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Mode of inheritance for resistance to FOC Race 1 and fruit quality traits in Sukali Ndizi cultivar of Banana

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Information on the genetic control of resistance to *Fusarium oxysporum f.sp.cubense* (FOC) race (1) and fruit quality traits in Sukali Ndizi cultivar of banana is key to its genetic improvement. The mode of resistance to Fusarium wilt in Sukali Ndizi was analyzed in 536 hybrids and 5 parental lines and quality attributes in 137 hybrids and two parental lines, grown in same environment. Fruit quality was assessed by physical measurements and fruit composition whereas resistance to Fusarium wilt was assessed by corm discoloration symptoms. All the assessed traits were quantitatively inherited. Flavor attributes, and pulp texture showed a predominance of additive inheritance with complementary gene action whereas total soluble solutes showed non-additive gene with dominant gene action. Fruit acidity had incomplete dominancy with the genetic model explained by both single gene and certain multiple genes. Resistance to Fusarium wilt showed dominant gene action and polygenic effects. Involvement of a few genes governing wilt resistance suggested the ease of breeding for this trait. Pedigree breeding method could be recommended for incorporating various traits in (cv. Sukali Ndizi) of banana.

Key words: Sukali Ndizi, quantitative inheritance, fruit quality, Fusarium wilt resistance.

INTRODUCTION

Bananas provide a starch staple across some of the poorest parts of the world (with consumption up to 400 kg per person per year), in Africa and Asia, while desert bananas are a major cash crop in many countries (FAOSTAT, 2007). Banana production in Uganda provides cash incomes and livelihoods to subsistence producers, transporters and dealers in its trade (FAO, 2002). Amongst the dessert bananas, the most popular in highlands is locally known as 'Sukali Ndizi' ('Apple and

most widely distributed dessert cultivar East African banana', AAB genome) (Pillay et al., 2003; Nsabimana and Van Staden, 2006). In other parts of the East African highlands this cultivar is known as 'Kameramasenge' or 'Calole'. An estimated 85% of all banana farmers in Uganda have 'Sukali Ndizi' (Gold et al., 2002). The banana crop suffers from many pests and diseases, mainly Fusarium wilt, bacterial wilt and black sigatoka.

Fusarium wilt, caused *by Fusarium oxysporum f. sp.*

cubense (FOC), is the most common and major disease in several desert banana producing areas worldwide (Poon and Teo, 2019). Wilt caused by *F. oxysporum f.sp cubens* is becoming more serious in Apple banana (Sukali-Ndizi), causing decline in yield and poor quality fruits (Tushemereirwe et al., 2000). Companies dealing in export business of apple bananas have lost their contract farmers because the disease has caused yield decline or wiped out their plantations (NBRP, 1999). Being soil borne, the control of Fusarium wilt by chemical management is expensive = inefficient and causes adverse effect on the physico-chemical and biological properties of soil, therefore important to develop cultivars with inbuilt resistance to the disease. All the genotypes that have been identified as source of resistance to *F. oxysporum f.sp cubense* may not necessarily have desirable agronomic traits and thus, may not be directly introduced for wide scale cultivation but can be used as donors for resistance genes under breeding programme. Knowledge on inheritance of the wilt resistance is important to decide the breeding strategies in cv.Sukali Ndizi of banana. Little work has been done about studies on inheritance of resistance and gene action involved, indicating the lack of knowledge on inheritance behavior for resistance to (Foc).

The considerable banana breeding efforts have mainly emphasized resistance to disease and pest, yield, fruit size and fruit appearance (Dufour et al., 2020). However, the consumers complain about the lack of pleasant sensory qualities of Ndizi hybrids (Dufour et al., 2020). According to a market survey, the sensory quality of a food product has been ranked higher than its nutritional value, price or safety, from a consumer point of view (Grunert 2005). It does not matter how resistant to diseases and pest or productive the banana may be, if the fruit is not of acceptable quality, it will not be a commercial success (Causse et al., 2003). Consumers evaluate Sukali Ndizi fruit quality according to pulp colour, pulp texture (firmness), flavor sugar content and fruit acidity (Van Asten et al., 2010). These parameters are the most important attributes that determine overall fruit quality (Van Asten et al., 2010). Firmness is considered a useful criterion for ascertaining the eating quality and ripeness of banana. Softening or loss of pulp firmness during ripening has been attributed to the solubilization of peptic substances in the cell wall and middle lamella (Dadzie and Orchard, 1997). Fruit taste is an important trait majorly controlled by organic acids and together with aromatic volatile compounds and soluble sugars, strongly facilitate overall organoleptic quality of a fruit (Carli et al., 2011). Three major organic acids that accumulate in most fruits include malic, citric and tartaric acid and their final concentration in ripening fruits depends on the balance between the biosynthesis of organic acids, their degradation, and their vacuolar storage. Different fruits accumulate different organic acids for example citric acid is the major organic acid in

