

Full Length Research Paper

Heterosis, combining ability and reaction of tomato parental lines and their F₁ hybrids to bacterial wilt caused by *Ralstonia solanacearum* in Kenya

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Strategies to manage bacterial wilt disease causing 64-100% yield loss have limited effectiveness. A 10×10 diallel mating design excluding reciprocals and self was employed in this study to evaluate combining ability effects, heterosis, and reaction to bacterial wilt in 10 tomato parents. Genotypes AVTO1424 (11.87%), AVTO1429 (12.29%) and AVTO1314 (13.53%) were found to have significantly lower disease incidence, demonstrating high levels of bacterial wilt resistance. Commercial varieties Roma VF (89.87%) and Cal J (79.60%) however had the highest disease incidence. Out of 45 F₁ hybrids, 10 had an incidence <20% and severity score <1, while 12 F₁ hybrids had an incidence >75% and severity score >4. The cross AVTO1429 x AVTO1314 had the lowest incidence (7%). Negative heterosis was recorded in 29 and 31% of the F₁ hybrids during long and short rain respectively, with AVTO1429 x AVTO1314 having the lowest at -50 and -37%. Cal J had the highest General Combining Ability while AVTO1314, AVTO1429 and AVTO1424 had the lowest. Cross UC82 x Valoria select and AVTO1429 x AVTO1424 had the highest Specific Combining Ability while cross Danny select x Riogrande had the lowest. Genotypes with bacterial wilt resistance trait and high combining ability have the potential in developing a breeding program.

Key words: Bacterial wilt, combining ability, heterosis, *Ralstonia solanacearum*, tomato

INTRODUCTION

Tomato (*Solanum lycopersicum* Mill) is produced globally at around 130 million tons and represents the largest vegetable category at 16% (FAOSTAT, 2021). In Kenya, tomato is consumed widely by many diets and is one of the most important vegetables, accounting for 14% of the horticultural production (FAO, 2020). Over the past

decade, the population growth and increasing demand for tomatoes have led to a sharp decrease in productivity from 25.5 t ha⁻¹ to 18.7 t ha⁻¹ during the same period (FAOSTAT, 2021). The estimated demand for tomatoes in Kenya is 300,000 tons, while production is averaged out at around 283,000 tons annually (Sigei et al., 2014).

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This disparity between the demand and production of tomato has caused the prices to skyrocket, with imports from neighboring countries such as Tanzania increasing (Ochilo et al., 2019). Decrease in tomato productivity which can contribute to losses in yields of up to 100% is mainly caused by biotic stresses, such as pests and diseases, and abiotic stresses, such as drought (Mwangi et al., 2020). In addition, 40% of the post-harvest losses are due to poor handling, storage and transportation which reduce the quality and shelf life of tomato fruits (Ochilo et al., 2019). Tomato crop grown under open fields and greenhouses in Kenya has been greatly constrained by bacterial wilt disease caused by the pathogen *Ralstonia solanacearum* which causes up to 100% yield losses (Mbaka et al., 2013). Bacterial wilt incidence in Kenya, which is more severe during the dry season, has been reported to range from 30 to 90% (Kiirika et al., 2013). *Ralstonia solanacearum* is recognized as an extremely virulent species complex pathogen with over 200 different host plant species globally, making it difficult to manage (Fentik, 2017). Several cultural methods have been utilized to manage bacterial wilt disease in tomato, such as crop rotation, field sanitation, and the use of soil amendments such as urea and lime-based fertilizers (Jitendra et al., 2012; Mbaka et al., 2013). Fumigation with copper oxychloride-based chemicals has also been used in suppressing the *R. solanacearum* pathogen (Jitendra et al., 2012). Still, success of these strategies to effectively manage bacterial wilt disease is limited (Fentik, 2017). Use of tomato varieties resistant to bacterial wilt has been reported in various studies as one of the most efficient and effective method (Kiirika et al., 2013; Aslam et al., 2017). Nonetheless, resistance of the varieties may be lost with change in region due to presence of several diverse strains of *R. solanacearum* (Onduso, 2014). Furthermore, resistant varieties in Kenya are very expensive because seed companies import them from overseas, some are not adapted to local environmental condition while some lack qualities preferred by consumers (Kitinoja et al., 2011). It is of great importance to establish a tomato breeding program in Kenya to develop bacterial wilt resistance varieties affordable to growers and with fruits qualities preferred by consumers. This study aimed to determine heterosis, combining ability and reaction of tomato parental lines and their F_1 hybrids to bacterial wilt disease under greenhouse and field conditions.

METHODS

Experimental site

Experiment was conducted in the field at Kirinyaga county and greenhouse at Kabete Field station, Kiambu county, Nairobi / Africa between 2017 and 2019. Both regions have dark brown to brown deep humic nitosols soils with good drainage and pH of 5 ideal for tomato production. Kiambu County is in the agro-ecological zone III

(01°15'S; 036°44'E) with 1059 mm rainfall annually, temperature range from 12.3 to 22.5°C and an altitude of 1820m (Lengai, 2016). Kirinyaga County is agro-ecological zone II (0.54°20' S, 37.27°35' E) with 1470 mm rainfall annually, temperature range from 15.6 to 28.6°C and an altitude of 1570m (Lengai, 2016).

Plant materials

Ten tomato genotypes were studied for combining ability and reaction to bacterial wilt. Genotypes AVT01424, AVT01429 and AVT01314 with bacterial wilt resistance trait were sourced from the repository of the World Vegetable Centre (Fufa et al., 2009). Cultivars Riogrande, Roma VF, Cal J VF and UC 82 were obtained from Continental Seeds Co. Limited and they lack bacterial wilt resistance trait. Cultivars Valoria, Danny and Eden were selected from farmer's selection lines. Valoria and Danny select are claimed but not evaluated to have resistance against bacterial wilt while Eden select is susceptible.

