Understanding the Consequences of Soil Amendments on Host Selection by a Maize Viral Vector (*Cicadulina mbila* Naudé)

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Abstract: The significance of applying different rates of soil elements on host selection by a viral vector was studied in a confined habitat, to understand the mechanism of host selection by the leafhopper (*Cicadulina mbila* Naudé), a vector of Maize Streak Virus Disease (MSV). Field collected leafhoppers were used in a screen house to assess insect settling preferences by evaluating insect behavior towards host plants, exposed to different rates of nitrogen and phosphorus fertilizers (0, 25, 50 and 75kg/ha.). Analysis of the two elements in the host plant tissues showed significant variation in levels of percent nitrogen (% N: p = 0.031) and phosphorus (% P: p = 0.001). Similarly, a significantly higher number of insects settled on plants treated with a higher rate of nitrogen (21%) and phosphorus (44%), compared to low rates of the same (9% and 28% respectively) (p = 0.019). Host choice by insects was significantly longer phosphorus treated hosts (four days) than nitrogen treated (three days). No significant differences were detected in the analysis of host plants for % neutral detergent fibers, acid detergent fibers, lignin and tannins. However, regression analysis revealed that neutral detergent fibers had significantly negative relationship with nitrogen fertilizer, while and phosphorus showed a negative relationship with lignin. This study showed that fertilizer amendments can critically affect host attack by leafhoppers with amplifications on viral disease transmission.

Keywords: Nitrogen, phosphorus, colonization, maize streak, transmission.

1. INTRODUCTION

In Africa, maize streak virus (MSV) disease, which causes up to 100% yield loss is primarily transmitted by leafhoppers *Cicadulina* (Homoptera: Cicadellidae) [1,2]. The current management options for controlling the MSV vectors are inadequate, with resultant disease surges [3]. Alyokhin and Sewell [4] stated that vector populations influence the spatial and temporal distribution of viral infections, and other studies indicate the existence of a correlation between the nutritive quality of host plants, temperature and wind on one hand and the percentage of infective leafhoppers [1,2].

The elaboration of the mechanisms involved in vector host selection are critical in understanding disease epidemiology, and therefore the management of the disease. Moreover, host selection behaviour has been studied within simplified tritrophic systems (one plant, one insect and one viral species). Lett [5] stated that inoculation of MSV into plant tissues is dependent on successful selection of a suitable host through a series of events using various stimuli, which consist of host-habitat location, classification, recognition and the final acceptance of a suitable host [6].

Host plants, conversely have evolved deterrents such as secondary plant metabolites to discourage insect attack [7]. Therefore, it is probable that the selection of hosts by leafhoppers depends on the content of the appropriate nutrients in plants. In this paper, we present data on the settling preferences of *C. mbila* reared on maize plants exposed to the different rates of inorganic fertilizers, and discuss the implications of host selection to MSV management.

2. MATERIALS AND METHODS

2.1. Insect Rearing

Cicadulina mbila was originally collected from Oyani region (01^o.112 S; 034^o 31.684 E; 1550m a.s.l) in South western Kenya, and was reared in the screen house on maize plants (*Zea mays* L. – hybrid variety H614), within insect-proof cages (70 × 60 × 60cm) (length × breadth × height) fitted with fine nylon netting, at 28 ± 3^{o}C, 70 ± 4% RH. The insects used in bioassays were reared for more than five generations before trials.

2.2. Fertilizer Application

The common field applied rates of 0, 25, 50 and 75kg (both for nitrogenous and phosphatic fertilizers) were computed (Table **1**) and applied separately in eight pots (four each for nitrogen and phosphorus). The two fertilizers were obtained from MEA Fertilizer

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Company, Kenya LTD. and applied as Calcium Ammonium Nitrate (C.A.N; that contains 26% Nitrogen) Triple Super Phosphate (T.S.P. that contains 46% P_2O_5) respectively. Each of the six fertilizer treatments were thoroughly mixed with 4kg of soil in plastic pots (12cm base diameter, 18cm top diameter, and 14cm height) for planting.

