

Inheritance of fusarium wilt resistance in pigeonpea [*Cajanus cajan* (L.) Millspaugh]

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Abstract

Fusarium wilt caused by *Fusarium udum* Butler is the most important disease of pigeonpea worldwide. Objectives of this study were to determine the mode of genetic inheritance of Fusarium wilt resistance in different pigeonpea accessions and to determine different genes governing resistance that exists in pigeonpea accessions. F₁, F₂ and backcross populations were developed by crossing resistant accessions (ICEAP 00554, ICEAP 00557) with susceptible accessions (KAT 60/8, ICP 7035). The Parents, F₁, F₂, backcrosses (BC₁F₁ and BC₂F₁) populations were evaluated for Fusarium wilt resistance. F₂ populations derived from ICEAP 00554 × KAT 60/8, ICEAP 00557 × KAT 60/8, ICEAP 00554 × ICP 7035, ICEAP 00557 × ICP 7035 crosses exhibited a 3:1 ratio which indicated that resistance to Fusarium wilt was under the control of major gene, however, a recessive gene was detected from ICP 7035 × KAT 60/8 cross. The genes detected could be valuable for wilt resistance breeding.

Key words: Pigeon pea, *Fusarium udum*, isolate

Introduction

Fusarium wilt (*Fusarium udum* Butler) is an important soil borne disease of pigeonpea [*Cajanus cajan* (L.) Millsp], which causes significant yield losses in susceptible cultivars throughout the pigeonpea growing areas [1, 2]. In the last two decades, ICRISAT has been conducting research in India to overcome the pigeon pea production constraints associated with Fusarium wilt [3]. Several Fusarium wilt resistant lines have been identified and developed, nonetheless, these germplasm are not adapted to Kenyan environment due to photoperiod and temperature sensitivity [4]. Among some resistant pigeon pea varieties, segregation for resistance to Fusarium wilt does occur in subsequent

generations because of variation in isolates [5, 6]. Consequently, development of durable and adaptable pigeonpea varieties is one of the most efficient and economical method to control Fusarium wilt.

The knowledge of genetic inheritance is essential for formulation of strategy on how to transfer the genes into adapted susceptible varieties. In pigeonpea, resistance to fusarium wilt has been reported to be under the control of two complementary genes [7], single dominant gene [8], 2 genes [9], major genes [7, 10], duplicate genes and even multiple factors [11] and a single recessive gene [12]. Apart from dominant, recessive and complementary gene action on the control of Fusarium wilt [5, 13] has been reported. Dominant epistatic gene interaction and a single dominant gene play a significant role in controlling resistance to wilt [7]. Digenic and quantitative genes that are resistant to Fusarium wilt have been observed although quantitative inheritance is often influenced by environment; the resistance depends on the source of the gene [14].

Information on allelic relationship for Fusarium wilt resistance in pigeonpea is inadequate. In a cross between two resistance lines, there is independence in the genes controlling resistance to Fusarium wilt [9]. Therefore, objectives of this study were to determine the inheritance of Fusarium wilt resistance in different pigeonpea backgrounds and to determine different resistant genes that exist in pigeonpea genotypes

Materials and methods

The study was conducted at Kenya Agricultural Research Institute (KARI)-Kiboko and KARI-Katamani

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Research Centre in Eastern Kenya (Table 1).

Seedling test

Fifty-one pigeonpea accessions/varieties of medium and long duration that originated from Kenya, Tanzania, Uganda, Mozambique and ICRISAT (India) were screened for resistance. The activity was carried out in a green house at KARI-Katamani research station. Varieties ICEAP 00040 from ICRISAT is resistant to Fusarium wilt. However, KAT 60/8 that is medium (but early) maturing is susceptible to Fusarium wilt. Three different isolates of the *Fusarium wilt* fungus from KM (Machakos), EM (Makueni) and KB (Makueni) pigeonpea growing areas in Kenya were used. The KM and EM isolates were collected from farmers' fields while the KB isolate was collected from the wilt-sick plot at Kiboko research station. In this study KB isolate which is the most virulent among the *F. udum* pathotypes was included to help identify accessions with resistance to more than one strain. Inoculum was prepared using diseased stems according to the modification of the protocol described by Laslie and Summerell [15]. The seedlings were inoculated using root-dip inoculation technique described by Okiror [16]. Observations were made and scoring done using a disease rating scale described by Nene *et al.* [17]