Mating design and hybridization

Ten parental genotypes sown in germination trays were transplanted in 2.4 x 2.4 m plots at a spacing of 60 cm x 60 cm after 28 days (after attaining pencil thickness) in the field and greenhouse. Griffin's 10 x 10 diallel mating design (males on one side and females on the other) with parents and F_1 's excluding reciprocals to produce $(p(p+1))/2$ cross combinations was used (Griffing, 1956). Hybridization led to the development of 45 F_1 hybrids. Crops were managed for pests and diseases through application of pesticides. Pythium, early and late blight were managed using Metalaxyl-M and propineb (700 gkg⁻¹) at the rate of 50g in 20 l water. Whiteflies were managed by mixing 45 gl⁻¹ of Imidaclopride and betacyfluthrin100 and applying at the rate of 0.2 lha⁻¹ every 7 days. Leaf miners were managed by Thiamethoxam at 25ml in 20 l of water per week.

Preparation of female parent

Emasculation was carried out following a protocol by (AVRDC, 2001) when 2 flowers in an inflorescence were fully grown using pointed forceps. Emasculation was done in the morning and evening at 21-25 and 15-20°C temperature range, respectively. Male and female parents were isolated at 3m. Pollen was harvested using modified electric toothbrush manufactured by VegiBee-Garden pollinators (model VBP-02) with a pollen collection cap. Pollination was carried out 2 days after anthesis at 21-23°C (Singh et al., 2004). Stigma was dipped into the pollen pool in the pollen container. To distinguish hand pollinated cluster from self's, two sepals were removed after hybridization and labelled with a waterproof tag. Eight fruits harvested manually at red stage were hand crushed and seeds extracted in 1 litre of water mixed with 10ml of 0.6M hydrochloric acid. The pulp and acid mixture stirred after every 15 for 45 min was drained. Seeds were rinsed thoroughly in distilled water and sun dried for 3 days to a moisture content not exceeding 8% following a modified protocol of Cheema and Dhaliwal (2005).

Evaluation of bacterial wilt infected field

Field with history of *R. solanacearum* was selected in Kirinyaga County during the long and short rain season in 2017. The pathogen load and severity index for the site was established using a susceptible cultivar Roma VF (Jitendra et al., 2012). Healthy Roma VF seedlings were transplanted 28 days after sowing into

850 m² blocks replicated thrice with 550 plants in each block. Bacterial wilt incidence was assessed by counting the number of wilted plants in each block and the location severity index (LSI) was calculated as percentage of wilted plants divided by the total plants within each block (Ayana et al., 2011). *R. solanacearum* infected field with location severity index of over 76% in susceptible varieties such as Roma VF is ideal for bacterial wilt evaluation (Jitendra et al., 2012).

Ralstonia solanacearum isolation and confirmation

The first confirmation test of *R. solanacearum* was bacterial streaming carried out following Kelman (1954) protocol. Tomato stems cut horizontally were dipped in clear water in universal bottles to allow streaming out of bacteria exudates from the diseased vascular bundle. *Ralstonia solanacearum* was isolated from diseased plants and plating on Kelman's TZC agar medium (2, 3; 5 Triphenyl Tetrazolium Chloride medium) then incubated for 48 h at 28°C (Kelman, 1954). Morphological characteristics of the colonies were observed.

Assessment of the amount of inoculum in the field

Scoops of 50g were randomly picked from each block at a depth of 10cm and composited in polythene bags for laboratory analysis. Three replicates of ten grams of soil from the composited sample were placed into 250ml conical flasks containing 90ml sterile water. After vigorous shaking for 30 min in a rotary shaker at 300rpm, the suspension was serially diluted up to 15 folds as described by Xu et al. (2012). One ml of the 14th and the 15th folds was plated on Kelman's TZC media and incubated for 48 h at 28°C. *R. solanacearum* colonies were counted and the colony forming units per gram of soil were calculated.

Evaluating the reaction of 45 F₁ hybrids and their parents to bacterial wilt disease in the greenhouse

Experiment was carried out in a complete randomized design with four replicates at Kabete greenhouse. Ten parents and 45 F₁ hybrids were studied. Five litre plastic pots that contained sterile forest soil, well decomposed compost manure and sand were used as planting media in the ration of 2:1:1. Pure cultures of *R. solanacearum* isolated from infected tomato plants were flooded with 10ml sterile distilled water and bacterial suspension was adjusted to 10⁷ cfu/ml by serial dilution technique (Kiirika et al., 2013). Avenues for bacterial entry were exposed by pricking tomato seedlings roots using sterile needle. 25 ml of the bacterial suspension were then inoculated around the root base.

Evaluating the reaction of 45 F₁ hybrids and their parents to bacterial wilt disease in the field

Experiment in the field was conducted in a randomized complete block design with three replicates during the short and long rain season. Selected field had location severity index of >76%. Ten parents and 45 F₁ hybrids were transplanted in a 1 x 4 m plot with 10 plants at a spacing of 60 x 60cm. Recommended agronomic practices for watering, fertilizer application and spraying with chemicals were carried out to ensure healthy crop in the field.

Data collection in greenhouse and the field

Data on wilted plants, healthy plants and scoring for severity was collected at 4 days' interval. Bacterial wilt disease incidence (DI)

was calculated as a percentage (%) of wilted plant divided by the total number of plants per plot. Disease severity index was determined using a score from 0 to 5 where: 0-no symptoms, 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). Disease evaluation followed the procedure of Jeger and Viljanen-Rollinson, (2001). Resistance was categorized as suggested by Shinji et al., (1997). Severity index of <1-high resistance, 1 to 1.5-resistance, 1.6 to 2-moderately resistance, 2 to 3-weak resistance and >3-susceptible. Area under disease progress curve (AUDPC) per plant in all the treatment was calculated as follows:

$$AUDPC = \sum_{i=1}^{n-1} [(x_i + x_{i-1}) / 2](t_i - t_{i-1})$$

Where x_i and x_{i-1} denote disease severity index and t_i and t_{i-1} are consecutive evaluation dates (t_1 to t_{i-1} equal to 1). Turkey test at $\alpha = 0.05$ was used to test the level of significance differences between treatments.

Heterosis for bacterial wilt resistance trait was estimated by the relative performance of the F₁ hybrids expressed as a percentage higher or lower performance of the new F₁ hybrid compared to the better parent (Virmani, 1997) viz:

$$BPH = \frac{F_1 - BP}{BP} \times 100 \quad (1)$$

Where: F₁ is the mean performance of a single cross and BP is the mean performance of the better parent.