Table 1: Type and Rate of Fertilizers Used in the Net Covered Screen House Plots

Fertilizer rates used by farmers	Code	Calculated rates used in experimental cages	
		Rate of C.A.N. (26% N) (g pot^{-1})	Rate of T.S.P (46% P_2O_5) (g pot^{-1})
1. 0kg (control)	N_1	0	0
2. 25kg ha^{-1}	N_2	0.22	0.12
3. 50kg ha^{-1}	N_3	0.43 0.70	0.25
4. 75kg ha^{-1}	N_4		0.37

Legend: C.A.N - Calcium ammonium nitrate; T.S.P – Triple super phosphates.

2.3. Plant Materials and Settling Preference Tests

Two maize seeds were planted in each of the eight fertilizer treated pots (representing the rates of 0, 25, 50 and 75kg for nitrogen and phosphorus) and later thinned to one plant after germination. A set of four pots (each for nitrogen or phosphorus) were positioned in a circle (30cm diameter, with a distance of 20cm between pots) around an insect release point in an insect-proof cage (70×70×70cm). The potted plants were watered after every 2 days with 150ml of distilled water.

2.3.1. No Choice Tests

Tests were carried out to determine the possible interference of light orientation in the screen house on the selection of host plants by the leafhoppers. Four potted maize plants were grown using a similar rate of nitrogen fertilizer and tested in a pilot trial (n = 4; all pots had a rate of N_2, which was replicated 4 times). The potted plants were set on a polythene floor, generating a homogeneous background to allow easy movement of insects among potted host plants. Twenty adult leafhoppers in a glass vial (ten males and ten females), taken from a laboratory culture, were released into the cage. Individual leafhoppers moved out of the remote end of a vertical vial without disturbance and selected different plants by their own free choice. The experiment was replicated four times and was conducted between 08:00 and 10:00 hours when leafhoppers were most active. Data on the number of leafhoppers on each plant / treatment were recorded at 1, 3 and 24 hours after insect release.

2.3.2. Multi Choice Tests

A free-choice test was carried out to determine the settling preferences of adult *C. mbila* among maize plants with different rates of nitrogen and phosphorus fertilizers. Each of the four potted maize plants grown using one of the specified rates: 0, 25, 50 and 75kg for nitrogen (N_1, N_2, N_3 and N_4) and phosphorus (P_1, P_2, P_3 and P_4) were arranged in a completely randomized design within a cage covered by a fine mesh as in the no-choice test. Twenty adult leafhoppers in a glass vial (ten males and ten females), taken from a laboratory culture, were released into the cage. The numbers of leafhoppers on the entire plant were counted at 1, 3, 24, 48, 72 and 96 hours after insect release. The experiment was replicated four times and was conducted between 08:00 and 10:00 hours when leafhoppers were most active.

2.3.3. Dual Choice Tests

To validate the results of the multi-choice tests, a series of dual choice tests were carried out in the screen house. Four potted plants for each of two different fertilizer rates (N_1 and N_4 and P_1 and P_4 treatments) were separately placed alternatively in a circle within a cage, and twenty adult leafhoppers released from a glass vial, as explained previously. Each of the pair-wise comparison was replicated 10 times. The number of leafhoppers on the entire plant was counted at 1, 3, 24, 48, 72 and 96 hours after insect release.

2.4. Analysis for Lignin and Tannins

After the mortality of a pair of *C. mbila* in the test cage, the plants that had supported leafhoppers (including plant materials from the control plants) were cut, packed and transported to the Plant Tissue Analysis Laboratories in Muguga, Kenya, using cooler boxes. Cutting of the plant material was done in the afternoons in order to standardize the cutting period for all the treatments. Total phenols (lignin and tannins) were estimated using the Folin-Ciocalteu reagent procedure [8]. Absorbency values were measured using a Novaspec II PHARMACIA LKB spectrophotometer (Biochrom Limited, Cambridge, UK) at 680nm and the total phenol concentration was expressed as nmol/mg dry weight.

2.5. Analysis for Nitrogen

Nitrogen in the sample of the plant material prepared above was determined using the Kjeldahl method described by Sillanpaa [9] and Rowell [10]. A sample of 1.0 ± 0.001 g of dried leaves was transferred to a 100ml Kjeldahl flask and 6ml of concentrated H_2SO_4 was added, along with a Kjeldahl tablet. This mixture was digested at 380°C for 2h, and then transferred to a 100ml volumetric flask. Two ml of this digest was steam-distilled with 200ml 40% NaOH. The distillate was collected in 5ml of 4% boric acid and was back-titrated with standard HCl (0.01M) using a few drops of mixed indicator. The solution was transferred into a 50ml volumetric flask, and filled to the mark with distilled water. The solution was then filtered through Whatman filter paper no. 541.

