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Inheritance of bacterial wilt resistance in five tomato cultivars

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Five tomato cultivars were studied for inheritance of bacterial wilt resistance. Lines AVTO1429, AVTO1424, and AVTO1314 have the resistance gene, Roma VF lacks the resistance gene, and Valoria Select is claimed to have resistance but has not been evaluated. The study, which was carried out in a split plot design, involved six generations and backcrosses that were conducted in a greenhouse and a field. Artificial inoculation of *Ralstonia solanacearum* was carried out in greenhouse. Parental lines AVTO1429, AVTO1424 and AVTO1314 had the lowest incidence of 37.78, 26.67 and 26.67%, respectively while Roma VF had the highest at 95%. F1 hybrids had lower incidence of ≤ 33.33% in all the crosses. Cross F1 x Parent 2 (BC2) had significantly lower disease incidence and severity compared to F2 hybrids, F1 x Parent 1 (BC1) and P1 (Roma VF) in all crosses. Computation of gene effects showed significant additive effects of 1.941 for cross Roma VF x AVTO1429 and 1.925 for cross Roma VF x Valoria select at p<0.01. Dominance effects, additive x additive, additive x dominance and dominance x dominance interaction in all the crosses were significantly different at p<0.01. The important gene effects for bacterial wilt resistance inheritance was in additive and dominance-additive portions which implied that the resistance trait was inherited.

Key words: *Ralstonia solanacearum,* tomato, resistance trait, inheritance, bacterial wilt.

INTRODUCTION

One of the most devastating bacterial diseases in tomatoes production in Kenya is bacterial wilt caused by *R. solanacearum.* The disease has been reported to cause between 64 and 100% losses in crops grown in open field and greenhouse, respectively (Mbaka et al., 2013). Among the most efficient and effective management strategies, use of resistant tomato varieties has gained popularity (Fufa et al., 2009; Jitendra et al., 2012; Kiriika et al., 2013). However, due to development of new strains of *R. solanacearum,* there is need to advance the available resistance varieties and develop new ones through breeding (Aslam et al., 2017). Seed companies in Kenya import resistant tomato varieties with qualities preferred by consumers at high costs which makes them expensive] and unaffordable to smallholder farmers (Kitinoja et al., 2011).

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Examples of such varieties include Riogrande, Cal J, Roma VF, UC82, Proster F_1, Kentom F_1, M-82 and Kilele F_1 (Monsanto, 2013; Ochilo et al., 2019). However, these varieties are related to various constraints such as exorbitant prices, susceptibility to diseases like bacterial wilt and pests like *Tuta absoluta,* and inadaptability to ecological condition in Kenya (Kitinoja et al., 2011). The increase in demand for tomato varieties that combine bacterial wilt resistance with good yields and agronomic characteristics from growers has prompted the need to advance the current cultivars to alleviate the gap (Muthoni et al., 2015). However, there are limited tomatos breeding program in East African region such as the World Vegetable Centre Regional Program centred in Tanzania (Fufa et al., 2009). The program has carried out several attempts to breed bacterial wilt resistance cultivars such as AVTO1429, AVTO1424 and AVTO1314 (AVRDC, 2017). Despite the efforts, the success of this breeding work has been hindered by variability in the pathogen strains and pathogen x genotype interaction influenced by the environment (Neto et al., 2002).

Generation means analysis has been extensively employed to estimate the main genetic variability, such as additive effects, dominance effects, and their digenic interactions, involved in the expression of traits such as resistance to bacterial wilt, yield, and yield-related traits (Jasmina et al., 2011). Resistance to bacterial wilt in tomato plants has been identified as monogenic, oligogenic or polygenic (Neto et al., 2002). Reports on polygenic nature of resistance, with the presence of partial dominance and epistasis, have been more frequent (Opena et al., 1992: Neto et al., 2002: Acharya et al., 2018). Breeders at AVRDC have generally treated bacterial wilt resistance as a polygenic trait despite the conflicting theories on the genetic systems (Opena et al., 1992). This implies that both additive and non-additive gene action is involved in the genetic system conditioning bacterial wilt resistance (da Silva Costa et al., 2018). The source of resistant gene, knowledge of inheritance scheme, types of resistance and the mechanism of tomato resistance to bacteria have been mastered by plant breeders, in development of breeding program for resistance tomato variety to bacterial wilt (Maulida et al., 2019).

The objective of this study was to evaluate inheritance of bacterial wilt resistance traits and identify potential parental crosses for further breeding.

METHODS

Experimental sites

Experimental sites were bacterial wilt infected field in Kirinyaga County during long rain season and greenhouse at Kabete Field Station, Kiambu County Nairobi / Africa, in 2019. Kiambu County is located at 01°15'S; 036°44'E, agro-ecological zone (AEZ) III. The region has temperature ranges from 12.3 to 22.5°C and receives rainfall distributed in two seasons of 1059 mm per year. The humic nitisols in the region are deep and well-drained with a pH of about 5.0 to 5.4 (Lengai, 2016). The farmer's field is located at 0.5420° S, 37.2735° E, and agro-ecological zone (AEZ) II. The region has temperature ranges from 15.6 and 28.6°C and receives rainfall distributed in two seasons of 1470 mm annually. The humic nitisols in the region are well-drained with a pH of about 5.0 (KARI, 2013).

Plant materials

Five tomato cultivars were studied for inheritance of bacterial wilt resistant trait. Lines AVTO1429, AVTO1424 and AVTO1314 with resistance gene sourced from the World Vegetable Centre (AVRDC), Roma VF lacks resistance gene and Valoria Select claimed having resistance but not evaluated sourced from Continental Seeds Company Limited.