Statistical analysis of data collected

Data were subjected to analysis of variance (ANOVA) using GenStat 15th edition and significant means separated using Fisher's protected Least Significant Difference (LSD) test at $P \leq 0.05$. General Combining Ability, Specific Combining Ability, variances and effects, relative importance of GCA/SCA and interaction of GCA and SCA with environments were conducted using genetic design tool in AGD-R (Analysis of Genetic Design with R) version 5.0, with genotypes as the fixed factors (Francisco et al., 2018). Estimation of variance components was developed on the expectation's values from the analysis of variance for combining ability (Equation 2).

$$gi = \frac{xi}{tr} - \frac{X}{ltr}n \quad (2)$$

Where: gi = General combining ability effect of ith line, Xi = Total of ith line overall including replications and X = Total of all hybrid combinations

Estimation of SCA effects was as elaborated in Equation 3.

$$Sij = \frac{xij}{r} - \frac{xi}{tr} - \frac{xj}{rl} + \quad (3)$$

Where: Sij = Specific combining ability of the ith line and jth parent cross, Xij = Total (ij)th combination for all replications

Overall performance of the male and female in the diallel design was equated to their respective general combining abilities (GCA) and their interactions equated to their respective specific combining abilities (SCA).

RESULTS

Evaluation of bacterial wilt infected field

Experimental field in Kirinyaga County was confirmed to



Figure 1. A; White, fluidal, pinkish red centred colonies of *R. solanacearum* with round irregular margin on Kelman's TZC medium. B; Wilted tomato plants of Roma VF, 60 days after transplanting in bacterial wilt infected plots in 2017. Source: Author.

Table 1. Reaction of 10 parental lines to bacterial wilt in the field and greenhouse.

Parents	Disease Incidence (%)				Disease severity score				Observation
	Field LR2017	Field SR2017	Green-house	Mean	Field LR2017	Field SR2017	Green-house	Mean	
Eden select	90.40	86.00	69.31	81.90	4.52	4.32	3.44	4.10	Susceptible
Roma VF	99.60	96.67	73.33	89.87	4.98	4.83	3.67	4.49	Susceptible
AVTO1429	17.87	19.00	0.00	12.29	0.89	0.94	0.00	0.61	Resistance
Cal J	84.47	84.33	70.00	79.60	4.22	4.22	3.50	3.98	Susceptible
AVTO1424	14.93	20.67	0.00	11.87	0.75	1.03	0.00	0.59	Resistance
Danny select	31.40	34.33	27.04	30.92	1.57	1.72	1.35	1.55	Moderate resistance
AVTO1314	14.47	23.33	2.78	13.53	0.72	1.18	0.14	0.68	Resistance
UC82	40.47	47.00	61.48	49.65	2.02	2.36	3.07	2.49	Moderate resistance
Valoria select	49.40	51.00	36.67	45.69	2.47	2.55	1.83	2.29	Moderate resistance
Riogrande	68.53	77.33	62.96	69.61	3.43	3.88	3.15	3.48	Susceptible
Grand mean	51.15	54.00	40.31	48.49	2.56	2.70	2.02	2.43	
CV (%)				5.43				0.27	
LSD (5%)				11.81				0.59	

Environments were bacterial wilt infected field LR2017 (long rain season) and SR2017 (Short rain season) and artificially inoculated greenhouse 2017. Source: Author.

have bacterial wilt causing pathogen (*R. solanacearum*). The pathogen population in the infected soil was estimated as 1.8×10^{15} colony-forming units (cfu) g^{-1} soil. The severity index of cultivar Roma VF planted in this field was 90%. Symptoms of bacterial wilt observed on the indicator cultivar Roma VF were pale yellow coloration on lower leaves, drooped leaves, wilted and dead plants (Figure 1). Milky white bacterial exudate and brown discoloration on the vascular bundle was also observed. Colonies of *R. solanacearum* isolated from diseased Roma VF plants on Kelman's TZC selective media were round, 8.0mm in diameter, white, fluidal with irregular margins and pinkish red centre (Figure 1).

Reaction of F₁ hybrids and their parents to bacterial wilt in the greenhouse and the field

The ten evaluated parental had high significant differences

in bacterial wilt incidence and severity at ($P \leq 0.05$) in the greenhouse. High significant difference in the genotypes was recorded across the long and short rains study seasons in the field which also validated the results observed in the greenhouse. High significant differences at $P \leq 0.05$ were also recorded in bacterial wilt incidence and severity for the environments x genotypes interactions (Table 1). Genotype AVTO1424, AVTO1429 and AVTO1314 had the lowest disease incidence of 11.87, 12.29 and 13.53%, respectively across the three environments. The genotypes also had the lowest disease severity score of 0.61, 0.59 and 0.68, respectively (Table 1). Farmer's selection genotype Danny and Valoria select were moderately resistance with disease incidence of 30.92 and 45.69% and severity score of 1.55 and 2.29, respectively across the study environments. Commercial varieties Roma VF followed by Cal J had the highest bacterial wilt incidence of 89.87