Screening of F_1 , F_2 and Backcross populations

Development of F_1 , F_2 and Backcrosses populations : Four medium duration genotypes were used as parents (Table 2). ICEAP 00554 and ICEAP 00557 were used as the resistant parents while KAT 60/8 and ICP 7035 as susceptible varieties (Table 3). ICEAP 00554 and ICEAP 00557 are selections from Tanzanian landraces; KAT 60/8 is a selection from local germplasm and a popular pigeonpea commercial variety in Kenya. ICP 7035 is an introduction from India. The first crossing was done in Feb.-April, 2008 using Griffin's mating design I, model I to generate F_1 populations. Resistant \times resistant and susceptible \times susceptible crosses were made to obtain information on the allelic relationship on the resistant and susceptible parents, respectively

Table 1. Description of experimental site

Site	Location	Average Temp. (°C)	Altitude (meter asl)	
			Feb.	Oct.
KARI-Katamani	37°14'E; 1°35'S	1600	27.9	26.4
KARI-Kiboko	2°10'S ;37° 40'E	975	26.3	24.9

Source: KMD, 2008

Table 2. Mating scheme of the four pigeonpea (*Cajanus cajan*) cultivars used to develop F_1 , F_2 populations for genetic analysis

	KAT 60/8	ICP 7035	ICEAP 00554	ICEAP 00557
KAT 60/8		x	x	x
ICP 7035	x		x	x
ICEAP 00554	x	x		x
ICEAP 00557	x	x	x	

KAT= Katumani 60/8; ICEAP= ICRISAT East African Pigeonpea

Table 3. Differential reaction of 13 pigeonpea (*Cajanus cajan*) accessions and 7 genotypes to three Fusarium wilt isolates KM, EM and KB.

Genotype	Country of origin	Isolate		
		KM	EM	KB
Accession 111	Tanzania	+	+	-
Accession 112	Tanzania	+	+	-
Accession 5	Tanzania	+	+	-
Accession 32	Tanzania	+	+	-
Accession 29	Tanzania	+	+	-
Accession 103	Tanzania	+	-	-
Accession 120	Tanzania	+	-	-
Accession 19	Tanzania	+	-	-
Accession 107	Tanzania	+	+	-
Accession 24	Tanzania	+	-	-
Accession 38	Tanzania	+	+	-
Accession 45	Tanzania	+	-	-
Accession 82	Tanzania	+	-	-
ICEAP 00040	Kenya	+	+	+
ICEAP 00020	Kenya	+	+	+
ICEAP 00554	Tanzania	+	+	+
ICEAP 00557	Tanzania	+	+	+
ICEAP 00576-1	Kenya	+	+	+
KAT 60/8	Kenya	-	-	-
ICP 7035	India	-	-	-

KM=Kimutwa, EM= Emali, KB=Kiboko; + = resistant (= 36.6% wilt incidence), - = susceptible (= 36.6% wilt incidence); KAT= Katumani 60/8; ICEAP= ICRISAT East African Pigeonpea

(Table 1). F_2 , BC_1F_1 and BC_2F_1 populations were derived from F_1 seeds. F_1 and F_2 populations derived from resistant \times resistant (ICEAP 00554 \times ICEAP 00557) and susceptible \times susceptible (KAT 60/8 and ICP 7035) crosses were developed for allelic study.