Development of study populations

The experiment was carried out in a split-plot design with three replicates. The experiment was conducted in two parts, development and evaluation of the study population. Four bi-parental crosses: Roma VF x AVTO1429, Roma VF x AVTAO1424, Roma VF x AVTO1314 and Roma VF x Valoria Select were developed in a 10 x10 half diallel mating design excluding reciprocals in April-August season, 2018 using a procedure by Griffing (1956). The F_1s' were backcrossed to both parents (BC_1P_1 and BC_1P_2) and also advanced to F_2 at Kabete Field Station during September-December, 2018 following a protocol by Sharma (1988). Screening for reaction of parents and their hybrids to bacterial wilt was conducted in field with history of *Ralstonia solanacearum* infection and in greenhouse that was artificially inoculated at Kabete Field Station from April to August, 2019.

Evaluation of study populations

Experimental layout

Seedlings were raised in germination 204-cells trays with a depth and width of 3.5 and 2.5 cm, respectively. The trays contained sterile peat moss as planting media and one seed per cell, raised under a propagation unit. Daily watering of seedlings was carried out. Seedlings having 4 true leaves were hardened by reducing watering and removing netting, 25 days after sowing, before transplanting. One-month-old seedlings were watered 12 hours before transplanting in the early morning to the farmer's fields and the greenhouse for evaluations. In the field, deep ploughing at 45cm, ridges of 30 cm high and 25 cm wide to raise the beds were prepared as described (KALRO, 2016). A split-plot design with four families as main plots and the six generations as subplot replicated three times was established. The main plot had a configuration of 36x54 meters with 18 subplots of 2m by 3m. Subplots had four rows each with five plants. Plants and rows number per plot differed with generations. More rows were assigned to segregating F_2 and backcross populations than the non-segregating F_1 and parental populations. F_2 generation had 40 rows with 200 plants, backcross had 20 rows with 100 plants and 4 rows with 20 plants were assigned to non-segregating generations (P_1, P_2 and F_1) using modified procedure of Checa et al. (2006).

Crop management

Hand-weeding was used to maintain the crop weed free at a 2-3 weeks' interval. Drip irrigation was used to supplement rainfall. On planting, both di-ammonium phosphate fertilizer (DAP 18:46:0) and N: P: K (17: 17: 17) were each applied at the rate of 12 g plant^{-1}

during transplanting. Calcium ammonium nitrate (CAN) at the rate of 100kg/ha was used as first top dress when plants were 25 cm high and second top dress, 55days after transplanting at the rate of 200kg/ha. Fertilizers were used to maintain crop health while preventing deficiency disorders (KALRO, 2016). Insecticide Metalaxyl-M and Propineb (700 g/kg) at the rate of 50g / 20 litres of water was applied at an interval of two weeks to manage against early and late blights. Imidaclopride (100 g l^{-1}) and betacyfluthrine (45g l^{-1}) at the rate of 0.2 l ha^{-1} and Thiamethoxam at the rate of 8g / 20 litres water were used to control aphids, whiteflies, and leaf miners during the crop growth cycle.

Greenhouse trial

Plastic pots with 5-litre capacity were filled with 2 parts of forest soil, 1 part well decomposed manure and 1part sand up to 2kg. The forest soil was obtained from *R. solanacearum* free fields and artificially inoculated with *R. solanacearum* pathogen.

Inoculum preparation: Followed the protocol described by Kiriika et al. (2013). Diseased material was collected from farmers' fields in Kirinyaga County. Isolation of the pathogen was conducted in Petri dishes with culturing media. The media contained nutrients glucose agar (NGA) with 5% bactopeptone, 0.25% D-glucose, 0.3% beef extract and 1.5% agar in one litre demineralised water (dH_2O). The culture was incubated at 30°C for 48 hours. Triphenyl Tetrazolium Chloride (TZC) medium was used for purification of the colonies and for distinguishing *R. solanacearum* from other bacteria (Fajinmi and Fajinmi, 2010).

Colony characterization of the pathogen: Colonies that measured 7.0-9.0mm, round, white, fluidal with irregular margins and pinkish-red centre were observed.

Inoculation: bacterial suspension for inoculation was obtained by flooding pure culture petri dishes, with 15ml sterile distilled water and serial dilution up to five folds. The bacterial suspension was adjusted to 10^7 cfu/ml by serial dilution technique. The bacterium was inoculated by pricking the tomato seedlings roots with a sterile needle to expose avenues for bacterial entry. Each tomato pot was inoculated with 25ml of the 10^7 cfu/ml bacterial suspension around the root base.

Data collection

Bacterial wilt incidence and severity score

Bacterial wilt incidence was evaluated in the field and in the greenhouse after inoculation. The number of wilted plants was counted after 28 days of transplanting and recorded at four days' interval up to 126 days after transplanting. To confirm the wilt was due to bacteria and not Verticillium or Fusarium wilt, bacterial streaming was carried by checking bacterial ooze from infected plants. Disease incidence (DI) was determined as a percentage of the average wilted plant over the plant population per treatment. Bacterial wilt severity on tomato was evaluated using a score from 0 to 5. Where: 0-no symptom, 1-one leaf wilted, 2-two leaves wilted, 3-three leaves wilted, 4-all leaves wilted except the tip and 5-entire plant wilted (death). The disease evaluation followed the procedure of Jeger and Viljanen-Rollinson (2001).

Data analysis

Data on bacterial wilt incidence and severity were subjected to analysis of variance (ANOVA) using Genstat software 15th edition. The analysis aimed to determine their significant differences. Means were separated using Tukey's procedure for multiple comparisons (P≤ 0.05). Further, significantly different variables were subjected to generation mean analysis (GMA). The variables were indicated by orthogonal contrasts between parents P_1 and P_2. The aim of this study was to establish if bacterial wilt is inherited quantitatively or qualitatively using the methodology proposed by Checa et al. (2006).