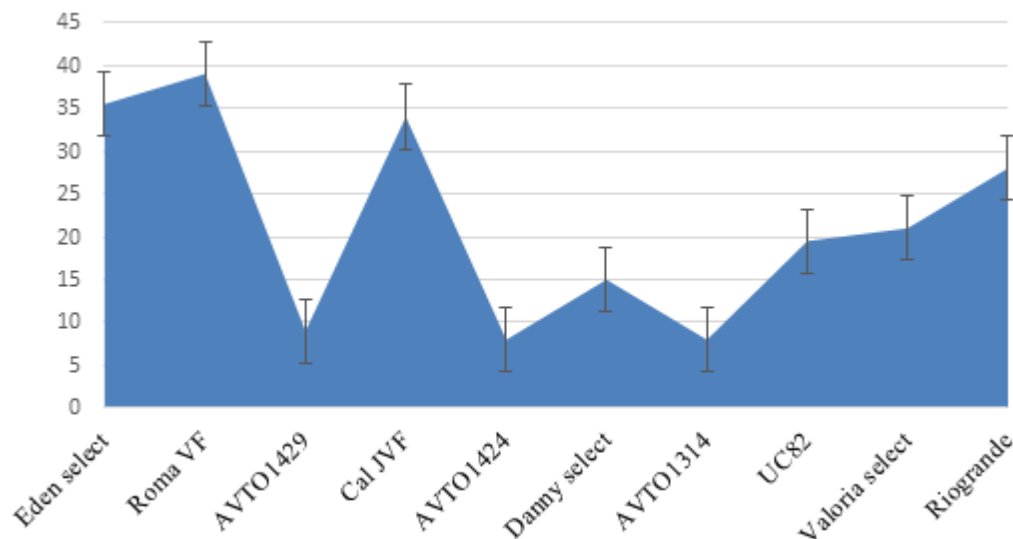


Figure 2. Mean areas under disease progress for 10 parental genotypes in the field. Source: Author.

and 79.60%, and severity score of 4.49 and 3.98, respectively. Eden select, a variety claimed to be susceptible to bacterial wilt also recorded significantly high disease incidence of 81.90% and severity score of 4.10. This genotype was the second most susceptible after Roma VF. All genotypes had significantly high disease incidence and severity during the short rain season compared to long rain season. The area under disease progress (AUDPC) was significantly lower at an average of 8 in AVTO1424, AVTO1429 and AVTO1314 while in genotype Roma VF, followed by Eden select and Cal J was significantly higher at average of 39, 35.5 and 34, respectively (Figure 2). Significant differences at $P \leq 0.05$ in bacterial wilt incidence and severity score were recorded in F_1 populations (Table 2). There were no significant environments x genotypes interactions in the F_1 populations. The lowest disease incidence of 7% followed by 12% was recorded in F_1 hybrids AVTO1429 x AVTO1314 and AVTO1429 x Danny select, respectively. The hybrids also had the lowest severity score of 0.26 and 0.46, respectively (Table 2). Out of the 45 F_1 hybrids evaluated, 10 namely, Roma VF x AVTO1424, AVTO1429 x Valoria select, AVTO1424 x AVTO1314, AVTO1424 x Riogrande, Danny select x AVTO1314, AVTO1314 x UC82, AVTO1314 x Valoria select and AVTO1424 x Valoria select had disease incidence of <20% and severity score of <1. The highest disease incidence of 90% was recorded in F_1 hybrids Eden select x Riogrande, UC82 x Valoria select and UC82 x Riogrande. The hybrids also had the highest severity score of 4.77, 4.73 and 4.58, respectively (Table 2). Out of the 45 F_1 hybrids evaluated, 12 namely, Eden select x Roma VF, Eden select x Cal J, Eden select x UC82, Roma VF x Cal J, Roma VF x UC82, Roma VF x

Riogrande, Cal J x UC82, Cal J x Valoria select and Cal J x Riogrande had disease incidence of >75% and severity score of >3.5.

Better parent heterosis for bacterial wilt resistance trait

Positive and negative heterosis percentage was recorded for bacterial wilt incidence and severity score (Table 3). Better parent heterosis for bacterial wilt disease index in the 45 F_1 hybrids evaluated varied from -50 to 280% and -37 to 181% during the long and short rain seasons. Heterosis implied that the F_1 hybrid had significantly lower disease incidence and severity than the better parent with low disease index which is desirable in a breeding program. In contrast, positive heterosis implied that the F_1 hybrid had significantly higher disease incidence and severity than the better parent with low disease index. Out of the 45 F_1 hybrids, 29 and 31% during the long and short rain seasons, respectively showed negative heterosis for disease incidence and severity score. F_1 hybrid AVTO1429 x AVTO1314 had the highest negative heterosis of -50 and -37% in long and short rain seasons, respectively. During the long seasons, F_1 hybrids Roma VF x Valoria select (-41%), AVTO1429 x Danny select (-38%), AVTO1429 x Valoria select (-22%), AVTO1314 x Valoria select (-21%) and AVTO1424 x Riogrande (-20%) recorded high negative heterosis of >-20% (Table 3). Similarly, during the short rain season, F_1 hybrids with negative heterosis >-20% were AVTO1314 x UC82 (-35%), Roma VF x Valoria select (-35%), AVTO1314 x Valoria select (-30%), Roma VF x AVTO1424 (-29%) and AVTO1429 x Danny select (-

Table 2. Reaction of 45 F₁ hybrids to bacterial wilt in the field and greenhouse.