Screening of Accessions, F_1 , Backcrosses and

Segregating Populations

Preparation of Inoculum and plant inoculation: A Kiboko (KB) isolate of the Fusarium wilt fungus was obtained from a highly susceptible *var.* KAT 60/8. Stems from diseased plants of this *var.* were used and the inoculum was prepared according to the modification of the protocol described by Laslie and Summerell [15]. Soil was mixed with sand at a ratio of 3:1 and the damp mixture was sterilized using soil sterilizer (THERMOFORCE LTD) for 1.5 hours at 82 °C. It was then placed in polythene bags (16cm × 16cm × 8cm) in the greenhouse. A total of 60 seeds each for F₁, BC₁F₁, BC₂F₁ and parents while 200 seeds for F₂ were evaluated. Four seeds were sown in each bag. The seeds were surface sterilized in 1% sodium hypochlorite for one minute and rinsed three times in sterile dH₂O. Seven days after germination, the seedlings were inoculated using root-dip inoculation technique described by Okiror [16]. For controls of both the susceptible and resistant lines, the distal end of the root system was cut, and the seedlings dipped in sterile dH₂O. Immediately after transplanting, watering was done at an interval of two days. The polythene bags were then placed in a greenhouse and maintained at about 22-32°C. The seedlings were sprayed with insecticide [Duduthrin (Lambda-cyhalothrin)] at the rate of 17.5g ha⁻¹ to control insect pests. Control of weed was done by hand weeding. The number of resistant and susceptible seedlings to Fusarium wilt was observed.

Data analysis

Chi-square analysis was performed using SAS software, SAS Institute [18] to test the goodness of fit between the theoretical models and observed ratios of resistant to susceptible plants.

Results and discussion

Inheritance studies

Among the pigeon pea parents used in this study, KB isolate of Fusarium wilt was virulent to *var.* KAT 60/8 and ICP 7035 but no susceptible reaction was noted on the resistant *var.* ICEAP 00554 and ICEAP 00557 (Table 3). All the F₁ progenies that were derived from ICEAP 00554 (resistant) × KAT 60/8 (susceptible), ICEAP 00557 (resistant) × KAT 60/8 (susceptible) and their reciprocal crosses were resistant to Fusarium wilt isolate KB at seedling stage (Table 4). Similar results were observed on the ICEAP 00557 (resistant) × ICP 7035 (susceptible), ICEAP 00554 (resistant) × ICP 7035 (susceptible) and their reciprocal crosses. Lack of

difference in disease reaction from crosses between resistant × susceptible and their reciprocals indicated that cytoplasmic effects did not play any role in the expression of resistance to Fusarium wilt isolate KB. The resistance conferred was located in the genome. No difference in disease reaction was observed in the resistant × susceptible and their reciprocal crosses.

The number of resistant and susceptible observed in F₂ populations derived from resistant × susceptible and their reciprocal crosses demonstrated a good fit to one gene model with a ratio of 3:1 (resistant: susceptible) (Table 4). Evidently, frequencies of their respective F₂ genotypes derived from reciprocal crosses did not differ significantly from the expected frequencies (Tables 4) and this suggests that resistance to Fusarium wilt is conferred by single gene [13]. When KAT 60/8 was used as a recurrent parent in a backcross program, BC₂F₁s segregated into a ratio of 1: 1. However, some of the BC₁F₁ populations where ICP7035 was used as a recurrent parent did not fit the expected segregation ratio. The disease reactions observed in the BC₁F₁ and BC₂F₁ populations with the KAT 60/8 as a recurrent parent confirmed the one gene model detected in the F₂ pigeonpea populations. In some of the BC₂F₁ populations with ICP7035 as a recurrent parent, the data deviated from the expected segregation ratio of 1: 1 (resistant: susceptible) and this may be due to variable penetrance of the spores during the inoculation. As positive control, fusarium wilt KB was virulent to the susceptible parents but avirulent to resistant parents.

Allelic Relationship of Genes in the Resistant and Susceptible Parents

The F₁ genotypes from resistant × resistant and susceptible × susceptible crosses of pigeon pea genotypes were resistant and susceptible to Fusarium wilt, respectively (Table 5). As expected, no F₂ genotypes from resistant × resistant crosses were susceptible to Fusarium wilt. Nevertheless, segregation was observed on F₂ genotypes derived from reciprocal crosses between susceptible (KAT 60/8) × susceptible (ICP7035) parents. The number of resistant and susceptible plants observed in the F₂ populations [KAT 60/8 and ICP7035 ($\chi^2_{0.05} = 0.166$, $P \geq 0.733$)] and its reciprocal ($\chi^2_{0.05} = 0.153$, $P \geq 0.696$) was conformed to a ratio of 1:3 (resistant: susceptible) phenotypic ratio one gene action (Table 5).