Analysis of generation means

Analysis followed the approach of Sharma (1988). Generation mean development was calculated by summing the number of observations for a trait in each generation and dividing by the total number (n) of sampled plant i.e $\ddot{\bar{X}}$=T/n. Calculating the variance and mean variance of each generation was: Variance for each generation =∑ SS/ (n-1) and Mean variance for each generation $\bar{V}$=V/n. Epistasis affects the estimation of additive and dominance components of variance. Scaling tests were used to determine epistatic effects for the trait studied and the appropriate model for genetic analysis. Four scales A, B, C, D were used to determine the presence of an additive, dominance, and the type of interaction effects. Computation of the scales was achieved as A= $\bar{P1}$ +$\bar{F1}$-2$\bar{BC}$1, B=$\bar{P2}$+$\bar{F1}$-2$\bar{BC}$2, C=$\bar{P1}$+$\bar{P2}$+2 $\bar{F1}$-4 $\bar{F2}$ and D=2$\bar{F2}$-$\bar{BC}$1-$\bar{BC}$2 Where: A= additive x dominance (P1), B= additive x dominance (P2); C= dominance x dominance; D=additive x additive. Test for significance of each scale was done using the equation t (A) = A/SE (A) Where: A= additive x dominance (P1) and SE= Standard error. This was done for each scaling test. Significance of even one of the 4 scales showed the presence of epistasis, therefore necessitated analysis of components of means. Analysis of components of means in crosses with epistasis was conducted using 6-parameters model since backcrosses were used following a procedure of Sharma (1988)

RESULTS

General mean analysis for bacterial wilt

Significant difference at P≤0.01 (**) was revealed by analysis of variance (ANOVA) among the generations for bacterial wilt incidence (Table 1) and severity (Table 5). Highly significant differences between the sites were noted in cross Roma VF x AVTO1429 at P≤0.05 (*) and Roma VF x Valoria select at P≤0.01.

Bacterial wilt incidence (%)

An increase in percent incidence from an average of 22.15 to 58.33% was noted from 18 to 65 days after transplanting. Disease incidence was higher by ≥10% in the field compared to the greenhouse in all the crosses (Table 2). Parent AVTO1429 had the lowest bacterial wilt incidence of 31.11% followed by BC2 (F1 x AVTO1429) at 45.56%. P_1 (Roma VF) had the highest incidence of 88.89% followed by BC_1 (F1 x Roma VF) at 54.44% in the greenhouse. Compared to better parent AVTO1429, F_1

Table 1. ANOVA Table for Bacterial wilt incidence in four crosses recorded for five weeks.

Source	df	Week 1	Week 2	Week 3	Week 4	Week 5
Roma VF x AVTO1429						
Replicate	2	1655.6	1384.7	592.86	265.02	126.77
Generation	5	1365.6**	2702.7**	2950.52**	2594.71**	2417.76**
Sites	1	926.7*	1443.9**	493.75*	565.38*	796.46**
Generation x Sites	5	84.8	137.8	66.43	41.39	20.36
Residue	22	117.4	123.9	98.21	91.68	73.84
Roma VF x AVTO1424						
Replicate	2	396.09	906.8	71.48	56.8	220.86
Generation	5	913.32**	2235**	4176.86**	3805.99**	3502.30**
Sites	1	12.64	17.3	71.34	9.65	8.99
Generation x Sites	5	44.05	146.9	29.97	151.46	158.04
Residue	22	74.79	108.7	68.77	79.82	99.37
Roma VF x AVTO1314						
Replicate	2	1443.09	1111.2	199.5	91.6	100.2
Generation	5	3683.04**	4683.6**	5193**	5078.6**	4637.1**
Sites	1	241.94	4410	183.7	89.2	10.4
Generation x Sites	5	40.5	56.1	58.1	22.5	23.7
Residue	22	97.51	124.2	175.3	126.3	156.4
Roma VF x Valoria select						
Replicate	2	2207.*5	1432.5	583.4	104.63	63.3
Generation	5	1091.2***	1602.0**	1459.6**	1581.91**	1393.0**
Sites	1	1360.9**	1801.8**	1103.7*	613.99**	290.9
Generation x Sites	5	46.9	103.7	50.4	15.7	11.3
Residue	22	187.1	103.2	137.9	71.18	100.7

Sites were Kabete greenhouse and Sick plot at Kirinyaga county during long seasons, 2019. *, ** Significant at 5 and 1% probability levels, respectively.
Source: Author's work

and F_2 hybrids had significantly higher incidence of 53.33 and 48.45%, respectively. Similar results were noted in the field where P_2 showed the lowest incidence of 37.78% and P_1 the highest at 100% followed by BC_1 at 70%. In the greenhouse, the F_1 hybrid from cross Roma VF x AVTO1424 had the lowest bacterial wilt incidence of 33.33% followed by BC_2 at 37.78%. Similarly, in the field, P_1, had the highest bacterial wilt incidence of 100% followed by BC_1 at 68.89 while P_2 (AVTO1424) had the lowest incidence of 26.67% followed by F_1 hybrids at 31.11% (Table 2).