citrus (Batista-Silva et al., 2018), while malic acid is the predominant organic acid in apple and banana (Centeno et al., 2011). Organic acids are the main soluble constituents which influence important fruit qualities such as fruit coloration, the shelf life of the fresh fruit, and ripeness; consequently, they can be used as an index of consumer acceptability (Mikulic-Petkovsek et al., 2012). This parameter can be used to predict the slightly acidic apple-like taste of Sukali Ndizi fruit pulp which is its unique characteristic (Van Asten et al., 2010).

The most inheritance studies done in bananas are resistance to black Sigatoka, nanism, albinism, apical dominancy and habit of buds formation, partenocarpy of the fingers and sterility, orientation of the bunch, wax in the pseudostem, male and female sterility, weight of the components of the bunch and other agronomic traits such as persistency of the male bracts and hermaphrodite flowers in the rachis. These studies have observed that such characteristics are governed by one or a few genes (Ortiz, 1995; Vuylsteke et al., 1996). There is lack of information on understanding the inheritance of traits like fruit size, soluble solids content (SSC), colour, firmness, acidity and starch in bananas. This has resulted into slow uptake or total rejection of the banana hybrids (Dufour et al., 2020).

Therefore, the knowledge of inheritance of various characters that determine fruit quality is important to achieve success in banana breeding in general and Sukali Ndizi breeding in particular. The inheritance of characters like fruit, pulp texture, flavor, colour and fruit acidity would be valuable information to breeders while selecting superior genotypes for desirable traits. Hence, this study was designed to understand the inheritance of resistance to Fusarium wilt. Other characters like fruit pulp texture, flavor, colour, taste and fruit acidity were also investigated.

MATERIALS AND METHODS

Experimental material

Inheritance of quality traits

The study was conducted to establish mode of inheritance of genes controlling fruit quality traits in a biparental cross of Sukali Ndizi and TMB2X8075-7 using Top cross. TMB2X8075-7 has poor flavor, no apple-like taste and not good pulp texture and was derived from across between two parents namely, hybrid SH-3362 "Musa AA" as a female parent and the wild banana Calcutta 4 "Musa AA as a male parent" (Dochez, 2004).

Inheritance of resistance to Fusarium wilt

The experiment was conducted from during March 2016 to August 2018 at National Agricultural Research Laboratories, Kawanda. During the period of 2013 to 2016, NAMU 1, NAMU 2 hybrids were selected from over 500 Ndizi hybrid lines in a field which had a history of severe Foc race 1 infestation therefore, a hot spot, to

avoid field escape of some plants to the pathogen due to uneven pathogen distribution, Foc race 1 inoculum at a concentration of 5 × 10^6 spores/ml was distributed around the banana stools (Buregyeya et al., 2020).

The two selected NAMU 1 and NAMU 2 lines were utilized as Foc resistant female parents and Sukali Ndizi as susceptible female parent, and TMB2x8075-7, Pisang lilin and Cultivar Rose were FOC race 1 resistant male parents during crossings.

During the period of 2016 to 2018, nine (9) cross combinations possible with the resistant parental plants (R), moderate resistant parental plants (MR), and susceptible parental parents (S) were carried out. North Carollina Design II (NCII) crossing design was utilized for the crosses NAMU 1(R)(♀) × TMB2x8075-7(R)(♂), NAMU 2(MR)(♀) × TMB2x8075-7(R)(♂), NAMU 1(R)(♀) × Cultivar Rose(R)(♂), NAMU 2(R)(♀) × Cultivar Rose(R)(♂), and Sukali Ndizi(s)(♀) × Pisang lilin (R)(♂), and the five F1 populations of Sukali Ndizi derived from the crosses were utilized in the study.

