394905.8 x Ingabire	-356481.14	19.82	-3.67	15.16	-1.96	-69.55	-1.74	1.53
392278.19 x Ingabire	23148.19	11.57	8.72	-9.23	-2.19	-401.01	8.68	-4.72
394895.7 x Ingabire	-412036.64	14.92	-14.81	-3.35	2.36	196.08	-5.49	-2.64
394903.5 x Ingabire	-689814.14	-84.39	7.14	-8.16	2.01	367.53	-2.99	-7.01
SE (females x males)	789812.24	110.88	6.65	5.53	3.58	324.08	5.64	2.79

TTN=Total tuber number per hectare; PSTTN= Percentage of symptomatic tubers (% of total tuber number per hectare); TTW= Total tuber weight (ton ha^{-1}); PWTTW= Percentage of ware sized tubers (% of total tuber weight in ton ha^{-1}); PSTTW= Percentage of symptomatic tubers (% of total tuber weight in ton ha^{-1}); AUDPC= Area under the disease progress curve; DTOW= Days to onset of wilting; DTM= Days to maturity.

Table 8. Analysis of variance of general and specific combining abilities for selected potato tuber traits at Kinale.

Source of variation	df	Mean squares							
		TTW	TTN	PSTTN	PWTTW	PSTTW	AUDPC	DTOW	DTM
Replications	2	581.79**	752087917305.3**	50.65*	87.34 ns	33.12 ns	1473160.9 ns	564.58 ***	69.97 ns
Crosses	47	449.85 ***	59290801374.0 ns	9.60 ns	292.62 ***	14.86 ns	2156849.0 ns	39.18 ns	40.42 ns
GCA Males	7	552.97***	71827207811.0 ns	18.11 ns	91.73 ns	21.85 ns	2262512.5 ns	20.24 ns	67.24 ns
GCA Females	5	496.37**	76811843318.7 ns	7.91 ns	156.39 ns	18.23 ns	1835623.6 ns	81.67 ns	21.42 ns
SCA	35	422.58***	54280514094.5 ns	8.13 ns	352.26 ***	12.98 ns	2181605.6 ns	36.91 ns	37.77 ns
GCA/SCA		0.45	0.48	0.52	0.19	0.51	0.39	0.48	0.44
Residual	94	116.61	35642937986.85	14.16	78.91	19.09	1971968.74	55.36	42.31

* = Significant at P≤ 0.05; **= Significant at P≤ 0.01; ***= Significant at P≤ 0.001; df=Degrees of freedom; TTW= Total tuber weight (t ha^{-1}); TTN=Total tuber number per hectare; PSTTN= Percentage of symptomatic tubers (% of total tuber number per hectare); PWTTW= Percentage of ware sized tubers (% of total tuber weight in t ha^{-1}); PSTTW= Percentage of symptomatic tubers (% of total tuber weight in t ha^{-1}); AUDPC= Area under the disease progress curve; DTOW= Days to onset of wilting; DTM= Days to maturity.

Table 9. General combining ability effects of parents for different traits at Kinale.

GCA Males	TTN	PSTTN	TTW	PWTTW	PSTTW	AUDPC	DTOW	DTM
Bishop Gitonga	-126758.15	-0.10	4.76	4.02	0.24	-89.13	-1.81	1.91
Cangi	73486.96	0.43	-1.98	0.05	-0.69	-208.02	0.97	1.35
Kenya Karibu	9290.24	-0.87	-1.41	-0.19	0.60	1.70	1.53	-0.31
Kihoro	48795.85	1.00	8.34	0.78	1.78	827.26	-0.14	0.52
Meru Mugaruro	-22808.65	-1.18	-9.01	-2.39	-1.41	-315.52	-0.69	2.47
Tigoni	43857.63	-0.24	4.33	0.65	0.58	2.81	-0.69	-3.09
Sherekea	11759.18	1.74	-1.07	0.60	0.33	-7.74	0.42	-1.98
Ingabire	-37623.04	-0.77	-3.97	-3.52	-1.41	-211.35	0.42	-0.87
SE(males' GCA)	86808.52	0.89	2.55	2.09	1.03	330.99	1.75	1.53
GCA Females								
391919.3	16697.53	-0.32	7.40	-0.95	-0.94	-212.81	2.92	-0.38
394904.9	-96449.76	0.95	-2.12	-4.50	1.08	43.02	-1.25	0.03
394905.8	-16635.60	0.35	-0.27	3.08	0.70	-59.27	-0.83	-1.42
392278.19	64845.07	-0.69	-6.04	0.80	0.35	-134.90	-0.83	1.49
394895.7	-11080.10	-0.09	-1.35	0.57	-1.06	-169.69	1.67	0.03
394903.5	42622.86	-0.21	2.38	1.01	-0.13	533.65	-1.67	0.24
SE (females' GCA)	75178.38	0.77	2.20	1.81	0.89	286.65	1.52	1.33