For cross Roma VF x AVTO1314 in the field, F_1 hybrids showed the lowest disease incidence of 22.22% followed by P_2 (AVTO1314) at 26.67% while P_1 (Roma VF) showed the highest incidence of 100% followed by BC_1 at 72.22%. F_2 hybrids and BC_2 had significantly higher incidence of 45.78 and 35.56%, respectively compared to better parent (AVTO1314). Similar trend of results was observed in the greenhouse. F_1 hybrids showed the lowest incidence of 57.78% followed by BC_2 at 60% in the field while Roma VF (P_1) had the highest incidence of 100% followed by BC_1 at 72.22%. There was no significant difference in bacterial wilt incidence for F_1, F_2, BC_2 and P_2 (Valoria select). This trend of results was also observed in the greenhouse but was lower than in the field.

Scale tests had significant differences at P≤0.01 in all the 4 crosses (Table 3). This means that there was additive x dominance interaction (A** and B**), dominance x dominance interaction (C**) and additive x additive interaction (D**).

The 6-parameter model computation of gene effects, showed significant differences ($p<0.01$) in additive effects at 1.941 and 1.925 in cross Roma VF x AVT01429 and Roma VF x Valoria select, respectively (Table 4). All the crosses showed significant differences ($p<0.01$) in dominance effects, additive x additive interaction, additive x dominance interaction and dominance x dominance interaction.

Bacterial wilt severity score

In the field, Parent AVTO1429 had the lowest bacterial

Table 2. Bacterial wilt incidence for six tomato generations in four crosses recorded for five weeks at Kabete Greenhouse and Sick plot at Kirinyaga County, 2019.

Generation	Week 1			Week 2			Week 3			Week 4			Week 5		
	Greenhouse	Field	Mean	Greenhouse	Field	Mean	Greenhouse	Field	Mean	Greenhouse	Field	Mean	Greenhouse	Field	Mean
Roma VF x AVTO1429															
P_2	6.67	8.89	7.78	8.89	13.33	11.11	22.22	22.22	22.22	26.67	33.33	30.00	31.11	37.80	34.44
P_1	40	60.00	50.00	57.78	84.44	71.11	77.78	93.33	85.56	84.44	100.00	88.89	92.22	100	94.44
F_1	17.78	35.56	26.67	28.89	48.89	38.89	42.22	57.78	50.00	48.89	62.22	53.33	55.56	68.90	61.11
F_2	14.67	24.44	19.55	23.11	36.89	30.00	36.00	42.67	39.33	45.78	51.11	48.45	48.45	53.80	51.11
BC_1P_1	12.22	21.11	16.67	20.00	30.00	25.00	37.78	41.11	39.44	48.89	52.22	50.55	54.44	64.50	59.45
BC_1P_2	11.11	13.33	12.22	17.78	18.89	18.33	28.89	32.22	30.56	43.33	46.67	45.00	45.56	53.30	49.45
Mean	17.07	27.22	22.15	26.07	38.74	32.41	40.82	48.22	44.52	49.67	57.59	53.63	53.63	63.00	58.33
CV (%)	44.4	36.6	48.9	34.3	22.6	34.4	24.9	15.1	22.3	18.1	15.8	17.9	17.8	9.6	14.7
LSD(P≤0.05)	16.34	18.15	18.35	20.45	15.92	18.85	18.48	14.25	16.78	16.36	13.41	16.21	17.33	11.1	14.55
Roma VF x AVTO1424															
P_2	13.33	4.44	8.89	26.67	8.89	17.78	26.67	24.44	25.56	46.67	26.67	36.67	46.67	26.70	36.67
P_1	40.00	42.22	41.11	64.44	68.89	66.67	88.89	95.56	92.22	91.11	100	95.56	91.11	100	95.56
F_1	13.33	13.33	13.33	17.78	17.78	17.78	22.22	20.00	21.11	26.67	26.67	26.67	33.33	31.10	32.22
F_2	27.11	29.78	28.45	36.44	41.33	38.89	45.33	46.67	46.00	53.78	54.22	54.00	58.67	60.50	59.56
BC_1P_1	23.33	27.78	25.56	35.45	44.44	39.94	48.89	56.66	52.78	64.44	63.34	63.89	70.00	68.90	69.44
BC_1P_2	8.89	15.55	12.22	15.56	23.33	19.44	26.67	32.22	29.45	33.33	38.89	36.11	37.78	44.40	41.11
Mean	21	22.18	21.59	32.72	34.11	33.42	43.11	45.93	44.52	52.67	51.63	52.15	56.26	55.30	55.76
CV (%)	34.2	39.4	40.1	34	29.4	26	18.4	18.7	18.6	14.7	18.4	17.1	16.9	18.50	17.9
LSD(P≤0.05)	13.05	15.92	14.64	20.26	18.27	17.66	14.41	15.62	14.04	14.05	17.31	15.12	17.31	18.60	16.88
Roma VF x AVTO1314															
P_2	4.44	6.67	5.56	8.89	13.33	11.11	20.00	22.22	21.11	22.22	26.67	24.44	28.89	28.90	28.67
P_1	64.44	73.33	68.89	73.33	91.11	82.22	88.89	100	94.44	95.56	100	97.78	95.56	100	97.78
F_1	6.67	4.44	5.56	11.11	13.33	12.22	20.00	15.56	17.78	24.44	22.22	23.33	28.89	24.4	26.67
F_2	18.67	20.89	19.78	27.11	28.00	27.56	39.56	40.00	39.78	45.78	45.78	45.78	52.00	52.90	52.44
BC_1P_1	35.56	44.45	40.00	46.67	55.56	51.11	56.67	63.33	60.00	63.33	72.22	67.78	68.89	75.60	72.22
BC_1P_2	7.78	18.89	13.33	14.44	22.22	18.33	21.11	32.22	26.67	32.22	35.56	33.89	38.89	37.80	38.33
Mean	22.93	28.11	25.52	30.26	37.26	33.76	41.04	45.56	43.3	47.26	50.41	48.83	52.19	53.30	52.72
CV (%)	44.7	35	38.7	42.3	26.3	28.5	39	24.9	30.6	25.9	22.2	23	24.7	23.8	23.7
LSD(P≤0.05)	18.64	17.9	16.72	23.28	17.83	18.87	29.08	20.61	22.42	22.28	20.32	19.03	23.41	23.1	21.18
Roma VF x Valoria select															
P_2	24.44	37.78	31.11	35.56	53.33	44.44	46.67	64.44	55.56	53.33	66.67	60.00	60.00	66.70	63.33

Table 2. Contd.