Experimental layout

The F1 progenies resulting from the cross Sukali Ndizi × TMB2X8075-7 were planted in the field in a complete Randomized Design with the parents in two replications, in a spacing of 3 m × 3 m, between plants in March 2015. All the banana management practices were observed as described in NBRP (2001). .

FOC assessment

On a monthly basis, beginning three months after planting, plants were observed for symptom development of FOC race 1. Plants which clearly portrayed Fusarium wilt symptoms were recorded as diseased and marked for future reference. Plants that died before yielding fruit were examined internally to confirm the presence of Fusarium wilt disease. Plants that yielded fruits, internal ratings of disease were carried out at harvest. Characteristic Fusarium wilt symptoms were evaluated according to the following symptoms scale (Mohamed et al., 2001) with some modifications (that is, the scale stopped at 6 instead of 8) for corm symptoms: 0, healthy plants without symptoms; 1, no discoloration of stellar region of corm, discoloration at junction of root and corm; 2, trace to 5% of steller region discoloured; 3, 6-20% of steller region discoloured; 4, 21-50% of steller region discoloured; 5, more than 50% of steller region discoloured; 6, discoloration of the entire corm stele. Disease symptoms based on pseudostem splitting were evaluated using a scale: 1, no cracking of the pseudostem; 2, slight cracking of the pseudostem; 3, advanced cracking of the pseudostem (Mohamed et al., 2001).

All plants from the five crosses were grouped into four classes viz., immune no symptoms, resistant, susceptible and highly susceptible with severe corm discoloration symptoms. These plants were further grouped into two classes that is resistant = immune + resistant and susceptible = susceptible + highly susceptible.

Physio-chemical assay

Physio-chemical assays were carried out as described in Liew and Lau (2012). Briefly, juice samples from the ripe banana fruits were extracted using a commercial fruit blender (8011E Model 38BL41 Made USA). Fifty (50) grams of fresh banana sample were diluted in 50 mL of distilled water and blended for 1 min until homogenized and turned juicy. The mixture was centrifuged (6000 rpm, 6 min) using the Hitachi centrifuge (Hitachi Germany).

The physio chemical assays involved the determination of the titratable acidity (% malic acid) using 0.1 M NaOH (AOAC, 2016), total soluble solutes (%Brix) using a refractometer (WZS 50 brix meter YANHE Shangai Chain) and pH using handheld pH meter (Model TDS Made China), fruit texture (pulp firmness) in kgf (Soltani et al., 2010), and the sugar/acid ratio, which was calculated using Equations 1 and 2, and 0.0067, a factor for malic acid multiplied since malic acid is the dominant acid in dessert bananas (AOAC, 2016):

$$Percentage\ Acid = \frac{Titre \times Acid\ Factor \times 100}{10\ (ml\ Juice)} \quad (1)$$

$$Sugar\ acid\ ratio = \frac{°Brix\ Value}{Percentage\ Acid} \quad (2)$$

Statistical analysis

FOC data analysis was performed using SAS version 8.2 for windows (2001). To compare the traits means, Fisher's protected least significant test at α ≤5% was performed. The estimated resistant susceptible ratios of the crosses were confirmed by application of χ^2 test for their significances (Fisher, 1971) using the standard formula χ^2.

The segregation ratios of the offsprings on wilt incidences were subjected to χ^2 analysis to test the goodness of fit between the observed and the expected means.

Observed segregation ratios of various traits were tested by Chi-square analysis against expected ratio for a single gene inheritance and level of significance tasted.

The χ^2 analysis was applied to determine the patterns of inheritance for various traits in the F_1 populations. The segregation ratios were applied to explore the mode of gene action.

RESULTS AND DISCUSSION

Inheritance and gene action of Fusarium wilt resistance in Sukali Ndizi

Screening of the progenies

Segregation pattern for Fusarium wilt resistance among crosses NAMU2 x TMB2X8075-7, NAMU1 x TMB2X 8075-7, NAMU2 x Cultivar Rose, Sukali Ndizi x Cultivar Rose and Sukali Ndizi x Pisanga lillin are given in Table 1.