Hybrid combinations	Disease incidence (%)				Disease severity score				Observation
	Field LR2017	Field SR2017	Green-house	Mean	Field LR2017	Field SR2017	Green-house	Mean	
Eden select x Roma VF	73	78	77	76	3.66	4.55	3.87	4.03	Susceptible
Eden select x AVTO1429	16	19	24	20	0.80	1.69	1.22	1.24	Resistance
Eden select x Cal J	81	84	94	86	4.19	5.08	4.72	4.66	Susceptible
Eden select x AVTO1424	57	59	67	61	2.85	3.74	3.33	3.31	Weak resistance
Eden select x Danny select	65	67	91	74	3.24	4.13	4.55	3.97	Susceptible
Eden select x AVTO1314	24	29	32	28	1.20	2.09	1.62	1.64	Moderate resistance
Eden select x UC82	84	87	94	88	4.19	5.08	4.72	4.66	Susceptible
Eden select x Valoria select	50	52	82	61	2.48	3.37	4.08	3.31	Weak resistance
Eden select x Riogrande	89	90	90	90	4.45	5.34	4.52	4.77	Susceptible
Roma VF x AVTO1429	26	31	28	29	1.32	1.55	1.42	1.43	Resistance
Roma VF x Cal J	74	79	92	82	3.72	3.95	4.62	4.10	Susceptible
Roma VF x AVTO1424	13	15	19	16	0.66	0.89	0.95	0.83	Resistance
Roma VF x Danny select	60	63	92	71	2.99	3.27	4.58	3.61	Susceptible
Roma VF x AVTO1314	21	22	39	27	1.07	1.38	1.93	1.46	Resistance
Roma VF x UC82	75	75	82	77	3.74	4.04	4.08	3.95	Susceptible
Roma VF x Valoria select	29	33	46	36	1.46	1.73	2.28	1.83	Moderate resistance
Roma VF x Riogrande	77	82	87	82	3.83	4.10	4.37	4.10	Susceptible
AVTO1429 x Cal J	25	27	32	28	1.23	0.98	1.62	1.28	Resistance
AVTO1429 x AVTO1424	31	33	20	28	1.57	1.52	1.00	1.36	Resistance
AVTO1429 x Danny select	11	14	11	12	0.55	0.64	0.18	0.46	Highly resistance
AVTO1429 x AVTO1314	7	12	3	7	0.32	0.41	0.03	0.26	Highly resistance
AVTO1429 x UC82	24	24	37	28	1.19	1.26	1.87	1.44	Resistance
AVTO1429 x Valoria select	14	17	17	16	0.73	0.80	0.45	0.66	Resistance
AVTO1429 x Riogrande	47	49	75	57	2.33	2.40	3.75	2.83	Weak resistance
Cal J x AVTO1424	42	41	31	38	2.12	2.19	0.98	1.77	Moderate resistance
Cal J x Danny select	69	74	69	71	3.46	3.53	2.57	3.18	Weak resistance
Cal J x AVTO1314	37	42	28	36	1.86	0.86	0.98	1.23	Resistance
Cal J x UC82	81	86	77	81	4.03	3.03	3.85	3.64	Susceptible
Cal J x Valoria select	77	79	75	77	3.85	3.11	3.77	3.58	Susceptible
Cal J x Riogrande	73	75	93	80	3.65	3.04	4.65	3.78	Susceptible
AVTO1424 x Danny select	30	35	20	28	1.49	1.34	0.82	1.21	Resistance
AVTO1424 x AVTO1314	17	22	8	16	0.83	0.63	0.33	0.60	Resistance
AVTO1424 x UC82	22	27	14	21	1.10	0.98	0.42	0.83	Resistance
AVTO1424 x Valoria select	20	25	10	18	0.94	0.98	0.12	0.68	Resistance
AVTO1424 x Riogrande	12	17	11	13	0.60	0.64	0.55	0.60	Resistance

Table 2. Contd

Danny select x AVTO1314	17	22	9	16	0.86	1.09	0.47	0.81	Resistance
Danny select x UC82	33	38	69	47	1.67	1.90	3.45	2.34	Moderate resistance
Danny x Valoria select	68	69	68	68	3.39	3.52	3.38	3.43	Weak resistance
Danny select x Riogrande	27	28	48	34	1.33	1.26	2.38	1.66	Moderate resistance
AVTO1314 x UC82	13	15	16	15	0.63	0.56	0.63	0.61	Resistance
AVTO1314 x Valoria select	11	18	13	14	0.57	0.65	0.47	0.56	Resistance
AVTO1314 x Riogrande	25	30	10	22	1.28	1.96	0.42	1.22	Resistance
UC82 x Valoria select	92	92	86	90	4.60	5.28	4.32	4.73	Susceptible
UC82 x Riogrande	89	91	89	90	4.44	4.82	4.47	4.58	Susceptible
Valoria select x Riogrande	55	60	68	61	2.75	2.97	3.40	3.04	Weak resistance
Grand mean	44	46	50	47	2.20	2.31	2.41	2.31	
CV (%)				11.59				0.63	
LSD (5%)				20.79				1.08	

Environments were bacterial wilt infected field LR2017 (long rain season) and SR2017 (Short rain season) and artificially inoculated greenhouse 2017.

Source: Author.

26%). Positive heterosis was recorded in 71 and 69% of the F_1 hybrids during the long and short rain seasons, respectively which indicated the F_1 hybrids had higher disease incidence and severity than their better parents. Eden select x AVTO1424 is an example with heterosis of 280% during long rains and 181% during short rains.

Combining ability effects for bacterial wilt resistance trait

The general combining ability (GCA) effects among the ten parental genotypes for bacterial wilt incidence and severity were significantly different at $P \leq 0.05$. In the greenhouse, GCA effects for disease incidence and severity varied from -36.23 to 25.36 and -1.80 to 1.36, respectively (Table 4). Genotype Eden select had the highest GCA effects of 25.36 followed by Cal J

with 17.82 in disease incidence while genotypes AVTO1314, AVTO1429 and AVTO1424 had the lowest GCA effects of -36.23, -24.98 and -31.23, respectively. The same trend in GCA effects was recorded in the genotypes for disease severity index. GCA effects in the field for disease incidence varied from -26.85 to 20.28 during the long and short rain seasons (Table 4). GCA effects for disease severity index varied from -1.40 to 1.02 and -1.47 to 1.65 during the long and short rain seasons, respectively. Similar to results recorded in the greenhouse, Cal J and Eden select had the highest GCA effects in disease incidence and severity while AVTO1314, AVTO1424 and AVTO1429 had the lowest GCA effects in both seasons. Significant differences in the specific combining ability (SCA) effects were recorded at $P \leq 0.05$ between the 45 crosses in bacterial wilt incidence and severity. In the greenhouse, SCA effects in disease incidence

varied from -25.95 to 34.71 while the range in severity index was from -1.28 to 1.76 (Table 5). AVTO1429 x Riogrande, AVTO1429 x AVTO1424 and AVTO1424 x AVTO1314 had the highest SCA effects in disease incidence of 34.71, 26.30 and 25.88, respectively. Eden select x AVTO1429, AVTO1424 x Riogrande and Danny select x Riogrande had the lowest SCA effects of -25.95, -23.04 and -20.95, respectively. Similar trend in SCA effects in the crosses was recorded in disease severity index. SCA effects in the field varied from -27.49 to 31.11 and -29.26 to 29.37 during the long and short rain seasons for disease incidence (Table 5). SCA effects in disease severity index varied from -1.89 to 1.56 and -1.63 to 2.11 during both seasons, respectively. Cross UC82 x Valoria select, AVTO1429 x AVTO1424 and Danny select x Valoria had the highest SCA effects in disease incidence while crosses Danny select x Riogrande and AVTO1424 x Riogrande

Table 3. Better parent heterosis for bacterial wilt resistant trait in the field and greenhouse.