P_1	44.44	64.44	54.44	62.22	86.67	74.44	75.56	93.33	84.44	91.11	100	95.56	93.33	100	96.67
F_1	13.33	24.44	18.89	26.67	33.33	30.00	37.78	42.22	40.00	46.67	55.56	51.11	51.11	57.80	54.44
F_2	21.33	26.22	23.78	32.00	39.11	35.56	44.00	49.33	46.67	52.89	56.89	54.89	57.78	61.80	59.78
BC_1P_1	18.89	26.67	22.78	30.00	36.67	33.33	45.55	55.55	50.55	55.56	64.44	60.00	63.22	72.20	67.72
BC_1P_2	11.11	27.78	19.44	26.67	48.89	37.78	43.33	54.44	48.89	54.45	60.00	57.23	58.89	60.00	59.45
Mean	22.26	34.56	28.41	35.52	49.67	42.59	48.81	59.89	54.35	59	67.26	63.13	64.06	69.70	66.90
CV (%)	71.4	35.1	47.7	30.5	20.4	23.9	25.2	19.7	12.8	14.3	13.1	13.4	16.5	12.5	15
LSD(P≤0.05)	28.92	22.09	23.16	19.7	18.45	17.21	22.41	21.49	19.89	15.38	16.08	14.29	19.23	15.9	16.99

Source: Author's work

Table 3. Scaling Tests for bacterial wilt Incidence.

		Roma VF x AVTO1429			Roma VF x AVTO1424			Roma VF x AVTO1314			Roma VF x Valoria selects		
	Df	Scale	S.E (Expectations)	t (Scale/S.E)	Scale	S.E (Expectations)	t (Scale/S.E)	Scale	S.E (Expectations)	t (Scale/S.E)	Scale	S.E (Expectations)	t (Scale/S.E)
A	9	36.65	12.776	2.869**	-11.1	11.366	-0.977**	-19.99	13.108	-1.525**	15.67	12.03	1.303**
B	9	-3.35	10.339	-0.324**	-13.33	15.204	-0.877**	-21.32	13.34	-1.598**	-1.13	11.254	-0.1**
C	20	46.66	19.56	2.385**	-41.57	21.818	-1.905**	-29.97	18.548	-1.616**	29.76	18.488	1.61**
D	24	-6.68	7.095	-0.942**	8.57	5.936	1.444**	-5.67	10.64	-0.533**	-7.61	4.864	-1.565**

*, ** Significant at 5 and 1 percent probability levels, respectively.
Source: Author's work

wilt severity score of 1.18 followed by F_1 at 1.31 while parent Roma VF had the highest score of 4.29 followed by BC_1 at 3.00 (Table 6). Compared to the better parent (AVTO1429), F_2 hybrids had significantly higher severity score of 2.33. Similarly, P_2 followed by BC1 showed the lowest severity of 0.8 and 1.67, respectively, while P_1 (Roma VF) had the highest score at 3.64 in the greenhouse, followed by F_1 and F_2 hybrids at 2.00. This implied that parent AVTO1429 had significantly lower severity compared to F_1 and F_2 hybrids. F_1 hybrid Roma VF x AVTO1424 had the lowest bacterial wilt severity score of 1.27 while Roma VF (P_1) had the highest score of 3.89 followed by BC_1 at 3.00. Similarly, in the field, F_1 hybrids followed by BC_2 showed the lowest severity of 1.27 and 1.67, respectively while P_1 and BC_1 had the highest severity score of 3.89 and 3.00, respectively. Roma VF x AVTO1314 F_1 had the lowest disease severity of 0.82 while Roma (P_1) had the highest score of 4.96 followed by BC_1 at 3.67 in the field. Parent AVTO1314 had had significantly lower severity score of 0.91 than F_2 hybrids at 2.00. Similar results were recorded in P_2 and F_1 which had significantly lower severity score of 0.91 in the greenhouse. Likewise, P_1 had the highest severity score of 4.53. F_1 and F_2 hybrids showed the lowest bacterial wilt severity score of 2.33 which was not significantly different from the severity score in BC_1, BC_2 and P_2 (Valoria select). Parent Roma VF had significantly higher severity score of 4.82 compared to other generations. This trend of results was also observed in the greenhouse.

Scale tests were significantly different at (P≤0.01) in all the crosses (Table 7). This meant that there was additive x dominance, dominance x dominance and additive x additive interaction. Computation of gene effects using 6-parameter model showed higher additive effects at 1.337** in Roma VF x AVTO1429 and -0.557** in Roma VF x Valoria select as shown by Table 8. All the crosses had significant differences in dominance effects, additive x additive, additive x dominance and dominance x dominance interaction at

Table 4. Components of means for bacterial wilt incidence.