The pattern of segregation in the population from the NAMU2♀ × TMB2x8075-7♂ cross was 5.5R: 10.25mr: 1s:3.16Hs In the evaluations of the response to Fusarium wilt in parental and F_1 population, different categories of symptoms were identified that describe the disease in the Sukali Ndizi (Jamil et al., 2020; Ploetz and Pegg, 2000). The phenotype evaluation was based on the symptom scale and the biological response of the different genotypes to the pathogen, in order to establish possible phenotype ranges in the populations. The results of disease severity assessment based on corm symptoms done using a scale of 0-6, on the parental lines, showed values of corm discoloration between 0 and 15% for the resistant parental lines, and values above 50% for the particular case of the

Table 1. Performance of progenies to Fusarium wilt under various Foc ratings.

Cross	No. of plants	Observed frequency			
		Immune	Resistant	Susceptible	Highly susceptible
NAMU2 × TMB2x8075-7	240	67	123	12	38
NAMU1 × TMB2X8075-7	80	0	72	3	5
NAMU2 × Cultivar Rose	85	31	26	7	21
Sukali Ndizi × Cultivar Rose	37	3	21	2	11
Sukali Ndizi × Pisanga lilin	94	0	74	4	16

Table 2. Reaction of Sukali Ndizi hybrid crosses to Fusarium wilt grown under wilt hot sport.

Cross	Plant No.	Observed frequency		Expected frequency	Ratio R:S	χ^2 value cal.	χ^2 tab	p-value 0.05
		Resistant	Susceptible					
NAMU2 × TMB2 × 0775-7	240	190	50	60	3.8:1	2.223	3.841	3:1
NAMU2 × Cultivar Rose	85	57	28	21.3	2:1	2.833	3.841	3:1
Sukali Ndizi × Cultivar Rose Sukali Ndizi	37	24	13	9.3	1.1:1	1.991	3.841	3:1
Sukali Ndizi × Pisanga lilin	94	74	20	23.5	3.7:1	0.667	3.841	3:1
NAMU1 × TMB2 × 8075-7	80	72	8	13.3	9:1	2.533	3.841	5:1

Sukali Ndizi the positive control. Meanwhile, the negative controls showed corm discoloration values of 0%, which present no symptoms related to the Fusarium wilt. These symptoms occur between 2 and 5 months after infection of roots (Stover, 1962), the long incubation period was influenced by the susceptibility or resistance of the host plant. According to Beckman (1990), the pathogen infects the roots of both susceptible and resistant cultivars, but the infection of vascularized fragment of the rhizome is more prominent in the susceptible genotypes. The time in which the symptoms were present, both in parental plants and in the five assessed populations, was variable, thus an indication of varietal reply in the pathogen response. The time of evaluation of the symptomatology (2 years) plus the sizes of the five populations assessed (NAMU2 × TMB2x8075-7 240 genotypes, NAMU1 × TMB2X8075-7 80 genotypes, NAMU2 × Cultivar Rose 85 genotypes, Sukali Ndizi x Cultivar Rose 37 genotypes, and Sukali Ndizi x Pisanga lilin 94 genotypes) proved the presence of a wide variety of situations, from genotypes that did not present any symptoms to genotypes that died from Fusarium wilt.

Results of detailed symptomatology tracking over time, for each genotype of the five evaluated populations, the phenotype ranges were estimated as resistant (R), moderately resistant (mr), susceptible (s) and highly susceptible (Hs). In the range R, genotypes that at the end of the symptom register time did not present any symptoms were placed (1-2). In the range mr, genotypes that presented symptoms in number three were placed, genotypes rated scale 4 were in range susceptible (s). And finally, in the range highly susceptible (Hs), the genotypes that presented symptoms in numbers 5 and 6 were placed,

namely wilting and death. The severity information of each genotype of the various assessed populations was used to characterize each phenotypic range (R, ms, s and Hs) for each population. The ranges explain the phenotypes of Fusarium wilt response that are evident in the populations across the symptomatology, and the time in which those symptoms are present. In the cross involving NAMU2♀ × TMB2x8075-7♂ of 240 progenies 67 resistant, 123 moderately resistant, 12 susceptible and 38 highly susceptible. The pattern of segregation in the population from the NAMU2♀ × TMB2x8075-7♂ cross was 5.5R: 10.25mr: 1s:3.16Hs (Table 1).