At seedling stage the resistance to *Fusarium* wilt is controlled by digenic [5, 9] and polygenes [14]. Contrary to the findings in this study major gene effect were detected in KAT 60/8 × ICEAP 00554, 00554 ×

Table 4. Genetic analysis of resistance to *Fusarium* wilt in pigeonpea populations derived from resistant x susceptible crosses

Pedigree	Observed frequencies					
	Generations	R	S	Ratio R:S	χ^2	P
<i>Crosses using KAT 60/8 x ICEAP 00554 as parents</i>						
KAT 60/8	P1		40			
ICEAP 00554	P2	40				
KAT 60/8 x ICEAP 00554	F ₁	60				
KAT 60/8 x ICEAP 00554	F ₂	159	51	3:1	0.057	0.811
ICEAP 00554 x KAT 60/8	F ₁	60				
ICEAP 00554 x KAT 60/8	F ₂	167	53	3:1	0.097	0.755
KAT 60/8 x ICEAP 00554* ¹	BC ₂ F ₁	22	25	1:1	0.191	0.662
ICEAP 00554 x KAT 60/8* ¹	BC ₂ F ₁	20	24	1:1	0.364	0.546
<i>Crosses using KAT 60/8 x ICEAP 00557 as parents</i>						
KAT 60/8	P1		40			
ICEAP 00557	P2	40				
KAT 60/8 x ICEAP 00557	F ₁	60				
KAT 60/8 x ICEAP 00557	F ₂	159	57	3:1	0.222	0.637
ICEAP 00557 x KAT 60/8	F ₁	60				
ICEAP 00557 x KAT 60/8	F ₂	153	56	3:1	0.359	0.549
KAT 60/8 x ICEAP 00557* ¹	BC ₂ F ₁	26	29	1:1	0.164	0.686
ICEAP 00557 x KAT 60/8* ¹	BC ₂ F ₁	21	26	1:1	0.532	0.466
<i>Crosses using ICP 7035 and ICEAP 00554 as parents</i>						
ICP 7035	P1		40			
ICEAP 00554	P2	40				
ICP 7035 x ICEAP 00554	F ₁	60				
ICP 7035 x ICEAP 00554	F ₂	156	47	1:1	0.369	0.543
ICEAP 00554 x ICP 7035	F ₁	60				
ICEAP 00554 x ICP 7035	F ₂	157	49	3:1	0.167	0.687
ICP 7035 x ICEAP 00554* ¹	BC ₂ F ₁	33	20	1:1	3.189	0.074
ICEAP 00554 x ICP 7035* ¹	BC ₂ F ₁	27	21	1:1	0.750	0.386
<i>Crosses using ICP 7035 x ICEAP 00557 as parents</i>						
ICP 7035	P1		40			
ICEAP 00557	P2	40				
ICP 7035 x ICEAP 00557	F ₁	60				
ICP 7035 x ICEAP 00557	F ₂	162	49	3:1	0.355	0.551
ICEAP 00557 x ICP 7035	F ₁	60				
ICEAP 00557 x ICP 7035	F ₂	167	51	3:1	0.300	0.584
ICP 7035 x ICEAP 00557* ¹	BC ₂ F ₁	26	18	1:1	1.455	0.228
ICEAP 00557 x ICP 7035* ¹	BC ₂ F ₁	35	19	1:1	4.741	0.029

KAT 60/8, KAT 60/8 x ICEAP 00557, ICEAP 00557 x KAT 60/8 (Table 4), ICP 7035 x ICEAP 00554, ICEAP 00554 x ICP 7035, ICP 7035 x ICEAP 00557 and ICEAP 00557 x ICP 7035 (Table 4). Single recessive gene action has also been shown to confer resistance to *Fusarium* wilt of pigeonpea [12]. In this study, it is hypothesized that a recessive resistant gene was present in accession ICP7035 and expressed when

placed in KAT60/8 background. Several factors may have contributed to these differences. First, the sources and genetic background of the resistant materials used in this study were different from those in earlier studies and this could have contributed to the differences. Resistant genes for *Fusarium* wilt in pigeon pea are expressed differently depending on the source and the background in which the gene is placed [14].