Components (gene effects)	df	Roma VF x AVTO1429			Roma VF x AVTO1424			Roma VF x AVTO1314			Roma VF x Valoria select		
		Expectation/ estimate	S.E	t(components /S.E)	expectation/ estimate	S.E	t(components /S.E)	expectation/ estimate	S.E	t(components /S.E)	expectation/ estimate	S.E	t(components /S.E)
Mean	14	51.11	2.439	20.955	59.56	1.52	39.184	52.44	3.481	15.065	59.44	1.14	52.14
Additive effects	10	10	5.152	1.941**	28.33	5.099	5.556	33.89	8.045	4.213	8.27	4.297	1.925**
Dominance effects	30	10.03	16.529	0.607**	-51.035	21.003	-2.43**	-25.165	22.144	-1.136**	-8.98	13.224	-0.679**
Additive x Additive interaction	24	13.36	14.19	0.942**	-17.14	11.873	-1.446**	11.34	21.28	0.533**	16.65	9.728	1.704**
Additive x Dominance Interaction	14	-40	12.11	-3.303**	-2.23	13.327	-0.167**	-1.11	17.045	-0.065**	-16.8	12.162	-1.381**
Dominance x Dominance Interaction	30	19.94	28.412	0.702**	-7.29	29.867	-0.244**	-52.43	37.145	-1.411**	-2.04	25.242	-0.081**

*, ** Significant at 5 and 1 percent probability levels, respectively.
Source: Author's work

(P≤0.01).

DISCUSSION

Bacterial wilt incidence and severity

Lowest bacterial wilt incidence and severity score was noted in lines AVTO1429 (37.78%), AVTO1424 (26.67%) and AVTO1314 (26.67%). Results confirmed Fufa et al. (2009) reports that the lines have gene for resistance to bacterial wilt. Similar findings have been reported by AVRDC, (2017) that genotype AVTO1429, AVTO1424 and AVTO1314 have gene for resistance to bacterial wilt. Roma VF (P_1) had significantly higher bacterial wilt incidence and severity is a bacterial wilt. This confirmed the susceptibility of the Roma VF line to bacterial wilt disease, with the lowest disease incidence of 33.33%, 22.22%, and 57.78% being observed in the F1 hybrids of Roma VF x AVTO1424, Roma VF x AVTO1314, and Roma VF x Valoria select, respectively. This was also observed for bacterial wilt severity score in the named crosses. Similarly, BC_2 had significantly lower disease incidence and severity score compared to F_2 hybrids, BC_1 and P_1 in all crosses. When the wilting value for Roma VF was 97.78 and for the AVTO1314 was 28.67 the wilting for the F1 plants of this crossing was 26.67%. This implies that there were additive and dominance-additive gene effects in cross Roma VF x AVTO1314 that led to inheritance of bacterial wilt resistance gene. Results implied significant expression of additive component as detected in the current study. These findings are similar to those reported by Neto et al. (2002) that expression of the additive component was approximately four times greater than the dominant component in their study on inheritance of bacterial wilt resistance in Brazil. Similarly, da Silva Costa et al. (2018), reported that inheritance of resistance of *Ralstonia pseudosolanacearum* in tomato involves two major genes with segregation independent of additive effects only and polygenes with additive and dominance effects at federal Rural University of Pernambuco. Otherwise when wilting value for Roma VF was 94.44% and for the AVTO1429 was 34.44%, the wilting for the F1 plants of this cross was 61.11%. This implies that resistance gene was not inherited because the F1 plants had higher disease incidence than in the better parent (AVTO1429). There were non-additive gene effects in cross Roma VF x AVTO1429.

A six-parameter model was identified as most suitable for data analysis for P_1, P_2, F_1, F_2 and backcrosses of the four crosses studied. This model was adopted because all the crosses showed epistasis and backcrosses were used. The six parameters in this model were; Mean, additive effect, dominance effect, Additive x Additive interaction, Additive x Dominance interaction and Dominance x Dominance interaction. Computation of gene effects revealed highly significant additive effects in Roma VF x AVTO1429 and Roma VF x Valoria select. In addition, all the crosses showed highly significant dominance effects, additive x additive, additive x

Table 5. ANOVA Table for Bacterial wilt severity score in four crosses recorded for five weeks.

Source	df	Week 1	Week 2	Week 3	Week 4	Week 5
Roma VF x AVTO1429						
Replicate	2	1.3412	0.8548	0.576	0.2423	0.156
Generation	5	0.6719**	2.1088**	3.2720**	5.6443**	6.6873**
Sites	1	1.1378*	2.8470**	3.2371**	2.9279**	3.4844*
Generation x Sites	5	0.0818	0.2142	0.1918	0.2346	0.1867
Residue	22	0.1136	0.1651	0.175	0.1887	0.2773
Roma VF x AVTO1424						
Replicate	2	0.8104	0.6826	0.0498	0.2381	0.4572
Generation	5	0.2927	0.7878**	1.7826**	3.7087**	6.8623**
Sites	1	0.0001	0.169	0.1186	0.0278	0.0011
Generation x Sites	5	0.0031	0.1717	0.1323	0.2112	0.2334
Residue	22	0.069	0.0974	0.1482	0.1328	0.1708
Roma VF x AVTO1314						
Replicate	2	1.3053	1.3823	0.1842	0.1431	0.0594
Generation	5	1.9186**	4.1500**	7.3936**	12.8713**	13.0328**
Sites	1	0.5216	0.3468	0.5878	0.7901	1
Generation x Sites	5	0.1219	0.1376	0.2059	0.172	0.2225
Residue	22	0.1569	0.1371	0.1791	0.3042	0.365
Roma VF x Valoria select						
Replicate	2	1.077	1.4693	0.4559	0.0657	0.0242
Generation	5	0.3256*	0.7267*	1.2592**	2.0754**	4.2303**
Sites	1	1.3872**	1.5764*	3.2801**	4.0446**	2.8900*
Generation x Sites	5	0.0737	0.212	0.3095	0.3794	0.0814
Residue	22	0.1135	0.1606	0.1521	0.2064	0.2402