Scrutinizing the results, it was revealed that the phenotype was distributed in the two extreme ranges, resistant and highly susceptible, and also in the intermediate range of moderately resistant, and susceptible showing that segregation for the resistance characteristic *to F. oxysporum f. sp. cubense* exists.

The phenotypic ranges were further grouped into two, resistant genotypes which included (resistant (R) and moderately resistant (mr)), and susceptible genotypes which included susceptible (s) and highly susceptible (Hs) in order to test *mendelian* monogenic inheritance model. In the cross NAMU2 × TMB2X8075-7 out of 240 plants screened against wilt 190 plants were resistant and 50 plants were susceptible (Table 2) in cross NAMU1 × TMB2X8075-7 progeny was classified as 72 resistant and 8 susceptible. The total number of plants counted in cross NAMU2 × Cultivar Rose was 85 out of which 57 was classified as resistant and 28 classified as susceptible, out of 37 progeny from across Sukali Ndizi × Cultivar Rose 24 were classified as resistant and the remaining

13 were susceptible. In cross Sukali Ndizi × Pisanga lillin out of 94 plants screened 74 plants recorded resistant reaction while remaining 20 plants were classified as susceptible. Segregation analysis of Fusarium wilt showed that the ratios of resistant to susceptible progenies in family NAMU2 × TMB2X8075-7 fit a 3:1 ratio (χ^2=3.841, p=0.05), and the NAMU2 × Cultivar Rose family observed segregation ratios (OSRs) fit 3:1 ratio, respectively (χ^2=3.841, p=0.05). In the Sukali Ndizi × Cultivar Rose family the resistant to susceptible progeny (χ^2=3.841, p=0.05) and Sukali Ndizi × Pisanga lillin progeny resistant to susceptible (χ^2=3.841, p=0.05) indicated a goodness of fit to ratio of 3R:1S inheritance pattern. Crosses of NAMU1 × TMB2X8075-7 segregated in (9R:1S) goodness to fit a ratio of 5:1 (χ^2=3.841, p=0.05) suggesting the involvement of major genes in expression of Fusarium wilt resistance in Sukali Ndizi where resistance is conferred by the dominant gene and susceptible controlled by recessive genes (Singh et al., 2016).

It was further observed that the proportions of the resistant progenies to the susceptible were always on the higher side indicating that dominant multiple genes governed Foc race 1 resistance trait in these hybrids (Haghdoust et al., 2018). Determination of the Foc race 1 segregation patterns for a particular parental combination, for example Sukali Ndizi × Cultivar Rose or Sukali Ndizi × Pisang Lilin, the progenies in F1 showed different patterns of resistance although the male parents used were resistant to Fusarium wilt suggesting that Sukali Ndizi was the double recessive and susceptible while the males are resistant dominant thus explaining the aforementioned distribution patterns (Singh et al., 2016). However, these results disagree with those earlier reported by Ssali et al. (2013) in a cross between TMB2X8075-7 and Sukali Ndizi which suggested that resistance to Fusaruim wilt in Musa was conditioned by a single recessive gene. In the case where both parents were resistant for example, NAMU2 × TMB2X8075-7 or NAMU2 × Cultivar Rose, the progenies showed different patterns of resistance with appearance of susceptible progenies. This can be explained by the heterozygous nature of the parents and/or due to the polygenic inheritance of resistance genes, similar findings were reported by Damodaran (2003) and Arinaitwe et al. (2019). The genetics of resistance to FOC can be presented as follows: three "dominant" capital letter genes (R_1, R_2 and R_3) confer resistance to Fusarium wilt. The "recessive" alleles of these three genes (r_1, r_2 and r_3) confer suceptability to Fusarium wilt in Sukali Ndizi. The letters dominant and recessive are placed in quotation marks because these pairs of alleles are not truly dominant and recessive as in some contest as that of Gregor Mendel. A genotype with all "dominant" capital genes ($R_1R_1R_2R_2R_3R_3$) has the maximum amount of resistance and immune to Fusarium wilt. A genotype with