2.6. Analysis for Plant Fibres

Simultaneously a sample of the plant material prepared as above was used to determine content of acid detergent fibre and neutral detergent fibres in the maize plant tissue samples. Plant material weighing 1.0 g was put into a 250ml round-bottom flask and 100ml of CTAB / sulphuric acid solution added, plus a few drops of ant-foam agent. The flask was connected to a condenser and refluxed for one hour. The contents were filtered through a vitreosil crucible (No. 1) of known weight under gentle suction. The residue was washed with three portions of 50ml boiling water, and then with acetone to remove the entire colour and to dry the fibre. The crucible and its contents were placed in an oven at 105^{o}C for 2 hours, and later cooled in a desiccators

2.7. Analysis for Phosphorus

For the determination of Phosphorus, 2 ± 0.01 g of the dried leaves was weighed in an evaporating basin and heated to 450–500°C in a muffle furnace. The grey ash was moistened with water, dried at 105°C, and similarly heated again at 450–500°C in the muffle furnace. Ten ml of 6 M HCl was added to the ash obtained, and was boiled to dryness. The residue was mixed with 2ml of concentrated HCl and boiled on a water bath for 2minutes. Ten ml of water was added and the mixture boiled again. This was then transferred to a 50ml volumetric flask and filled to the mark with distilled water. The solution was then filtered through Whatman filter paper no. 541. The phosphorus in the solution was determined by spectrophotometry (Cecil CE 2010 Spectrophotometer; Cecil Instruments Ltd., Cambridge, UK) using ammoniummolybdate solution and ascorbic acid [9,10]. Measurements were made at the visible wavelength of 880nm, using a standard calibration curve.

2.8. Statistical Analysis

An analysis of variance (ANOVA) was conducted using the general linear model (GLM) procedure (SAS, 1999–2000) to assess the effects of nitrogen and phosphorus fertilizers on leafhopper settling preference. Least squares mean values were separated using the Student–Newman–Keuls (SNK) test at $p < 0.05$. Total nitrogen and phosphorus in plant tissues, acid and neutral detergent fibers, lignin and tannins levels were compared between leafhopper settling preference and fertilizer treatments. Pearson correlation coefficient was calculated and regression analyses conducted for neutral detergent fibre and nitrogen, and phosphorus and lignin, where response to fertilizer was noted.

3. RESULTS

The no-choice test in these experiments indicated that plant positioning within a cage, relative to light orientation in the screen house, did not influence selection of a host ($F = 2.791_{3,60}$; $p = 0.089$). Successive multi-choice tests showed that a higher percentage of leafhoppers settled on plants treated with a high rate of nitrogen (21%) and phosphorus (44%) when compared to the low rates (9% and 28% respectively) ($F = 3.477_{3,92}$; $p = 0.019$) (Table **2** and **3**). The order of settling preference ranking due to the effect of nitrogen treatments was consistent at all recording periods. The leafhoppers required up to four days to select and settle on the appropriate nitrogen treated test plants ($F = 3.852_{3,12}$; $p = 0.038$).

Likewise, significant treatment effects by phosphorus fertilizer on host selection by *C. mbila* were only registered at 72 hours after exposure ($F = 6.616_{3, 12}$; $p = 0.007$) (Table **3**). However, the effects did not show similar uniformity in the ranking order as in the nitrogen treated plants.