Sites were Kabete greenhouse and Sick plot at Kirinyaga county during long seasons, 2019. *, ** Significant at 5 and 1% probability levels, respectively.
Source: Author's work

dominance and dominance x dominance interaction. The additive and dominance model explained the variations among the generation means. Moreover, significant differences observed in the scaling tests revealed the presence of epistatic effects for bacterial wilt resistance trait. Similar findings were reported by Acharya et al. (2018) that significance of scaling tests revealed the involvement of duplicate epistasis for inheritance pattern for tolerance to bacterial wilt disease in tomato in India. The findings of presence of epistatic effects in the current study are contrary to those reported by Neto et al. (2002), who reported that there was no evidence of significant epistatic gene action from the estimate of bacterial wilt resistance trait. Results from the scale test with 6-parameter model revealed that genes showing additive genetic effects predominantly control genetic resistance to bacterial wilt, although there may also be some dominance. Similarly, Mualida et al. (2019), also reported that based on the combined scale test method with 3-parameters (mean, additive and dominance effects) showed that the additive-dominant concept was completed and that controlling the resistance to bacterial wilt was influenced by additive gene and dominant gene.

Conclusion

Significantly lower bacterial wilt incidence and severity was noted in cultivar AVTO1429, AVTO1424 and AVTO1314. The genotypes had genes for resistance to bacterial wilt and hence are valuable parental lines in a breeding program.

There was significantly lower bacterial wilt incidence and severity in the F1 hybrids and BC1. This showed that trait for resistance to bacterial wilt was inherited in the first and third generations. When the wilting value for Roma VF was 97.78 and for the AVTO1314 was 28.67 the wilting for the F1 plants of this crossing was 26.67%. This implies that there were additive and dominance-additive gene effects in cross Roma VF x AVTO1314 that

Table 6. Bacterial wilt severity score for six tomato generations in four crosses recorded for five weeks at Kabete Greenhouse and Sick plot at Kirinyaga County, 2019.

Generation	Week 1			Week 2			Week 3			Week 4			Week 5		
	Greenhouse	Field	Mean	Greenhouse	Field	Mean	Greenhouse	Field	Mean	Greenhouse	Field	Mean	Greenhouse	Field	Mean
Roma VF x AVTO1429															
P_2	0.07	0.09	0.08	0.13	0.24	0.19	0.36	0.60	0.48	0.58	0.84	0.71	0.80	1.11	0.96
P_1	0.58	1.33	0.96	1.18	2.33	1.75	2.04	3.18	2.61	2.96	4.09	3.52	3.64	4.69	4.17
F_1	0.31	0.67	0.49	0.56	1.33	0.94	1.00	1.89	1.44	1.53	2.56	2.04	2.00	3.04	2.52
F_2	0.00	0.33	0.17	0.33	1.00	0.67	1.00	1.33	1.17	1.67	2.00	1.83	2.00	2.33	2.17
BC_1P_1	0.00	0.33	0.17	0.33	0.67	0.50	0.67	1.33	1.00	1.33	1.67	1.50	2.00	2.67	2.33
BC_1P_2	0.00	0.33	0.17	0.00	0.33	0.17	0.67	1.00	0.83	1.00	1.33	1.17	1.67	2.00	1.83
Mean	0.00	1.00	0.00	0.00	1.00	1.00	1.00	2.00	1.00	2.00	2.00	2.00	2.00	3.00	2.00
CV (%)	52.80	53.60	99.20	43.30	39.00	37.90	47.00	15.90	17.70	27.40	15.00	24.20	24.90	11.90	22.60
LSD(P≤0.05)	0.30	0.50	0.60	0.70	0.70	0.70	0.80	0.05	0.70	0.80	0.60	0.70	0.90	0.60	0.90
Roma VF x AVTO1424															
P_2	0.00	0.00	0.09	0.47	0.13	0.30	0.87	0.44	0.66	1.51	0.84	1.18	1.89	1.18	1.53
P_1	1.00	1.00	0.62	1.22	1.24	1.23	2.00	2.02	2.01	2.93	3.09	3.01	3.89	4.29	4.09
F_1	0.00	0.00	0.19	0.33	0.47	0.40	0.58	0.67	0.62	0.89	1.07	0.98	1.27	1.31	1.29
F_2	0.00	0.00	0.33	0.67	1.00	0.83	1.00	1.33	1.17	2.00	2.00	2.00	2.00	2.33	2.17
BC_1P_1	0.00	0.00	0.33	0.67	0.67	0.67	1.33	1.67	1.50	2.00	2.33	2.17	3.00	3.00	3.00
BC_1P_2	0.00	0.00	0.00	0.00	0.67	0.33	0.67	1.00	0.83	1.00	1.33	1.17	1.67	1.67	1.67
Mean	0.00	0.00	0.00	1.00	1.00	1.00	1.00	1.00	1.00	2.00	2.00	2.00	2.00	2.00	2.00
CV (%)	106.5	99.80	99.50	56.70	46.20	49.70	28.80	35.50	34.00	9.50	25.40	20.80	15.40	20.00	18.00
LSD(P≤0.05)	0.05	0.50	0.40	0.60	0.60	0.50	0.60	0.80	0.70	0.30	0.80	0.60	0.60	0.80	0.70
Roma VF x AVTO1314															
P_2	0.07	0.09	0.08	0.13	0.22	0.18	0.33	0.49	0.41	0.56	0.84	0.70	0.91	1.24	1.08
P_1	1.22	1.67	1.44	1.93	2.69	2.31	2.78	3.56	3.17	3.80	4.69	4.24	4.53	4.96	4.74
F_1	0.07	0.04	0.06	0.16	0.16	0.16	0.38	0.31	0.34	0.60	0.53	0.57	0.91	0.82	0.87
F_2	0.00	0.00	0.00	0.67	0.67	0.67	1.00	1.00	1.00	1.67	1.67	1.67	1.67	2.00	1.83
BC_1P_1	0.33	1.00	0.67	1.33	1.33	1.33	1.67	2.33	2.00	2.67	3.00	2.83	2.67	3.67	3.17
BC_1P_2	0.00	0.33	0.17	0.33	0.67	0.50	0.67	0.67	0.67	0.67	1.00	0.83	1.67	1.67	1.67
Mean	0.00	1.00	0.00	1.00	1.00	1.00	1.00	1.00	1.00	2.00	2.00	2.00	2.00	2.00	2.00
CV (%)	91.90	83.60	0.70	48.50	38.10	43.20	44.50	25.40	33.50	38.50	24.00	30.50	31.50	25.70	27.10
LSD(P≤0.05)	0.60	0.80	82.10	0.70	0.70	0.60	0.90	0.60	0.70	1.20	0.90	0.90	1.20	1.10	1.00
Roma VF x Valoria select															
P_2	0.00	1.00	0.47	1.00	1.24	1.02	1.31	2.04	1.68	1.82	2.80	2.31	2.33	3.13	2.73

