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Grasshopper Incidence and Severity of Damage as Influenced by Cyanogenic Potential in Leaf Tissue of Cassava (*Manihot esculenta* Crantz)

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Abstract

This study assessed the effect of cyanogenic potential (CNP) in leaf tissue on grasshopper incidence and severity of damage in cassava for the identification of parents with desired complementary traits for crossing. The experiment was conducted at the Foya Wulleh, Njala experimental site in Sierra Leone during 2020 and 2021 cropping seasons in a randomized complete block design with three replications. A total of 30 genotypes comprising 26 breeding lines, two improved and two local genotypes were assessed. Results showed a significant ($p < 0.05$) linear relationship between leaf CNP and grasshopper infestation (incidence and severity of damage) among cassava genotypes. Findings showed that the higher leaf CNP, the lower the grasshopper infestation in cassava genotypes. About two genotypes (Cooksoon and Cocoa) had low leaf CNP; three genotypes (TR0020, TR0037 and TR0013) CNP had moderately low leaf CNP; eight genotypes (SLICASS 6, TR0029, TR0032, TR0011, TR0012, TR0016-1/17, TR0002 and TR0010) had intermediate leaf CNP; seven (TR0009, TR0015-1/17, TR0036, TR0022-1/17, SLICASS 4, TR0007 and TR0026-1/17) had moderately high leaf CNP; eight (TR0008, TR0019-1/17, TR0006, TR0005, TR0021, TR0021-1/17, TR0022 and TR0024-1/17) had high leaf CNP; and two genotypes (TR0001 and TR0018-1/17) had very high leaf CNP. This suggests the indirect dependence of leaf cyanogenic potential on grasshopper infestation (incidence and severity of damage) in cassava that could be exploited for the genetic improvement of cassava for improved resistance to grasshopper

infestation, nutrition and utilization of the crop.

Keywords

Cassava, Cyanogenic Potential, Grasshopper Infestation, Regression, Correlation Analysis

1. Introduction

Cassava (*Manihot esculenta* Crantz) is the sixth most economically important storage root crop in the world [1] utilized as food, feed and industrial applications. Cassava is known as the third most important source of carbohydrates in Africa [2] and the second most important staple crop in Sierra Leone [3]. The crop meets the food needs of more than 800 million people in the world [4], accounting for about 500 calories daily for over 70 million people [5]. According to FAO [1], about 250 million people in sub-Saharan Africa (SSA) derive half of their daily calories from cassava. Cassava leaves and storage roots are available throughout the year [6], which makes it an important food security crop, even in drought-prone areas [5]. Cassava leaves are consumed as vegetables since they contain protein such as lysine, but lack the amino acid methionine and possibly tryptophan [7] [8]. The fresh storage root of cassava contains mainly starch and other food nutrients including calcium (0.16 g/kg), phosphorus (0.27 g/kg), vitamin C (0.206 g/kg), and minute quantities of protein among others [9]. Other cassava products utilized in Sierra Leone include cassava pellets for animal feed, cassava starch for sweeteners, thickeners and textile paper industry [7].

Despite the enormous importance of cassava, increase production and productivity of the crop are constrained by both biotic and abiotic factors [10]. Some of the key insect pest biotic factors affecting the economic yield of the cassava are variegated grasshopper (*Zonocerus variegatus* L.), cassava green mite, and cassava mealy bug. The variegated grasshopper defoliates and destroys the stem bark of food crops at the end of the dry season [8]. The fecundation of this pest results in the reduction in fresh storage root yield and quality as well as the destruction of cassava cuttings [11]. Although grasshoppers are considered as a polyphagous pest, they are selective to some degree, exhibiting definite plant preferences [12]. Studies carried out by Song [13] have shown that grasshoppers could be conveniently classified as grass-feeders (Graminivorous), forb-feeders (Forbivorous) or a mixture of the two (Ambivorous or mixed feeders).

According to Braima *et al.* [11], grasshoppers are deterred from feeding on cassava due to the presence of cyanogenic glucosides. The concentration of this plant secondary compound differs among cassava clones ranging between 80 mg and 167 mg CN per 100 g of fresh leaf [14]. Control of the variegated grasshoppers has generally involved use of chemical pesticides. However, due to the growing concern over its effect on non-target organisms, exorbitant cost and persistence in the

environment, there is the need of utilizing environmentally friendly alternative. Thus, host plant resistance is strongly advocated for the control of pests and diseases than the continual use of pesticides due to its adverse effects on the environment, ecosystem and unsustainability for low-income smallholder farmers [15]. Host plant resistance is any reduction in the population growth of a target pest as influenced by inheritable characteristic of the host plant compared to a standard genotype [16]. Host plant resistance is achieved through the existence of secondary compounds in plants; and the nature and concentration of these compounds differ in time, space and plant genotypes [17].