TTN=Total tuber number per hectare; PSTTN= Percentage of symptomatic tubers (% of total tuber number per hectare); TTW= Total tuber weight (t ha^{-1}); PWTTW= Percentage of ware sized tubers (% of total tuber weight in ton ha^{-1}); PSTTW= Percentage of symptomatic tubers (% of total tuber weight in t ha^{-1}); AUDPC= Area under the disease progress curve; DTOW= Days to onset of wilting; DTM= Days to maturity.

Table 10. Specific combining ability effects of crosses for different traits at Kinale.

Cross	TTN	PSTTN	TTW	PWTTW	PSTTW	AUDPC	DTOW	DTM
391919.3 x Bishop Gitonga	15648.03	1.67	-13.09	7.44	-0.23	134.76	2.64	-1.28
394904.9 x Bishop Gitonga	-6019.35	1.18	-14.76	-11.94	-0.50	203.92	0.14	-0.03
394905.8 x Bishop Gitonga	48981.15	-0.78	5.46	0.67	2.32	256.22	-3.61	3.09
392278.19 x Bishop Gitonga	-151016.85	-1.65	3.81	-16.10	2.50	196.84	-0.28	3.51
394895.7 x Bishop Gitonga	13796.32	-1.29	15.35	12.22	-2.06	61.63	-2.78	-1.70
394903.5 x Bishop Gitonga	78610.69	0.87	3.23	7.70	-2.04	-853.37	3.89	-3.58
391919.3 x Cangi	22808.25	-1.96	7.64	2.29	-2.62	-148.02	-0.14	-2.40
394904.9 x Cangi	91511.54	-0.58	-9.25	-14.99	0.69	19.48	0.69	2.19
394905.8 x Cangi	56141.38	-0.07	-5.09	5.64	0.90	498.44	0.28	-1.35
392278.19 x Cangi	4290.04	2.36	-7.20	6.80	1.52	434.06	-3.06	-0.94
394895.7 x Cangi	-23487.46	-0.31	15.69	-11.95	2.60	210.52	1.11	-1.15
394903.5 x Cangi	-151263.75	0.56	-1.79	12.22	-3.10	-1014.48	1.11	3.65
391919.3 x Kenya Karibu	12932.64	-0.58	1.44	-19.31	0.30	3.92	-0.69	0.94
394904.9 x Kenya Karibu	-155399.74	1.88	3.74	3.89	0.30	474.76	0.14	-1.15
394905.8 x Kenya Karibu	-101881.90	0.62	-13.29	2.68	-0.13	-49.62	-0.28	0.31
392278.19 x Kenya Karibu	127745.43	-1.18	1.48	-1.17	0.25	187.67	-0.28	-5.94
394895.7 x Kenya Karibu	55523.93	-1.77	-17.74	7.24	-1.84	-79.20	0.56	3.85
394903.5 x Kenya Karibu	61079.64	1.03	24.37	6.67	1.13	-537.53	0.56	1.98
391919.3 x Kihoro	225275.36	0.99	1.08	11.16	-1.11	-876.63	4.31	3.44
394904.9 x Kihoro	-209720.01	-1.74	-1.08	-6.49	0.66	-972.47	-4.86	1.35
394905.8 x Kihoro	6759.15	-1.74	27.13	0.30	-0.55	-923.51	-1.94	-0.52
392278.19 x Kihoro	162313.15	1.34	-14.09	1.70	2.50	-457.88	4.72	-0.10
394895.7 x Kihoro	16018.32	-0.36	-10.85	4.76	-1.68	-838.09	2.22	1.35
394903.5 x Kihoro	-200645.97	1.52	-2.19	-11.43	0.19	4068.58	-4.44	-5.52
391919.3 x Meru Mugaruro	-73486.81	2.03	-9.06	-9.94	0.68	291.15	-5.14	3.16
394904.9 x Meru Mugaruro	54475.15	0.33	19.59	17.44	0.91	300.31	2.36	2.74
394905.8 x Meru Mugaruro	211695.65	-1.84	-5.88	-4.23	-1.63	-27.40	-1.39	-0.80
392278.19 x Meru Mugaruro	-240151.68	-0.78	9.10	10.67	-2.10	-91.77	5.28	-5.38
394895.7 x Meru Mugaruro	-30894.51	2.19	-0.79	-13.86	3.09	431.35	-3.89	2.74
394903.5 x Meru Mugaruro	78362.19	-1.93	-12.95	-0.08	-0.96	-903.65	2.78	-2.47
391919.3 x Tigoni	-80894.42	0.51	6.40	2.09	0.09	72.81	1.53	-1.28
394904.9 x Tigoni	-86264.46	-1.03	-10.57	15.39	-1.56	-241.35	-0.97	-3.37