Secondly, some of the studies were carried out in the wilt boxes [5, 9] and others under field conditions [12]. In the field, the environmental and edaphic factors may influence both the disease severity and the expression of the resistance. As a result, methods of assessing this disease resistance often affect the conclusions of the genetic studies. *Fusarium udum* isolates from the same sites (country) and diverse geographical origin has been shown to exhibit high variability in pathogenicity on pigeonpea genotypes [16, 18, 19].

In the allelic test, the resistant reaction in F_1 plants and lack of susceptible segregates among the F_2 populations from crosses between resistant \times resistant parents suggests that the wilt resistant genes in the two genotypes ICEAP 00554 and ICEAP 00557 were allelic. Because F_1 population were resistant to Fusarium wilt this was evidence that resistance is controlled by dominant. This evidence is supported by the segregation pattern of 3:1 of F_2 populations. As expected all F_1 progenies from crosses between susceptible and susceptible parents were susceptible indicating that each of the two genotypes carried a gene for susceptibility and there was no novel genes from recombination. Segregation for resistant was observed in the F_2 populations derived from the crosses between susceptible and susceptible parents (Table 5). However, no complementary gene action reaction was observed. The susceptibility of F_1 to Fusarium isolate KB and segregation of F_2 genotypes derived from KAT 60/8

(susceptible) \times ICP 7035 (susceptible) crosses gave a ratio of 48 : 136 (resistant : susceptible) while F_2 genotypes from its reciprocal cross exhibited a ratio of 57: 161 (resistant: susceptible) both of them giving a fit of 1: 3 (resistant : susceptible). This clearly indicates the presence of a recessive gene that result from recombination between the two accessions (Table 5). It is therefore suggested that a novel recessive gene was detected from the crosses between the two susceptible accessions. Introgression of recessive resistance genes from ICP7035 with those from ICEAP 00554, ICEAP 00557 could be valuable source of resistant for pigeonpea breeders.

Screening pigeonpea seedlings by artificial inoculation in the greenhouse permits examination of a large number of populations for resistance under uniform disease pressure. Although this was the best approach for identifying major genes in genetic studies there could be differences in seedling and adult reaction to Fusarium wilt. It is therefore advisable to screen pigeon pea at seedling and adult stages. This study confirms that resistant to Fusarium wilt is controlled by a single dominant and a recessive gene. Breeding programs can therefore easily incorporate these genes for resistance into cultivars where Fusarium wilt is a problem after ascertaining isolate resistant. The recessive gene detected suggest that ICP7035 could be one of the sources of resistance.

Table 5. Genetic analysis of resistance to Fusarium wilt in pigeonpea (*Cajanus cajan*) populations derived from resistant \times resistant and susceptible \times susceptible crosses

Pedigree	Generations	Observed frequencies			χ^2	P
		R	S	Ratio R:S		
<i>Populations derived from crosses between ICEAP 00554 and ICEAP 00557</i>						
ICEAP 00554	P1					
ICEAP 00557	P2					
ICEAP 00554 \times ICEAP 00557	F_1	60				
ICEAP 00554 \times ICEAP 00557	F_2	174				
ICEAP 00557 \times ICEAP 00554	F_1	60				
ICEAP 00557 \times ICEAP 00554	F_2	162				
<i>Populations derived from crosses between KAT 60/8 and ICP 7035</i>						
KAT 60/8	P1		40			
ICP 7035	P2		40			
KAT 60/8 \times ICP 7035	F_1		48			
KAT 60/8 \times ICP 7035	F_2	48	136	1:3	0.116	0.733
ICP 7035 \times KAT 60/8	F_1		51			
ICP 7035 \times KAT 60/8	F_2	57	161	1:3	0.153	0.696

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