all "recessive" small case genes ($r_1r_1r_2r_2r_3r_3$) has no resistance thus highly susceptible e.g. Sukali Ndizi. Each "dominant" capital gene produces one unit of resistance, so that a wide range of intermediate resistance to Fusarium wilt are produced, depending on the number of "dominant" capital genes in the genotype. The genotype with three "dominant" capital genes and three small case "recessive" genes ($R_1r_1R_2r_2R_3r_3$) had a medium amount of resistance to Fusaruim wilt and the genotypes classified as moderately resistant. It was clearly evident that resistant × resistant crosses produced both resistant and susceptible hybrids. This makes it clear that resistance to FOC is also under polygenic control and segregation for resistance and susceptibility was expected because of the heterozygous nature of the parents involved (Mostafavi et al., 2004). Multiple gene (polygenic) inheritance explains resistance to Fusaruim wilt Sukali Ndizi and further supported by the wide variation between extreme phenotypes, with most individuals having intermediate phenotypes.

Physio-chemical variability in crosses

All the characters (pH, pulp texture, total soluble solutes, and sugar/acid ratios) measured were highly variable in the Sukali Ndizi × TMB2X8075-7 F_1 populations (Figure 1A, 1B, 1C, and 1D). Sukali Ndizi the female parent had slightly higher sugar content (24.8% Brix) than the diploid male parent TMB2X8075-7 (22.133% Brix). The range in total sugar content of the progenies ranged from 10% Brix (34-6HB) to 26.8% Brix (4-5) which was 2.68 folds, however, the highest percentage of the progeny population was consistently in the same range of sugars as the parents. The parental results of pH were Sukali Ndizi pH 3.4 and TMB2X8075-7 pH 4.8 while the range for progeny population for fruit acidity content 2.9 (Figure 1B). Statistically significant differences (p<0.05) were detected among the parental cultivars and the progeny population for sugar/acid ratio and the progenies population range was 56 (30-3HB) to 257.2 (8-5) and whereas the pulp texture of the parental was TMB2x8075-7(1.64 kgf) and Sukali Ndizi (0.89 kgf), the range of the progenies was 0.7 to 3.9 kgf which was a difference of 3.2 kgf. Results shown variation in fruit quality attributes composition in progeny population and all characters studied appeared to be under polygenic control.

Distributions of parental and F_1 populations (Figure 1A, 1B, 1C, and 1D) indicated that at least more than one gene operates to control in each of the studied character.