394905.8 x Tigoni	-210522.63	-0.89	0.18	-16.25	-1.65	-30.73	5.28	-0.24
392278.19 x Tigoni	152436.71	0.99	1.25	-6.19	1.36	334.90	-4.72	5.17
394895.7 x Tigoni	80215.21	0.24	11.93	10.23	-1.19	-138.65	6.11	-3.37
394903.5 x Tigoni	145029.58	0.19	-9.20	-5.27	2.95	3.02	-7.22	3.09
391919.3 x Sherekea	-33981.31	-0.20	-2.04	2.37	-1.14	26.70	0.42	0.94
394904.9 x Sherekea	153239.32	-0.13	9.36	-5.37	1.15	279.20	1.25	-4.48
394905.8 x Sherekea	43795.82	1.48	-1.41	-0.82	0.17	339.83	0.83	0.31
392278.19 x Sherekea	-82128.85	0.53	1.39	13.70	-1.28	-221.22	0.83	4.06
394895.7 x Sherekea	38240.32	-1.30	-0.38	-8.61	1.35	105.24	-1.67	-6.15
394903.5 x Sherekea	-119165.31	-0.38	-6.92	-1.28	-0.25	-529.76	-1.67	5.31
391919.3 x Ingabire	-88301.75	-2.46	7.63	3.90	4.03	495.31	-2.92	-3.51
394904.9 x Ingabire	158177.54	0.10	2.97	2.07	-1.66	-63.85	1.25	2.74
394905.8 x Ingabire	-54968.63	3.22	-7.10	12.02	0.57	-63.23	0.83	-0.80
392278.19 x Ingabire	26512.04	-1.61	4.26	-9.41	-4.75	-382.60	-2.50	-0.38
394895.7 x Ingabire	-149412.13	2.61	-13.22	-0.04	-0.27	247.19	-1.67	4.41
394903.5 x Ingabire	107992.92	-1.86	5.46	-8.54	2.08	-232.81	5.00	-2.47
SE (females x males)	212636.57	2.17	6.23	5.13	2.52	810.75	4.3	3.76

TTN=Total tuber number per hectare; PSTTN= Percentage of symptomatic tubers (% of total tuber number per hectare); TTW= Total tuber weight (t ha^{-1}); PWTTW= Percentage of ware sized tubers (% of total tuber weight in t ha^{-1}); PSTTW= Percentage of symptomatic tubers (% of total tuber weight in t ha^{-1}); AUDPC= Area under the disease progress curve; DTOW= Days to onset of wilting; DTM = Days to maturity.

at the recommended rate of 500 kg ha^{-1}. Weeding, ridging and pests and late blight control were carried out as per recommendations for potato production in Kenya (KARI, 2008). When the crop was mature, it was harvested, each plant separately. From each family, 150 plants were randomly sampled and from each selected plant, two tubers were retained. (The rest were later planted at KARI-Tigoni in the following season so as to generate more tubers for the second season bacterial wilt evaluation trial). One tuber from each of the 150 selected plants was picked and bulked together so as to come up with one bulked sample of 150 tubers. This was repeated again to generate a second bulked sample. Each of the two bulked samples consisted of 150 tubers. The two bulked samples were later planted out at KARI-NARL and Kinale respectively for determining the combining ability for bacterial wilt resistance and tuber yield and its components. To break tuber dormancy, the samples were treated by dipping them in a big container containing GA_3 at 5 ppm for ten minutes. Thereafter, they were air-dried and covered with a black polythene sheet for one month. They were then uncovered until sprouting.