Cyanogenic glucosides (CNGs) are phytoanticipins that have been noted to be widely distributed in the plant kingdom [18]. The CNGs exist in more than 2500 different plant species including ferns, gymnosperms and angiosperms indicating that the ability of plants to produce CNGs is ancient. Moreover, CNGs have been found in a few arthropod clades. CNGs are β-glucosides of α-hydroxynitriles derived from the aliphatic protein amino acids l-valine, l-isoleucine and l-leucine, from the aromatic amino acids l-phenylalanine and l-tyrosine and from the aliphatic non-protein amino acid cyclopentenyl-glycine [19]. In plants, CNGs are stored in the vacuoles [20]. Disruption of plant tissue by herbivore attack causes the CNGs to come into contact with β-glucosidases and α-hydroxynitrile lyases that hydrolyze the CNGs, thereby releasing the toxic hydrogen cyanide (HCN). This binary system of two sets of components that, when separated, are chemically inert, provides plants with an immediate defense against intruding herbivores and pathogens that cause tissue damage [19].

Cyanide is a toxic substance, mainly due to its affinity for the terminal cytochrome oxidase in the mitochondrial respiratory pathway [21]. The lethal dose of cyanide for vertebrates lies in the range of 35 - 150 $\mu mol \cdot kg^{-1}$, if applied in a single dose. Much higher amounts of HCN can be tolerated if consumed or administered over a longer period [22]. Biosynthesis and degradation of CNGs are well documented in many plants [23] [24].

For most plants, it has been hypothesized that CNGs are involved in plant defense against herbivores due to release of toxic HCN [25]. The CNGs are, however, also known to act as both feeding deterrents and phagostimulants for herbivores that are specialists on plants containing CNGs [26]. For cassava, little is known about the functional relationship between HCN and grasshopper infestation in cassava. Thus, the objective of this study was to determine the effect of cyanogenic potential in leaf tissue on grasshopper incidence and severity of damage in cassava.

2. Materials and Methods

2.1. Experimental Site

The study was established at Foya Wulleh (Forest Transition) in the Kori chiefdom, Moyamba District, Southern province during 2020/2021 and 2021/2022

cropping seasons. The trial sites experience distinct dry and wet seasons. The rainy season starts from April to November and the dry season starts from October to May. The mean monthly air temperature ranges from 21˚C to 23˚C for greater part of the day and night especially during the rainy season.

2.2. Experimental Materials, Layout, Design and Management

The experimental materials utilized in this study were stem cuttings of 30 genotypes comprising 26 breeding lines, two improved and two local genotypes. The improved genotypes were introduced from the International Institute of Tropical Agriculture (IITA). The experiment was laid out in a randomized complete block design with three replications. Planting was done in May, 2020/21 and repeated at the same month in 2021/22 to coincide with the outbreak period of the grasshoppers. About 40 stem cuttings per genotype each measuring 30 cm long were planted at 1 m × 1 m spatial arrangement in a plot measuring 4 m × 10 m (40 m^2). Hand weeding was done regularly with no applications of fertilizers, pesticides and/or herbicides (Table 1).

Table 1. List of genotypes utilized for the study.

SN	Genotype	Status	SN	Genotype	Status
1	Cocoa	Landrace	16	TR0015-1/17	Breeding line
2	Cooksoon	Landrace	17	TR0016-1/17	Breeding line
3	SLICASS 4	Improved released	18	TR0018-1/17	Breeding line
4	SLICASS 6	Improved released	19	TR0019-1/17	Breeding line
5	TR0001	Breeding line	20	TR0020	Breeding line
6	TR0002	Breeding line	21	TR0021	Breeding line
7	TR0005	Breeding line	22	TR0021-1/17	Breeding line
8	TR0006	Breeding line	23	TR0022	Breeding line
9	TR0007	Breeding line	24	TR0022-1/17	Breeding line
10	TR0008	Breeding line	25	TR0024-1/17	Breeding line
11	TR0009	Breeding line	26	TR0026-1/17	Breeding line
12	TR0010	Breeding line	27	TR0029	Breeding line
13	TR0011	Breeding line	28	TR0032	Breeding line
14	TR0012	Breeding line	29	TR0036	Breeding line
15	TR0013	Breeding line	30	TR0037	Breeding line