Hybrid combinations	Disease incidence (%)		Disease severity score	
	Field LR2017	Field SR2017	Field LR2017	Field SR2017
Eden select x Roma VF	-19	-9	-19	5
Eden select x AVTO1429	-11	0	-10	80
Eden select x Cal J	-4	0	-5	17
Eden select x AVTO1424	280	181	280	263
Eden select x Danny select	110	97	106	140
Eden select x AVTO1314	71	26	67	77
Eden select x UC82	110	85	107	115
Eden select x Valoria select	2	2	0.4	32
Eden select x Riogrande	29	17	30	38
Roma VF x AVTO1429	44	63	48	65
Roma VF x Cal J	-12	-6	-12	-6
Roma VF x AVTO1424	-13	-29	-9	-14
Roma VF x Danny select	94	85	90	90
Roma VF x AVTO1314	50	-4	49	17
Roma VF x UC82	88	64	85	71
Roma VF x Valoria select	-41	-35	-41	-32
Roma VF x Riogrande	12	6	12	6
AVTO1429 x Cal J	39	42	38	4
AVTO1429 x AVTO1424	107	74	109	62
AVTO1429 x Danny select	-38	-26	-38	-32
AVTO1429 x AVTO1314	-50	-37	-56	-56
AVTO1429 x UC82	33	26	34	34
AVTO1429 x Valoria select	-22	-11	-18	-15
AVTO1429 x Riogrande	161	158	162	155
Cal J x AVTO1424	180	95	183	113
Cal J x Danny select	123	118	120	105
Cal J x AVTO1314	164	83	158	-27
Cal J x UC82	103	83	100	28
Cal J x Valoria select	57	55	56	22
Cal J x Riogrande	5	-3	6	-22
AVTO1424 x Danny select	100	67	99	30
AVTO1424 x AVTO1314	21	5	15	-39
AVTO1424 x UC82	47	29	47	-5
AVTO1424 x Valoria select	33	19	25	-5
AVTO1424 x Riogrande	-20	-19	-20	-38
Danny select x AVTO1314	21	-4	19	-8
Danny select x UC82	6	118	6	10
Danny x Valoria select	119	103	116	105
Danny select x Riogrande	-13	-18	-15	-27
AVTO1314 x UC82	-7	-35	-13	-55
AVTO1314 x Valoria select	-21	-30	-21	-36
AVTO1314 x Riogrande	79	30	78	66
UC82 x Valoria select	130	96	128	124
UC82 x Riogrande	123	94	120	104
Valoria select x Riogrande	12	18	11	16

Environments were bacterial wilt infected field LR2017 (long rain season) and SR2017 (Short rain season) and artificially inoculated greenhouse 2017.

Source: Author.

Table 4. General combining ability effects of parental genotypes for bacterial wilt resistance trait.

Parents	Disease incidence (%)			Disease severity score		
	Field LR2017	Field SR2017	Greenhouse	Field LR2017	Field SR2017	Greenhouse
Eden select	17.49	17.49	25.36	0.89	1.65	1.36
Roma VF	6.67	6.67	14.11	0.33	0.47	0.80
AVTO1429	-24.94	-24.94	-24.98	-1.22	-1.31	-1.27
Cal J	20.28	20.28	17.82	1.02	0.52	0.81
AVTO1424	-18.95	-18.95	-31.23	-0.96	-1.10	-1.65
Danny select	-1.82	-1.82	3.36	-0.11	-0.13	0.08
AVTO1314	-26.85	-26.85	-36.23	-1.40	-1.47	-1.80
UC82	13.68	13.68	14.48	0.72	0.65	0.76
Valoria select	2.21	2.21	1.94	0.12	0.10	0.07
Riogrande	12.22	12.22	15.38	0.61	0.60	0.85
CV (%)	57.6	57.6	43	46.4	23	68.4
LSD (5%)	0.1006	0.1006	0.0684	0.1661	0.0875	0.2602

Environments were bacterial wilt infected field LR2017 (long rain season) and SR2017 (Short rain season) and artificially inoculated greenhouse 2017.

Source: Author.

had the lowest. Similar trend in SCA effects in the crosses was recorded in disease severity index.

DISCUSSION

Evaluation of bacterial wilt infected field

Assessment of the amount of inoculum in the field confirmed that the selected field had history of *Ralstonia solanacearum*. In addition, more than 90% of wilted Roma VF in the field indicated the location had a high bacterial wilt severity index, comparable to the findings reported by Jitendra et al. (2004). This implied that the site was ideal for *R. solanacearum* evaluation because the location severity index of was more than the required standard of 76%. Symptoms of bacterial wilt observed on indicator cultivar Roma VF in this study were similar to bacterial wilt symptoms reported by (Champoiseau and Momol, 2008) and (Tinatin and Saykal, 2016) that included yellow, drooped and shrivelled leaves, wilted and dead tomato plants. Presence of bacterial exudate and vascular bundle brown discoloration confirmed the wilt was due to bacteria and no other pathogens such as fusarium. Bacterial streaming is one of the most important confirmatory tests characterized by white bacterial ooze visible as white strands of bacterial cells in clear water. Similar findings have been reported by Seleim et al. (2011) and Garcia et al. (2019). Colony characteristics of *R. solanacearum* observed on Kelman's TZC selective media in this study were similar to the white, large, elevated, fluidal, pale red to pink centred colonies reported by Khasabuli et al. (2017). According to Fajinmi and Fajinmi (2010), Triphenyl Tetrazolium Chloride (TZC) is a selective medium for *R.*

solanacearum. Moreover, the medium distinguishes *R. solanacearum* from other bacteria and virulent colonies from avirulent mutant during isolation. Virulent colonies are fluidal with a pink centre while avirulent mutant are butyrous, deep red with bluish border (Khasabuli et al., 2017).