Determination of combining abilities for bacterial wilt resistance and tuber yield and its components

Using the first clonal generation, combining ability effects for bacterial wilt resistance and, yield and related traits were determined at the KARI-NARL and at a farmer's field at Kinale. Once the two bulked tuber samples sprouted, they were planted out in the field at KARI-NARL and at Kinale during the 2013 short rains season so as to determine their reaction to bacterial wilt. Planting was done on 1st October 2013 at KARI-NARL and 2nd October at Kinale. At each site, the experimental materials consisted of the 48 families. These were planted in a 6 x 8 alpha lattice design replicated three times. Each plot consisted of 50 plants i.e. 5 rows each consisting of 10 plants. The tubers were planted in furrows at a spacing of 75 x 30 cm. During planting, DAP (18% N: 46% P_2O_5) was applied at the recommended rate of 500 kg ha^{-1}. Weeding, ridging and pests and late blight control were carried out as per recommendations for potato production in Kenya (KARI, 2008). To ensure uniform distribution of bacterial wilt at KARI-NARL and Kinale, a bacterial suspension concentrated at 3.0 x 10^9 cfu ml^{-1} was poured into the planting furrows at a rate of 1 litre per plot. The inoculated bacteria were confirmed as bacterial wilt biovar 2 by Plantovita, South Africa based on the ability of the bacteria to produce acid from several disaccharides and sugar alcohols (Buddenhagen and Kelman, 1964). For proper disease expression, supplemental watering using overhead irrigation was done during the dry times.

Data collection

Data collected include the number of days from planting to maturity (DTM), days to onset of wilting (DTOW) and bacterial wilt incidence (BWI). Time to maturity was counted as the number of days from planting to when 75% of the plants had senesced. These data were taken on a plot basis. The BWI scores were used to calculate area under the disease progress curve (AUDPC) (CIP, 2007) using the formula:

$$\text{AUDPC} = \sum_{i=1}^{n-1} \frac{(S_i + S_{i+1})(t_{i+1} - t_i)}{2}$$

Where S_i is the BWI at days *i*, and *n* is the total number of sampling times, *t* is the number of days after planting

During harvesting, the twenty four middle plants per plot were harvested, each plant separately. Total number of tubers was counted from each of the 24 plants. In addition, the number of symptomatic tubers (i.e. showing rotting or bacterial ooze in the tuber eyes or soil adhering to the eyes of the tubers) and healthy looking tubers (asymptomatic) were determined. The healthy looking tubers were then categorized based on size i.e. ware ($\geq$45mm diameter) and, seeds (<45mm diameter). Their number and weights were recorded. The weights of symptomatic and ware tubers were expressed as percentage of the total yields. The percentage of symptomatic tubers was expressed both in weight, a value which is useful to determine yield losses (t ha^{-1}), and as a number of infected tubers, a value which is used for the calculation of infection tuber rates. Only healthy-looking tubers selected above were analyzed for latent infection by *R. solanacearum.* For each plot, 60 healthy-looking tubers were placed in sugar paper bags and delivered to the laboratory for latent infection analysis. The tubers were washed and disinfected. They were then divided into five groups of 12 tubers each. Sap from each group was extracted to constitute a sample which was then analyzed for latent infection using the post-enrichment enzyme-linked immunosorbent assay on nitrocellulose membrane (NCM-ELISA) test (Priou et al., 1999a).

Analysis of variance

Data on days to maturity (DTM), days to onset of wilting (DTOW), area under the disease progress curve (AUDPC), total tuber numbers (TTN), total tuber weight in t ha^{-1}(TTW), percentage of symptomatic tubers based on total tuber numbers (PSTTN), percentage of symptomatic tubers based on total tuber weight (PSTTW), and percentage of ware sized tubers based on total tuber weight (PWTTW) values were subjected to analysis of variance using the lattice procedure of Statistical Analysis Systems (SAS 9.1) statistical package (SAS, 2003).