Table 6. Contd.

P_1	1.00	1.00	0.83	1.00	1.87	1.53	1.82	2.64	2.23	2.87	3.73	3.30	3.98	4.82	4.40
F_1	0.00	0.00	0.26	1.00	0.58	0.54	0.96	1.02	0.99	1.49	1.67	1.58	1.91	2.33	2.12
F_2	0.00	0.00	0.18	1.00	1.00	0.83	1.00	1.33	1.17	2.00	2.00	2.00	2.00	2.33	2.17
BC_1P_1	0.00	1.00	0.33	1.00	0.67	0.67	1.00	1.33	1.33	1.67	2.33	2.00	2.33	2.67	2.50
BC_1P_2	0.00	1.00	0.33	0.00	1.33	0.83	0.67	2.00	1.17	1.33	2.67	2.00	2.33	3.00	2.67
Mean	0.00	1.00	0.00	1.00	1.00	1.00	1.00	2.00	1.00	2.00	3.00	2.00	2.00	3.00	3.00
CV (%)	93.90	62.10	84.20	70.30	28.70	44.30	32.80	23.40	27.30	27.50	16.80	20.70	21.90	15.60	17.70
LSD(P≤0.05)	0.50	0.70	0.60	0.90	0.60	0.70	0.70	0.70	0.07	0.90	0.80	0.80	1.00	0.90	0.80

Source: Author's work

Table 7. Scaling test for bacterial wilt Severity.

	df	Roma VF x AVTO1429			Roma VF x AVTO1424			Roma VF x AVTO1314			Roma VF x Valoria select		
		Scale	S.E (Expectations)	t (Scale/S.E)	Scale	S.E (Expectations)	t (Scale/S.E)	Scale	S.E (Expectations)	t (Scale/S.E)	Scale	S.E (Expectations)	t (Scale/S.E)
A	9	2.03	0.906	2.241**	-0.62	0.412	-1.505**	-0.73	0.721	-1.012**	0.43	0.648	0.664**
B	9	-0.18	0.52	-0.346**	-0.52	0.592	-0.878**	-1.39	0.557	-2.496**	0.07	0.6	0.117**
C	20	1.49	0.985	1.513**	-0.48	0.86	-0.558**	0.24	1.063	0.226**	1.1	0.872	1.261**
D	24	0.18	0.424	0.425**	-0.33	0.283	-1.166**	-1.18	0.539	-2.189**	-0.3	0.361	-0.831**

*, ** Significant at 5 and 1 percent probability levels, respectively.
Source: Author's work

Table 8. Components of Means for Bacterial wilt severity.

Components (gene effects)	df	Roma VF x AVTO1429			Roma VF x AVTO1424			Roma VF x AVTO1314			Roma VF x Valoria select		
		expectation /estimate	S.E	t (components/ S.E)	Expectation/ estimate	S.E	t (components/ S.E)	Expectation/ estimate	S.E	t (components/ S.E)	Expectation/ estimate	S.E	t (components /S.E)
Mean	14	2.167	0.1	21.67	2.167	0.1	21.67	1.833	0.2	9.165	2.167	0.1	21.67
Additive effects	10	0.5	0.374	1.337**	1.333	0.2	6.665	1.5	0.361	4.155	-0.167	0.3	-0.557**
Dominance effects	30	-0.376	1.387	-0.271**	-0.856	0.682	-1.255**	0.292	1.133	0.258**	0.222	0.819	0.271**
Additive x Additive interaction	24	-0.336	0.849	-0.396**	0.666	0.566	1.177**	2.336	1.077	2.169**	1.666	0.721	2.311**
Additive x Dominance Interaction	14	-2.211	0.81	-2.73**	0.11	0.548	0.201**	-0.666	0.806	-0.826**	-2.001	0.775	-2.582**
Dominance x Dominance Interaction	30	2.171	1.792	1.211**	-1.8	1.175	-1.532**	-4.448	1.792	-2.482**	-0.623	1.483	-0.42**

*and ** Significant at 5 and 1% probability levels, respectively.
Source: Author's work

led to inheritance of bacterial wilt resistance gene. Bacterial wilt resistance was controlled by additive-dominance effects and cross families Roma VF x AVTO1314 and Roma VF x AVTO1429 has great potential for use in a breeding program in Kenya.

CONFLICT OF INTERESTS

The authors have not declared any conflict of interests.

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