Results of TSS distribution showed that the highest percentage of the progeny population was consistently in the same range of sugars as the parents (Figure 1A). All the F1 population presented total sugar content concentrations with continuous variation which implies that TSS concentration was inherited quantitatively. The
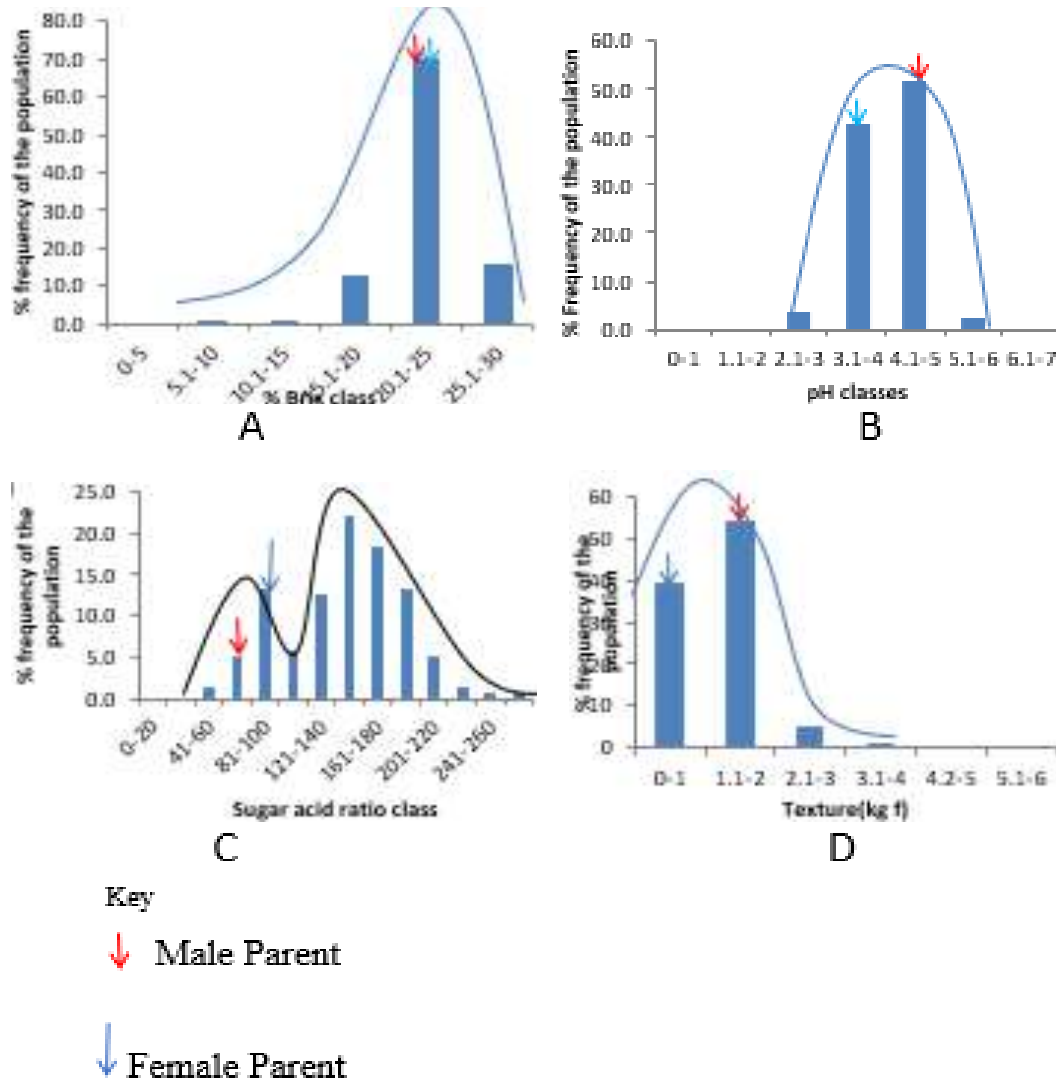
Figure 1. Frequency distribution of the studied traits in the progeny population (A) TSS, (B) acidity, (C) sugar/acid ratio, and (D) texture.

trait showed transgressive segregants with 16.2% positive segregates and 13.9% negative segregates. These shows that there are chances of improving the %Brix values beyond the parents values thus a high possibility of selecting breeding lines with better %Brix value from among the progenies generated in the cross. It was further observed that %Brix was negatively skewed in this population (Figure 1A) indicating the predominance of dominant gene action and thus there was a difficulty in immediate fixing of desirable alleles in early generation. The negatively skewed phenotypic distribution for the trait also indicated non-additive gene action for the character (Dinesh et al., 2018). The total sugar content concentration in pulp of F_1 population was skewed to the low values but some progenies had extraordinarily high TSS concentration. Therefore, improvement of Sukali Ndizi cultivars for high TSS

concentration is possible by crossbreeding as the transgressive segregants in F_1 generation, suggests that they could produce superior lines (Cazzola et al., 2020). The total sugars and soluble solids of Sukali Ndizi progenies were quantitative characters controlled by many minor genes and expressed additive and non-additive genetic effects and cross breeding was an effective way for improving Sukali Ndizi sugar content. Baojiang et al. (1995) reported that sweetness in apple fruits was governed by multiple genes that showed additive and non-additive genetic effect, and the segregation of the soluble solids, total sugar and reducing sugar contents of hybrids all showed continuous variance tending to normal distribution.