Data on TTN, TTW, PWTTW, PSTTN and PSTTW were first averaged on a plot basis; the average value was then used to extrapolate values per hectare. Data on latent infection (LI) level were subjected to the Kruskal-Wallis non-parametric test procedure using SPSS for Windows Release Version 18.0 (SPSS Inc., 2009). Data for different sites were analyzed separately. Families' resistance to bacterial wilt was determined using ranking based on % LI, AUDPC, DTOW, PSTTW and PSTTN and the percentage of total infected tubers (PTIT). Small values of % LI, AUDPC, PSTTW and PSTTN as well as, high values DTOW indicates high resistance. The PTIT was calculated as suggested by CIP (2007):

$$\text{PTIT} = \text{PSTTN} + \frac{(\text{\% healthy looking tubers x \% LI})}{100}$$

Where PTIT is the percentage of total infected tubers, PSTTN is the percentage of symptomatic tubers based on total tuber numbers and %LI is the % latent infection. Small values of PTIT indicates high resistance. Based on PTIT, bacterial wilt resistance levels are categorized as indicated in table 2 (CIP, 2007).

Estimation of general and specific combining ability effects

Parents were considered as fixed effects in the test of significance. The GCA and SCA values for each trait were calculated following the NC II mating design across sites (Hallauer et al., 1988) as follows:

$$Yijk = \mu + gi + gj + sij + \varepsilon ijk$$

Where, Yijk = observed value of the ijth genotype in the kth environment

μ = overall mean;

gi = the GCA effects of the i^{th} parent;

gj = the GCA effects of the j^{th} parent;

Sij = the SCA effects for the cross between the i^{th} parent and the j^{th} parent

εijk = experimental error associated with ij^{th} genotype in the k^{th} environment.

As the parents were considered fixed, inferences drawn from this study cannot be generalised. The relative importance of GCA and SCA in influencing performance of the crosses was estimated using the general predicted ratio (GPR) for all the traits (Baker, 1978);

$$\frac{GCA}{SCA} = \frac{\text{MSQ GCA (pooled)}}{\text{MSQ GCA (pooled)+MSQ SCA}}$$

$$\text{MSQ GCA (pooled)} = \frac{(MSQ\ GCA\ male + MSQ\ GCA\ female)}{number of replications}$$

Where; MSQ GCA and MSQ SCA are the mean squares for GCA and SCA, respectively. When the ratio >0.5, GCA is more important than SCA in the inheritance of the character concerned, while the reverse is true when the ratio is <0.5(Baker, 1978).

Conclusions

Significant (P≤ 0.001) GCA effects were observed for males for total tuber weight (TTW) and days to maturity (DTM) while the GCA effects for females were significant (P≤ 0.001) for TTW and total tuber numbers ha^{-1}(TTN) (P≤ 0.01) at KARI-NARL. Among the crosses, the nine crosses with the highest SCA effects for TTW at KARI-NARL were 394905.8 x Kihoro (31.94), 394903.5 x Kenya Karibu (31.46), 394904.9 x Meru Mugaruro (25.73), 394895.7 x Bishop Gitonga (15.37), 394905.8 x Cangi (13.06), 394895.7 x Tigoni (12.23), 394904.9 x Sherekea (11.44), 394895.7 x Sherekea (10.92) and 391919.3 x Tigoni (10.32) in that order. At Kinale, the nine crosses with the highest SCA effects for TTW were 394905.8 x Kihoro (27.13), 394903.5 x Kenya Karibu (24.37), 394904.9 Meru Mugaruro (19.59), 394895.7 x Cangi (15.69), 3948957 x Bishop Gitonga (15.35), 394895.7 x Tigoni (11.93), 394904.9 x Sherekea (9.36), 392278.19 x Meru Mugaruro (9.10) and 391919.3 x Cangi (7.64) in that order. These crosses were selected for high tuber yield and will be evaluated in future. For bacterial wilt resistance, the best general combiners were Ingabire, Meru Mugaruro, 391919.3, 394895.7 and 394903.5. These parents were selected for future crosses.

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