2.3. Data Collection

Data on cyanogenic potential in the leaf organ, grasshopper incidence and severity damage were collected using procedures described in cassava descriptor [27]. The cyanogenic potential of the leaf was done after 10 h of suspension of the picrate-

saturated filter paper above the cut leaves in the glass tube; and scoring for color intensity was done using the 1 - 9 scale. Where 1 = very mild; 2 = mild; 3 = low; 4 = moderately low; 5 = moderate; 6 = moderately high; 7 = high; 8 = very high. Assessment of the genotypes for susceptibility to grasshopper was based on the injury done to each genotype by the pest. The grasshopper severity damage was expressed as the total area of the cassava plant tissue affected over the total area of the plant tissue. The severity of damage was done using the visual rating scale of 1 to 5; where: 1 = 0% to 20% of foliage damaged, 2 = 21% to 40% of foliage damaged, 3 = 41% to 60% of foliage damaged, 4 = 61% to 80% of foliage damaged and 5 = 81% to 100% of foliage damaged as described by Capinera [28]. Pest assessments were done at 6, 9 and 12 months after planting (MAP) as there was no visible symptom of the pest at 3 MAP. Percentage incidence was expressed, as the number of infested cassava plants over the total number of cassava stands planted expressed as percentage. Data collection was done on plants in the two middle rows per plot.

2.4. Data Analysis

All data were subjected to analysis of variance (ANOVA) using General Linear Model procedure (PROC GLM) of SAS version 9.4 (SAS, 2013). The treatment averages were compared using the (SNK) at the level of 5% of probability. Statistical analyses for column charts and scattered plots were performed using Excel 2010. The statistical relationships among selected variables were determined through correlation and regression analysis. The total variations in the dependent variable explained by the independent variables were evaluated through the coefficient of determination (R^2) [29]. The simple linear regression and multiple linear regression analyses were done for determination of the effect of leaf hydrogen cyanide content on grasshopper infestation (incidence and severity damage) in cassava.

3. Results and Discussion

3.1. Genetic Variability among Cassava Genotypes for Leaf Cyanogenic Potential

Leaf cyanogenic potential significantly ($p < 0.05$) differed among genotypes (**Table 2**). Of the 30 genotypes assessed for leaf cyanogenic potential, two genotypes (Cooksoon and Cocoa) had low leaf CNP; three genotypes (TR0020, TR0037 and TR0013) CNP had moderately low leaf CNP; eight genotypes (SLICASS 6, TR0029, TR0032, TR0011, TR0012, TR0016-1/17, TR0002 and TR0010) had intermediate leaf CNP; seven (TR0009, TR0015-1/17, TR0036, TR0022-1/17, SLICASS 4, TR0007 and TR0026-1/17) had moderately high leaf CNP; eight (TR0008, TR0019-1/17, TR0006, TR0005, TR0021, TR0021-1/17, TR0022 and TR0024-1/17) had high leaf CNP; and two genotypes (TR0001 and TR0018-1/17) had very high leaf CNP. This suggests the indirect dependence of leaf cyanogenic potential on grasshopper infestation (incidence and severity of damage) in

cassava.

Table 2. Mean leaf cyanogenic potential as affected by genotypes.

Genotype	Leaf cyanogenic potential	Category	Genotype	Leaf cyanogenic potential	Category
Cooksoon	3.3	Low	TR0036	7.3	Moderately high
Cocoa	2.7	Low	TR0022-1/17	7.0	Moderately high
TR0020	4.3	Moderately low	SLICASS 4	6.7	Moderately high
TR0037	4.3	Moderately low	TR0007	6.7	Moderately high
TR0013	4.0	Moderately low	TR0026-1/17	6.7	Moderately high
SLICASS 6	6.3	Intermediate	TR0008	8.3	High
TR0029	6.3	Intermediate	TR0019-1/17	8.3	High
TR0032	6.3	Intermediate	TR0006	8.0	High
TR0011	5.3	Intermediate	TR0005	7.7	High
TR0012	5.3	Intermediate	TR0021	7.7	High
TR0016-1/17	5.3	Intermediate	TR0021-1/17	7.7	High
TR0002	5.0	Intermediate	TR0022	7.7	High
TR0010	4.7	Intermediate	TR0024-1/17	7.7	High
TR0009	7.3	Moderately high	TR0001	8.7	Very high
TR0015-1/17	7.3	Moderately high	TR0018-1/17	8.7	Very high
Mean	6.4				
l.s.d.	0.91				
CV(%)	2.4				

3.2. Effect of Leaf Cyanogenic Potential on Grasshopper Incidence and Severity Damage Based on Simple Regression Analysis