Reaction of F₁ hybrids and their parents to bacterial wilt in the greenhouse and the field

Genotypes AVTO1424, AVTO1429 and AVTO1314 were resistant to bacterial wilt with significantly lower disease incidence of less than 14% and severity scores of less than 1. These three genotypes sourced from the World Vegetable Center were reported to possess bacterial wilt resistance traits (Fufa et al., 2009). Results showed that commercial varieties Roma VF, Cal J and Riogrande were susceptible to bacterial wilt, indicated by the high disease incidence of 89.87, 79.60, and 69.61%, respectively, and severity scores of 4.49, 3.98, and 3.48, respectively. The results confirm the claims by farmers of the susceptibility of these varieties to bacterial wilt. Similarly, Eden Select, which has been claimed to be susceptible to bacterial wilt, recorded a significantly high disease incidence of 81.90% and severity score of 4.10, which further validates the claims. It is known that levels of *R. solanacearum* in a field can build up over time if left unmanaged (Seleim et al., 2011; Garcia et al., 2019).

This could explain the high disease incidence and severity recorded during the short rain season, compared to the long rain season. The experiment was conducted first during the long rains and repeated on the same field during the short rains. F₁ hybrid AVTO1429 x AVTO1314 had a significantly lower disease incidence (7%) than

Table 5. Specific combining ability effects of for bacterial wilt resistance trait.

Hybrid combinations	Disease incidence (%)			Disease severity score		
	Field LR2017	Field SR2017	Greenhouse	Field LR2017	Field SR2017	Greenhouse
Eden select x Roma VF	4.81	6.79	-12.04	0.24	0.01	-0.71
Eden select x AVTO1429	-21.38	-20.75	-25.95	-1.07	-1.07	-1.28
Eden select x CAL J	-1.51	-1.08	1.25	-0.08	0.34	0.14
Eden select x AVTO1424	14.29	12.94	22.63	0.72	0.78	1.21
Eden select x Danny select	5.20	4.35	12.05	0.26	0.20	0.68
Eden select x AVTO1314	-9.61	-8.76	-6.70	-0.49	-0.50	-0.36
Eden select x UC82	7.56	8.64	4.59	0.38	0.36	0.18
Eden select x Valoria select	-14.60	-15.23	4.46	-0.73	-0.79	0.24
Eden select x Riogrande	15.25	13.10	-0.29	0.76	0.68	-0.11
Roma VF x AVTO1429	0.28	2.08	-10.70	0.01	-0.02	-0.52
Roma VF x Cal J	3.49	5.30	3.17	0.17	0.55	0.60
Roma VF x AVTO1424	-18.49	-19.42	-13.79	-0.92	-0.90	-0.61
Roma VF x Danny select	11.31	10.51	24.30	0.57	0.52	1.29
Roma VF x AVTO1314	-1.28	-4.90	10.88	-0.07	-0.04	0.52
Roma VF x UC82	9.78	7.46	3.17	0.49	0.50	0.11
Roma VF x Valoria select	-23.86	-23.41	-20.29	-1.19	-1.25	-1.00
Roma VF x Riogrande	13.95	15.59	7.96	0.70	0.62	0.31
AVTO1429 x Cal J	-15.31	-15.87	-10.41	-0.77	-0.64	-0.33
AVTO1429 x AVTO1424	30.87	29.37	26.30	1.55	1.52	1.51
AVTO1429 x Danny select	-6.48	-6.44	-16.95	-0.32	-0.34	-1.04
AVTO1429 x AVTO1314	15.00	16.15	14.63	0.74	0.78	0.69
AVTO1429 x UC82	-10.31	-12.27	-2.08	-0.52	-0.51	-0.03
AVTO1429 x Valoria select	-7.65	-7.13	-9.54	-0.38	-0.41	-0.76
AVTO1429 x Riogrande	14.97	14.86	34.71	0.75	0.69	1.76
Cal J x AVTO1424	-2.93	-7.52	-5.83	-0.14	0.36	-0.58
Cal J x Danny select	6.87	8.46	-2.41	0.34	0.73	-0.73
Cal J x AVTO1314	0.91	1.60	-3.50	0.04	-0.38	-0.02
Cal J x UC82	1.78	4.40	-5.20	0.09	-0.55	-0.13
Cal J x Valoria select	10.18	9.09	5.67	0.51	0.08	0.48
Cal J x Riogrande	-3.49	-4.39	9.92	-0.18	-0.49	0.58
AVTO1424 x Danny select	6.82	8.32	-2.04	0.35	0.15	-0.03
AVTO1424 x AVTO1314	19.61	20.21	25.88	0.98	0.78	1.37
AVTO1424 x UC82	-17.45	-14.92	-19.16	-0.86	-0.99	-1.11
AVTO1424 x Valoria select	-7.64	-5.56	-10.95	-0.42	-0.43	-0.71
AVTO1424 x Riogrande	-25.09	-23.42	-23.04	-1.25	-1.28	-1.06
Danny select x AVTO1314	3.37	3.70	-7.70	0.16	0.28	-0.23
Danny select x UC82	-22.99	-20.72	1.25	-1.15	-1.04	0.19
Danny select x Valoria select	23.38	21.08	12.46	1.17	1.13	0.82
Danny select x Riogrande	-27.49	-29.26	-20.95	-1.38	-1.63	-0.96
AVTO1314 x UC82	-17.83	-19.24	-12.16	-0.89	-1.03	-0.74
AVTO1314 x Valoria select	-7.32	-6.41	-2.62	-0.35	-0.30	-0.21
AVTO1314 x Riogrande	-2.85	-2.34	-18.70	-0.13	0.41	-1.04
UC82 x Valoria select	31.11	29.18	20.00	1.56	2.11	1.07
UC82 x Riogrande	18.36	17.47	9.59	0.91	1.15	0.44
Valoria select x Riogrande	-3.61	-1.62	0.80	-0.18	-0.15	0.07
CV (%)	15.5	80.4	14.7	20.5	33.9	10.6
LSD (5%)	0.1173	0.1276	0.2773	0.1017	0.0759	0.1644

Environments were bacterial wilt infected field LR2017 (long rain season) and SR2017 (Short rain season) and artificially inoculated greenhouse 2017.
Source: Author.