Fewer insects settled during the first hour of choice, although most of them settled during the 48 h period (Table **3**), additionally the insects needed at least four days to make significant selection choices, which was faster than in the nitrogen treated plants (Table **2**). A comparison of the individual sampling periods indicated no significant differences for each of the nitrogen treatments; N_1 ($p = 0.692$), N_2 ($p = 0.251$), N_3 (p

Table 2: Mean ± SE Percentage of *C. mbila* Adults Settled on Maize Plants Treated with Rates of Nitrogen Fertilizer. Means in Columns Followed by the Same Letter do not Differ Significantly ($p < 0.05$) According to SNK Test

Treatment (kg/ha^{-1})	Time/Percentages				
	1 h	24 h	48 h	72 h	96 h
N_1	16 ± 0.08[a]	16 ± 0.55[a]	13 ± 0.05[a]	15 ± 0.02[a]	09 ± 0.04[b]
N_2	08 ± 0.02[a]	13 ± 0.25[a]	10 ± 0.05[a]	19 ± 0.02[a]	06 ± 0.04[b]
N_3	20 ± 0.11[a]	19 ± 0.38[a]	16 ± 0.05[a]	19 ± 0.03[a]	19 ± 0.01[a]
N_4	23 ± 0.07[a]	14 ± 0.38[a]	16 ± 0.38[a]	19 ± 0.06[a]	21 ± 0.05[a]

Table 3: Mean ± SE Percentage of *C. mbila* Adults Settled on Maize Plants Treated with Rates of Phosphorus Fertilizer

Treatment (kg/ha^{-1})	Time/Percentages				
	1 h	24 h	48 h	72 h	96 h
P_1	18 ± 0.05[a]	38 ± 0.10[a]	33 ± 0.14[a]	28 ± 0.01[b]	19 ± 0.04[a]
P_2	16 ± 0.04[a]	35 ± 0.10[a]	30 ± 0.06[a]	19 ± 0.06[b]	20 ± 0.04[a]
P_3	09 ± 0.04[a]	26 ± 0.04[a]	36 ± 0.08[a]	29 ± 0.04[b]	21 ± 0.07[a]
P_4	19 ± 0.04[a]	25 ± 0.08[a]	33 ± 0.06[a]	44 ± 0.32[a]	26 ± 0.07[a]

Means in columns followed by the same letter do not differ significantly ($p < 0.05$) according to SNK test.

= 0.991), N_4 (p = 0.622), however, for phosphorus treatments, only P_3 (p = 0.020) showed significant differences compared to others: P_1 (p = 0.451), P_2 (p = 0.260), P_4 (p = 0.083).

Dual-choice tests conducted in the screen house showed similar trends to the preceding multi-choice tests. There were no significant differences between percentages of *C. mbila* that settled on N_1 and N_4, at 1 h, 24 h, 48 h, 72 h, and 96h ($F = 0.580_{1,14}$; p = 0.459, $F = 0.625_{1,14}$; p = 0.625; $F = 0.509_{1,14}$; p = 0.487 $F = 0.190_{1, 14}$; p = 0.669; $F = 0.840_{1, 14}$; p = 0.375 respectively) (Figure **1**). On the contrary, the percentage of *C. mbila* on P_1 were significantly fewer than on P_4 at 24 and 48 hours after insect release P_1 ($F = 13.263_{1,14}$; p = 0.003 and $F = 42.176_{1,14}$; p = 0.001 respectively).

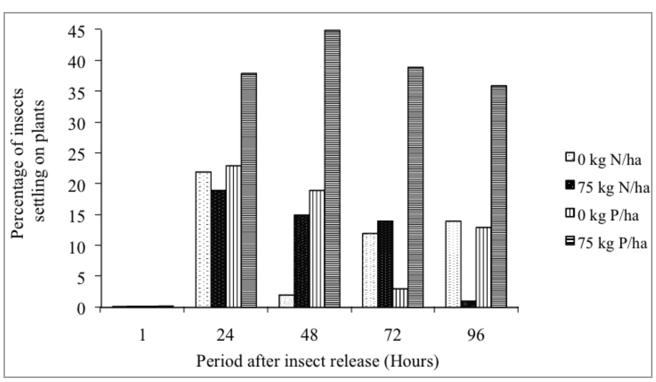


Figure 1: Mean percentage of *C. mbila* settled on maize plants treated with two rates of nitrogen and phosphorus fertilizers (Dual-choice test).