Figures 1-3 present relationships between leaf hydrogen cyanide content and grasshopper incidence, and between leaf hydrogen cyanide content and severity damage on cassava genotypes sampled at 6, 9 and 12 months after planting (MAP). At 6 MAP, the regression between leaf hydrogen cyanide content and grasshopper incidence accounted for 18.02% ($R^2 = 0.1802$; $p = 0.05$) (Figure 1(a)); and between leaf hydrogen cyanide content and grasshopper damage accounted for 3.48% ($R^2 = 0.0348$; $p = 0.05$) (Figure 1(b)). At 9 MAP, the regression between leaf hydrogen cyanide content and grasshopper incidence accounted for 0.47% ($R^2 = 0.0047$; $p = 0.05$) (Figure 2(a)); and between leaf hydrogen cyanide content and grasshopper damage accounted for 1.49% ($R^2 = 0.0149$; $p = 0.05$) (Figure 2(b)). At 12 MAP, the regression between leaf hydrogen cyanide content and grasshopper incidence accounted for 4.22% ($R^2 = 0.0422$; $p = 0.05$) (Figure 3(a)); and between leaf hydrogen cyanide content and grasshopper damage accounted for

0.02% (R^2 = 0.0002; p = 0.05) (Figure 3(b)). These findings imply that the remaining percent variabilities are possibly attributed to environmental errors.

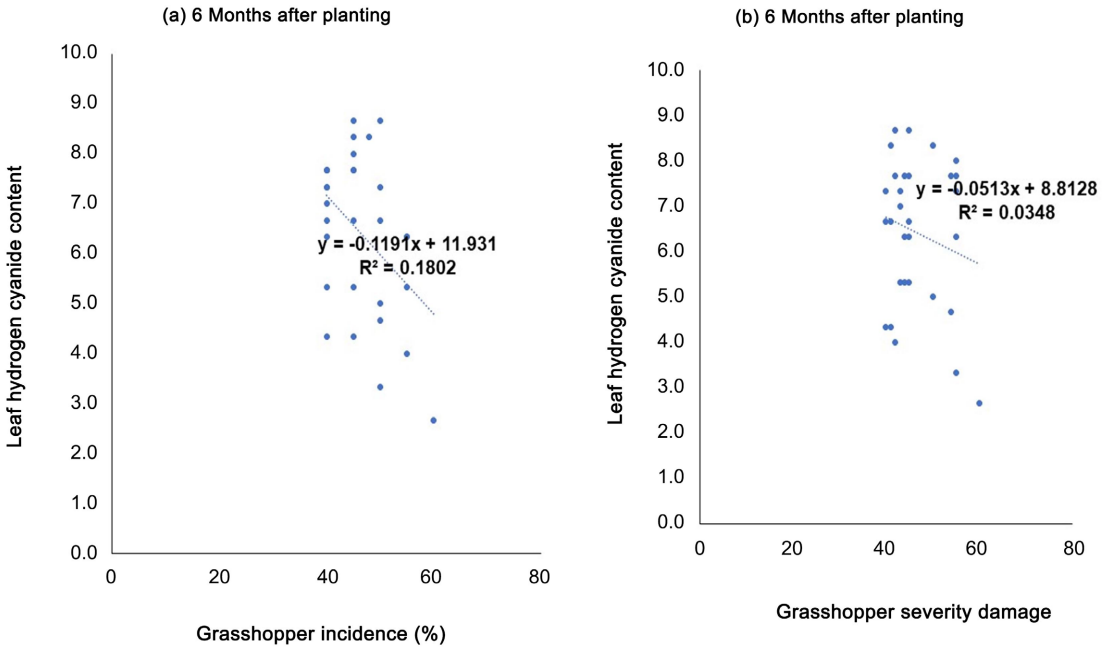

Figure 1. Relationships between leaf hydrogen cyanide content and grasshopper incidence (a) and severity damage (b) sampled at 6 months after planting. The x-axis = grasshopper incidence and severity damage ((a) and (b)); and the y-axis = leaf hydrogen cyanide content.