both parents AVTO1429 (12.29%) and AVTO1314 (13.53%). Similarly, F1 hybrid AVTO1429 x Danny select which had a significantly lower incidence of 12% was crossed between the resistance parent AVTO1429 (12.29%) and moderately resistant Danny select (30.92%). The results implied that there were additive gene effects in crosses between the highly and medium resistant genotypes. According to Fufa et al. (2009), and Onduso (2014), resistance to bacterial wilt is compounded after crossing parents with genes conferring resistance in their qualitative trait loci, which explains the results observed in this study. Studies conducted by Kathimba et al. (2023) have also reported that the inheritance of the bacterial wilt resistant trait is regulated by additive and dominance gene effects. Comparable findings were reported earlier by Opena et al. (1992) in their test of over 100 strains of *R. solanacearum* using a seven parent diallel experiment. Their findings also reported that F1 hybrids developed from resistant parents had higher resistance than those developed from susceptible x resistant genotypes, similar to results observed in AVTO1429 x AVTO1314 (7%) and Eden select x AVTO1429 (20%). Non-additive gene effects were also inferred in the present study in crosses between a susceptible and a resistant genotype, which resulted in the development of F1 hybrids with resistance comparable to that of the resistant parent. This was indicated in crosses Eden select x AVTO1429 (20%) and Roma VF x AVTO1429 (29%), where the parent Eden select and Roma VF had disease incidences of 81.90 and 89.87%, respectively. Susceptible parent Roma VF with an 89.87% incidence, crossed with resistant parents AVTO1424 (11.87), AVTO1429 (12.29%) and AVTO1314 (13.53%) developed F1 hybrids with higher resistance than the parent (Roma VF). These results implied that the inheritance of bacterial wilt resistance in this case was due to dominance gene effects. Comparable findings have been reported by Sharma and Sharma (2015) in their studies on the inheritance of the bacterial wilt gene was dominant over susceptible. Similar reports supporting this study's results on additive and dominance inheritance of bacterial wilt resistance trait in tomato were recorded by Da Silva Costa et al. (2018). Their findings pointed out that two major quantitative traits loci segregating independently of additive effects plus polygenes with additive and dominance effects regulate inheritance of bacterial wilt resistance gene.

Better parent heterosis for bacterial wilt resistance trait

Negative better parent heterosis in bacterial wilt disease index is desirable in selecting genotypes for breeding programs. Out of the 45 F1 hybrids, 29 and 31% during the long and short rain seasons respectively showed negative heterosis for disease incidence and severity score. This implies that the F1 hybrids had lower disease

incidence and severity compared to the better parent. These results are in line with the findings that the desirable heterosis for bacterial wilt disease index is a negative percent reported by Chattopdhyay et al. (2012) and Narayan et al. (2018). This infers that both parents had higher disease incidence and severity compared to their F1 hybrids. The highest negative heterosis of -50% was recorded in the F1 hybrid AVTO1429 x AVTO1314 in bacterial wilt disease incidence. Similarly, Singh and Asati (2011) reported a maximum negative heterosis of -66.7% in bacterial wilt incidence in their desirable F1 hybrid FEB-4 x BT-1 17-5-3-1. Heterosis has been used to evaluate the role of combining ability in various studies (Singh and Asati, 2011; Chattopdhyay et al., 2012; Narayan et al., 2018). This is because the role of combining ability and genetic effects is indicated by majority of heterotic crosses involving poor and good combiners.

Combining ability effects for bacterial wilt resistance trait

Large and positive general and specific combining ability is desirable in selecting genotypes for utilization in tomato breeding programs for bacterial wilt resistance trait (Singh and Asati, 2011). This implies that genotypes Eden Select (25.36), Cal J (17.82), Riogrande (15.38), UC82 (14.48) and Roma VF (14.11) with the largest positive GCA effects are good general combiners for use in heterotic crosses in developing hybrids with bacterial wilt resistance. Similarly, crosses AVTO1429 x Riogrande, AVTO1429 x AVTO1424, and AVTO1424 x AVTO1314 which recorded the highest SCA effects are desirable specific combiners. Comparable findings have been reported by Chattopdhyay et al. (2012), showing that positive values show required specific and good general combining ability that could be utilized in breeding programs. Similar findings have also been reported by Narayan et al. (2018). Previous studies on crosses between two bacterial wilt resistant and susceptible cultivars by Osiru et al. (2001), reported that GCA six times as large as specific combining ability (SCA) indicates a high proportion of additive gene effects in conferring bacterial wilt resistance. The development of bred progeny with bacterial wilt resistance greater than that of the parents requires hybridization of parents with good sources of resistance, and subsequent selection of the segregating population (Narayan et al., 2018). Utilizing a parent that is a good combiner and another that is a poor combiner increases the effectiveness of developing hybrids that are more resistant than their parents in a breeding program.

Conclusion

Parental lines AVTO1424, AVTO1429, and AVTO1314

were resistant to *Ralstonia solanacearum* UC82, while Danny and Valoria select had moderate resistance and Roma VF, Cal J, Riogrande and Eden select were susceptible. There were additive gene effects in the cross between highly and medium resistant genotypes, AVTO1429 x Danny select. Crosses between susceptible Roma VF and resistant lines AVTO1424, AVTO1429 and AVTO1314 had dominance gene effects. The highest heterosis percentage was in crosses with genotypes AVTO1429 and AVTO1424 as the better parents. Cal J had the highest GCA effects while AVTO1314, AVTO1429 and AVTO1424 had the lowest. The highest SCA effects were observed in UC82 x Valoria select and AVTO1429 x AVTO1424 during the long and short rain seasons, respectively. The resistance parental lines have potential for use in developing a tomato breeding program in Kenya.

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ABBREVIATIONS

AEZ: Agro-ecological zones; AVRDC: World Vegetable Centre; Cfu: colony forming unit; CV: Coefficient of variation; g: grams; ha: Hectares; l: litres; LSD: Least significant differences of means at ($P \leq 0.05$); m: meters; ml: millilitre; t: tonnes.

CONFLICT OF INTERESTS

The authors have not declared any conflict of interests.

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