Likewise, the highest percentage of the progeny population 51.5% was consistently in the same range of fruit acidity as the male parent TMB2x8075-7 (pH4.1-5),

42.6% of the progeny population in the same range as the female parent Sukali Ndizi (pH3.1-4), 3.7% showed negative transgressive segregation and lastly 2.2% of the progeneis were positive transgressive segregants (Figure 1B). It was observed that the F1 population showed fruit acid content concentrations with a continuous variation (Figure 1B) indicating that fruit acid concentration was inherited quantitatively. The frequency distribution of fruit acidity in this population showed continuous and unimodel curve which is indicative of polygenic control. However the presence of high acid, medium acid and low acid phenotypic classes in the progenies indicated that fruit acidity may be controlled by major gene with incomplete dominance effects, the homozygous dominant, heterozygote, and homozygous recessive corresponding to the pH classes (Hiroshi et al., 2012). Further, the results indicated that fruit acidity was jointly governed by two genetic models, a single major gene and certain multiple genes (Hiroshi et al., 2012). Visser and Verhaegh (1978) reported the effect of the multiple genes on fruit acidity was so great that it can cancel the effect of the major gene and make progenies drift off from the typical segregation. Liu et al. (2007) studied three grape progeny populations derived from crosses involving the same maternal parent and reported that malic acid inheritance in grape was strongly additively inherited with significant transgressive segregation. Visser and Verhaegh (1978) indicated that the mode of inheritance of acidity could be explained by an additive genetic action model (polygene). Liu et al. (2004) reported that fruit acidity is governed by two cooperative genetic models, which divided a single major gene and certain multiple genes, and the genetic effect of the major gene was completely dominant with additive genetic effects of the multiple genes. Baojiang et al.. (1995) reported that fruit acidity in apples was jointly governed by two genetic models, a single major gene and certain multiple genes and the genetic effect of the major gene (Ma-ma) was incomplete dominance. The homozygous dominant, heterozygote, and homozygous recessive showed high acid, sub acid and low acid phenotypes respectively. The effect of the multiple genes on fruit acidity was so great that it can cancel the effect of the major gene and make progenies drift off from the typical segregation (Baojiang et al., 1995).

In the case mean sugar/acid result showed that all the F_1 population presented sugar/acid ratio with continuous variation (Figure 1c). The frequency distribution of the sugar/acid ratio as an estimate of flavor in the population formed bimodal curve, with positive transgressive seggregant accounting 80.2% and 1.5% negative transgressive seggregants. The frequency distribution for sugar/acid ratio was positively skewed to the right for the population indicating that majority of the progenies had sugar/acid ratio higher than both parents. The presence of positive skewness for this traits indicated predominance of additive gene action and desirable alleles could be fixed in early generations. The presence of transgressive

segregants for this character indicated complementally gene action between the parents.

Like the other two parameters, fruit pulp texture behaved similarly with the highest proportion of the progeny population in the same range of fruit texture as the male parent TMB2x8075-7(1.64 kgf), the second ranked was in the same range as the female parent Sukali Ndizi (0.89kgf), while the rest showed positive transgressive segregation (Figure 1D). The frequency distribution for texture was continuous in the population meaning the trait was quantitatively controlled. Some progenies had pulp texture similar to or higher than that of the parents indicating positive transgrassive segregation with positive skewness (Figure 1D), thus complementary gene action (Ajay et al., 2016). The transgressive segregation was an indication of complementally gene action between the parents, positive skewness indicated predominance of additive gene action and desirable alleles could be fixed in early generations (Roy, 2000). It is known that firmness was quantitatively inherited with sufficient additive effects to permit gain from selection, also in a separate experiment generation means analysis was used to assess the mode of gene action in 2 crosses: 'Green F' × 'Chipper', and 'Gy3' × 'Green F' and additive genetic effects accounted for 98.8% and 99.3% of the total genetic variation within each cross (Peterson et al., 1978).

Conclusion

The genetics of Fusarium wilt resistance as well as quality determining characters like pH, pulp texture, total soluble solutes, and sugar/acid ratios are polygenic and quantitatively inherited. However, the acidity inheritance is associated with incomplete dominance effects and explainable by two genetic models. Fusarium wilt resistance and TSS are controlled by both dominant as well as non-additive genes suggesting improving these traits through cross breeding and recurrent selection. Sugar/acid ratio and pulp texture are governed by additive effects and complementally gene action indicating the improvement through pedigree method of selection. The two to three genes governing Fusarium wilt resistance in musa germplasms suggest the ease of incorporating resistance in Sukali Ndizi genotypes during the breeding process. Pedigree breeding would be recommended for conferring Fusarum wilt resistance and quality controlling traits in Sukali Ndizi.

CONFLICT OF INTERESTS

The authors have not declared any conflict of interests.

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