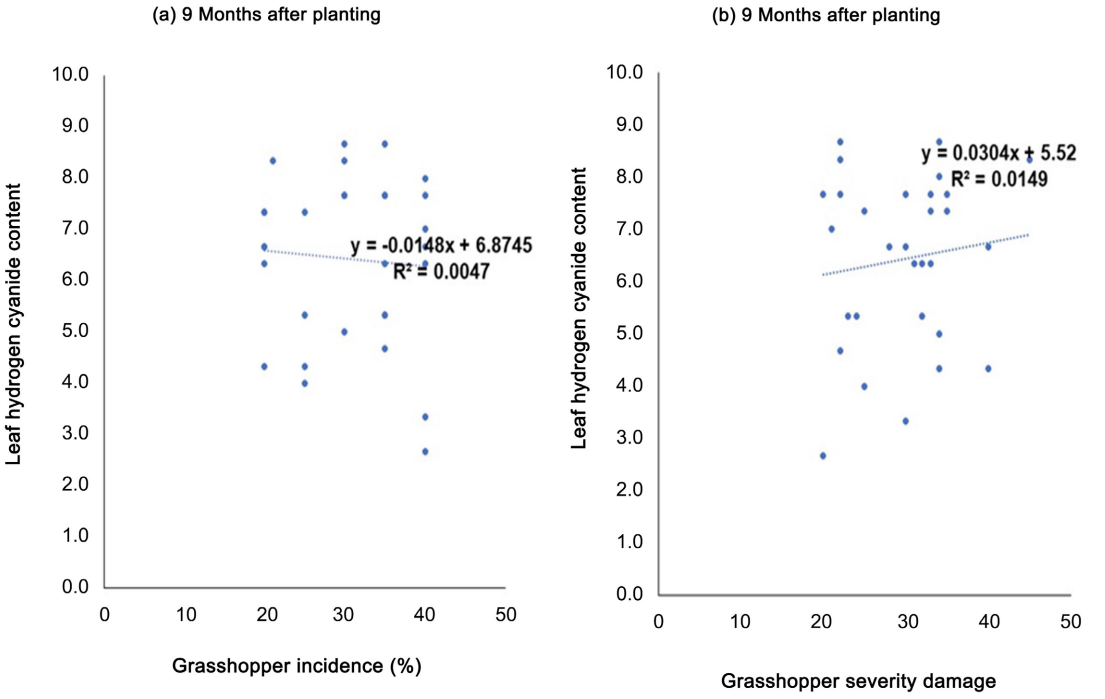

Figure 2. Relationships between leaf hydrogen cyanide content and grasshopper incidence (a) and severity damage (b) sampled at 9 months after planting. The x axis = grasshopper incidence and severity damage ((a) and (b)); and the y-axis = leaf hydrogen cyanide content.

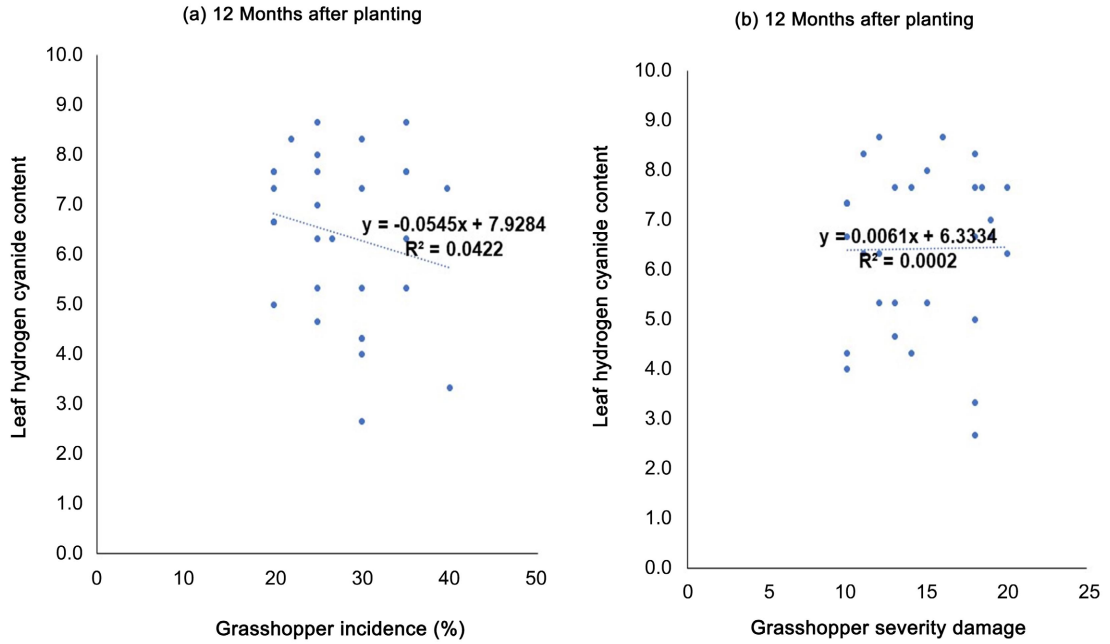

Figure 3. Relationships between leaf hydrogen cyanide content and grasshopper incidence (a) and severity damage (b) sampled at 12 months after planting. The x axis = grasshopper incidence and severity damage ((a) and (b)); and the y-axis = leaf hydrogen cyanide content.

3.3. Effect of Leaf Cyanogenic Potential on Grasshopper Incidence and Severity Damage Based on Multiple Regression Analysis

The fitted regression model for the influence of leaf cyanogenic potential on grasshopper incidence and severity damage is given below.

$$y = 13.48 - 0.106X_1 + 0.031X_2 - 0.065X_3 - 0.035X_4 + 0.016X_5 - 0.011X_6$$

Here, y = response variable (leaf cyanogenic potential); X = explanatory variables: X_1 to X_3 = grasshopper incidence at 6, 9 and 12 MAP; X_4 to X_6 = grasshopper severity damage at 6, 9 and 12 MAP, respectively. There was a significant ($p < 0.005$) linear relationship between leaf cyanogenic potential and grasshopper pest attack among cassava genotypes (Table 3).

Table 3. Regression parameter estimates of leaf cyanogenic potential, grasshopper incidence and severity damage in cassava genotypes.

	Estimate	Standard error	t (23)	t pr.
Constant	13.48	4.35	3.10	**0.005**
Ginc_6MAP	−0.106	0.056	−1.91	0.068
Ginc_9MAP	0.031	0.054	0.57	0.576
Ginc_12MAP	−0.065	0.059	−1.10	0.282
Gsev_6MAP	−0.035	0.058	−0.60	0.557
Gsev_9MAP	0.016	0.052	0.31	0.757
Gsev_12MAP	−0.011	0.103	−0.11	0.913

Gsev_6MAP, Gsev_9MAP and Gsev_12MAP represent grasshopper severity damage at 6, 9 and 12 months after planting, respectively.

The regression equation for mean leaf cyanogenic potential indicated that for every increase in the leaf cyanogenic potential of cassava, grasshopper incidence at 6 and 12 MAP decreased by 0.106 and 0.065 units, respectively. Similarly, for every increase in the leaf cyanogenic potential of cassava, grasshopper severity damage at 6 and 12 MAP decreased by 0.035 and 0.011 units, respectively. The accumulated analysis of variance of grasshopper incidence and severity damage in cassava genotypes revealed significant difference among cassava genotypes for grasshopper incidence sampling at 6 MAP (Table 4).

Table 4. Accumulated analysis of variance of leaf cyanogenic potential, grasshopper incidence and severity damage in cassava genotypes.

Change	d.f.	s.s.	m.s.	v.r.	F pr.
Ginc_6MAP	1	13.324	13.324	5.10	**0.034**
Ginc_9MAP	1	0.217	0.217	0.08	0.776
Ginc_12MAP	1	3.421	3.421	1.31	0.264
Gsev_6MAP	1	0.899	0.899	0.34	0.563
Gsev_9MAP	1	0.256	0.256	0.10	0.757
Gsev_12MAP	1	0.003	0.003	0	0.974
Residual	23	60.128	2.614		
Total	29	78.248	2.698		

Ginc_6MAP, Ginc_9MAP and Ginc_12MAP represent grasshopper incidence at 6, 9 and 12 months after planting, respectively; Gsev_6MAP, Gsev_9MAP and Gsev_12MAP represent grasshopper severity damage at 6, 9 and 12 months after planting, respectively.

The results generally indicate that depending on the sampling regime, increasing cyanogenic potential in leaf organ leads to decreasing incidence and severity of damage of grasshopper on the cassava.

The fitted regression model for the influence of leaf cyanogenic potential on grasshopper incidence is given below:

$$y = 13.02 - 0.118X^1 + 0.012X^2 - 0.054X^3$$

Here, y = response variable (leaf cyanogenic potential); X = explanatory variables; X_1 to X_3 = grasshopper incidence at 6, 9 and 12 MAP, respectively.

There was a significant ($p < 0.001$) linear relationship between leaf cyanogenic potential and grasshopper incidence among cassava genotypes (Table 5).

The regression equation for mean leaf cyanogenic potential indicates that for every increase in the leaf cyanogenic potential of cassava, grasshopper incidence at 6 and 12 MAP decreased by 0.118 and 0.054 units, respectively. The accumulated analysis of variance of grasshopper incidence in cassava genotypes revealed significant difference among cassava genotypes for grasshopper incidence sampling at 9 MAP (Table 6). Findings indicate that depending on the sampling regime, increasing cyanogenic potential in leaf organ leads to decreasing incidence of grasshopper attack on the cassava.

Table 5. Regression parameter estimates of leaf hydrogen cyanide content and grasshopper incidence assessed across three sampling regimes in cassava genotypes.

	Estimate	Standard error	t (23)	t pr.
Constant	13.02	2.61	4.98	**<0.001**
Ginc_6MAP	−0.118	0.049	−2.40	**0.024**
Ginc_9MAP	0.012	0.040	0.30	0.764
Ginc_12MAP	−0.054	0.048	−1.12	0.274

Ginc_6MAP, Ginc_9MAP and Ginc_12MAP represent grasshopper incidence at 6, 9 and 12 months after planting, respectively.

Table 6. Accumulated analysis of variance of leaf cyanogenic potential and grasshopper incidence assessed across three sampling regimes in cassava genotypes.

Change	d.f.	s.s.	m.s.	v.r.	F pr.
Ginc_6MAP	1	3.421	3.421	1.45	0.239
Ginc_9MAP	1	13.324	13.324	5.65	**0.025**
Ginc_12MAP	1	0.217	0.217	0.09	0.764
Residual	26	61.286	2.357		
Total	29	78.248	2.698		

Ginc_6MAP, Ginc_9MAP and Ginc_12MAP represent grasshopper incidence at 6, 9 and 12 months after planting, respectively.

The fitted regression model for the influence of leaf cyanogenic potential on grasshopper incidence is given below:

$$y = 7.41 - 0.0467X_1 + 0.0268X_2 + 0.054X_3$$

Here, y = response variable (leaf cyanogenic potential); X = explanatory variables; X_1 to X_3 = grasshopper severity damage at 6, 9 and 12 MAP, respectively.

There was a significant (p = 0.049) linear relationship between leaf cyanogenic potential and grasshopper severity damage among cassava genotypes (Table 7).

The regression equation for mean leaf cyanogenic potential indicates that for every increase in the leaf cyanogenic potential of cassava, grasshopper severity at 6 MAP decreased by 0.0467 units. The accumulated analysis of variance of grasshopper severity damage in cassava genotypes revealed a nonsignificant difference among cassava genotypes (Table 8).

Table 7. Regression parameter estimates of leaf cyanogenic potential and grasshopper severity damage assessed across three sampling regimes in cassava genotypes.

	Estimate	Standard error	t (23)	t pr.
Constant	7.41	3.58	2.07	**0.049**
Gsev_6MAP	−0.0467	0.0537	−0.87	0.392
Gsev_9MAP	0.0268	0.051	0.53	0.603
Gsev_12MAP	0.027	0.0936	0.29	0.775

Gsev_6MAP, Gsev_9MAP and Gsev_12MAP represent grasshopper severity damage at 6, 9 and 12 months after planting, respectively.

Table 8. Accumulated analysis of variance of leaf cyanogenic potential and grasshopper severity damage assessed across three sampling regimes in cassava genotypes.

Change	d.f.	s.s.	m.s.	v.r.	F pr.
Gsev_6MAP	1	2.666	2.666	0.93	0.344
Gsev_9MAP	1	0.795	0.795	0.28	0.603
Gsev_12MAP	1	0.022	0.022	0.01	0.931
Residual	26	74.765	2.876		
Total	29	78.248	2.698		

Gsev_6MAP, Gsev_9MAP and Gsev_12MAP represent grasshopper severity damage at 6, 9 and 12 months after planting, respectively.

3.4. Relationship among Leaf Cyanogenic Potential, Grasshopper Incidence and Severity of Damage Traits

The relationship among leaf cyanogenic potential, grasshopper incidence and severity damage traits measured in cassava genotypes is shown in **Table 9**. A low negative and significant correlations between leaf cyanogenic potential and grasshopper incidence at 12 MAP ($r = -0.209$, $p = 0.05$), between leaf cyanogenic potential and grasshopper incidence at 6 MAP ($r = -0.423$, $p = 0.05$), between leaf cyanogenic potential and grasshopper incidence at 9 MAP ($r = -0.062$, $p = 0.05$), and between leaf cyanogenic potential and grasshopper severity at 6 MAP ($r = -0.183$, $p = 0.05$). These findings indicate that higher level of leaf cyanogenic potential in cassava leaf organ decreases the grasshopper pest attack. Higher levels of leaf cyanogenic potential may also serve as a defense mechanism by the plant in causing increased mortality and decreased reproduction in the insect population.

Table 9. Pearson correlation coefficients among leaf hydrogen cyanide content, grasshopper incidence and severity damage traits measured in cassava genotypes.

Trait	GI12MAP	GI6MAP	GI9MAP	GS12MAP	GS6MAP	GS9MAP	HCN
GI12MAP	1.000						
GI6MAP	0.054^{ns}	1.000					
GI9MAP	0.293^{*}	0.139^{*}	1.000				
GS12MAP	-0.303^{*}	0.137^{*}	0.323^{*}	1.000			
GS6MAP	-0.008^{ns}	0.273^{*}	0.388^{*}	0.053^{ns}	1.000		
GS9MAP	0.060^{*}	-0.240^{*}	-0.362^{*}	-0.303^{*}	-0.162^{*}	1.000	
HCN	-0.209^{*}	-0.423^{*}	-0.062^{*}	0.017^{ns}	-0.183^{*}	0.117^{*}	1.00

GI = grasshopper incidence, GS = grasshopper severity, MAP = months after planting, HCN = hydrogen cyanide; * = $p < 0.05$, ns = not significant at $p < 0.05$.

The cyanogenic potential in cassava plays a key role in resistance mechanism to a polyphagous African grasshopper, *Zonocerus variegatus* L. [30]. Findings of the present study are in concurrence with the view that cyanogenic potential in cassava

limit grasshopper extensive feeding activity on flaccid compared with the turgid leaf cuttings [30]. Accordingly, damage by grasshopper feeding on flaccid leaves of cassava rapidly lost the capacity to produce detectable quantities of hydrogen cyanide, whereas turgid leaves retained their capacity to produce hydrogen cyanide [30]. Findings also agree with Rajamma *et al.* [31] who found negative relationship between storage insects of cassava and high levels of cyanogenic potential (900 ppm, as hydrogen cyanide, dry weight) compared with low levels of cyanogenic potential (39 ppm, as hydrogen cyanide, dry weight). High levels of cyanogenic potential in cassava cause significant increase and decrease in mortality and reproduction, respectively [30].

Induction of cyanogenesis in cassava under stress conditions and wounding has been noted in the literature [30]. In cassava, drought stress [32] and disease infection stress [33] increase the cyanogenic potential, though genotype effects are strongest in controlling root cyanogenic potential [34]. Riis *et al.* [30] reported increased cyanogenic potential in wounded fresh cassava storage roots, especially in the outer parenchyma tissue next to the cortex. Enhancement of the cyanogenic potential of root parenchyma caused by infestation by Cassava green mite (*Mononychellus tanajoa* Bondar) and Cassava mealybug (*Phenacoccus manihoti* Matile-Ferrero) relative to non-infested plants sprayed with insecticides was established by Ayanru and Sharma [35]. Accordingly, the average cyanogenic potential of the entire plants did not differ between infested and non-infested plants and concluded that translocation of cyanogen from other tissues to the root parenchyma must have occurred as a response to the biotic stresses.

In some monophagous or oligophagous herbivores, cyanogenic glycosides in the host plant can be phagostimulatory, especially when the chemical exists in low concentrations [30], consequently playing a role in host-plant recognition. Insects have been also noted in some instances sequestering cyanogenic compounds from plants [36].

Acquisition of an ability to detoxify hydrogen cyanide in some insect species early in their evolution, has offered the opportunity to feed on plants that deter other herbivores, subsequently exploiting the availability of such new host plants to radiate at the expense of competing species, as typified in moth and butterfly groups. The ability to sequester cyanogenic glucosides from host plants for detoxification of hydrogen cyanide provides such insects with the additional benefits of an improved defense system. Simultaneously, these insects then become more or less dependent on the availability of cyanogenic host plants. In this situation, it is imperative that plants maintain some acyanogenic genotypes that will not be preferred by the specialized insects. The ability to de novo synthesize cyanogenic glucosides is probably a basic trait within some insect pests. Accordingly, these insects only need cyanogenic host plants to minimize their own biosynthesis of cyanogenic glucosides. Consequently, some moth and butterfly species probably feed on plants that deter other herbivores without being absolutely dependent on such plants for their own predator defense. The ability to transfer genes across

species using genetic engineering enables the design of plants with an altered qualitative and quantitative content of natural products thereby bypassing millions of years of co-evolution of plants and their herbivores. The chemical warfare between plants and insects can be followed closely through metabolite profiling (LC-MS) and transcript profiling, which provide a better understanding of the relative importance of complete metabolism, detoxification and sequestering of cyanogenic glucosides.

4. Conclusion

The study demonstrates genetic variability among cassava genotypes for leaf cyanogenic potential, grasshopper infestation and influence of leaf cyanogenic potential on grasshopper infestation (incidence and severity of damage). Findings suggest indirect dependence of leaf cyanogenic potential on grasshopper infestation (incidence and severity of damage) in cassava that could be exploited for the genetic improvement of cassava for improved resistance to grasshopper infestation, nutrition and utilization of the crop. Further studies on the long-term effect of cyanogenic potential (CNP) in cassava on grasshopper infestation, extent of possible recovery of oviposition after short and long-term exposure to CNP in cassava and labeling studies to determine fate and possible metabolism of cyanogens as related to increased survival should be considered.

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Conflicts of Interest

The authors declare no conflicts of interest regarding the publication of this paper.

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