A comparison of the number of *C. mbila* that settled on plants at different periods showed that there was no significant difference in the N_1 treatment ($F = 1.642_{5, 42}$; p = 0.170). However, a significantly higher number of insects settled on N_4 treated plants at 1 h and 24 h after insect release ($F = 3.751_{5, 42}$; p = 0.007) (Figure **2**). Similarly, no significant differences were recorded on P_1 treatment ($F = 2.482_{5, 42}$; p = 0.059), but the number of insects that settled on P_4 at 1 hour after insect release was significantly different from the other sampling periods ($F = 4.308_{5, 42}$; p = 0.003) (Figure **2**).

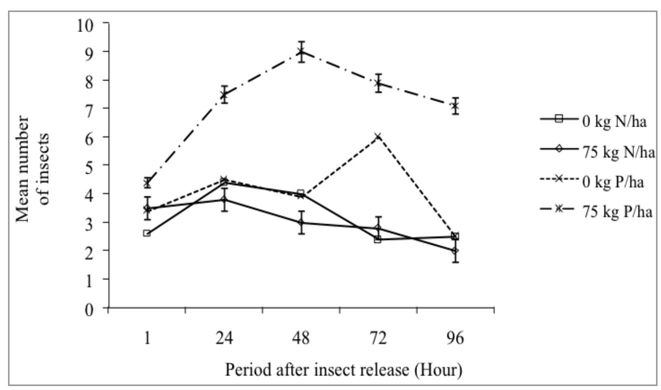


Figure 2: Preference of *C. mbila* adults for the maize plants exposed to different rates of nitrogen and phosphorus, measured as the number of adults per plant at different periods.

Pre-plant soil analysis performed on soil used in the potted plants showed that the mean N and P levels were low (0.27% and 19.9 parts per million respectively). Subsequent application of C.A.N to the potted plants resulted in significantly higher levels of nitrogen in plants treated with N_4 compared to N_1 ($F = 4.157_{3, 12}$; $p = 0.031$, Figure **3**). Similarly, treatment of plants with P_2, P_3 and P_4 significantly increased the level of total phosphorus in plant tissues compared to P_1 ($F = 17.111_{3, 12}$; $p = 0.001$) (Figure **3**).

The treatment of plants with different rates of nitrogen and phosphorus fertilizers resulted in differences in leaf tissue % nitrogen ($F = 4.\ 157_{3, 12}$; $p = 0.031$) and phosphorus ($F = 17.111_{3, 12}$; $p = 0.001$). The differences in % neutral detergent fibers ($F = 2.286_{3,12}$; $p = 0.131$ and $F = 0.704_{3,12}$; $p = 0.568$

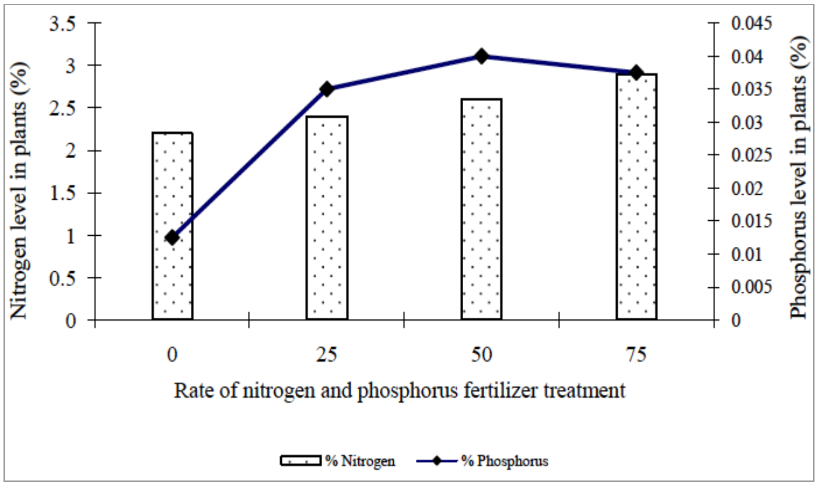


Figure 3: Nitrogen and phosphorus levels in plants treated with different rates of fertilizers. Bars with different letters indicate significant differences among treatments ($P = 0.05$, SNK test). The data presented combine those of 4 treatment plants, replicated 4 times.

Table 4: Mean Nutrient Levels in Maize Plant Tissues for Nitrogen and Phosphorus Treatments (Control, Low, Medium, and High) Established in a Screen House

Treatment (Kg/ha)	% Nitrogen	Phosphorus	NDF	% ADF	Lignin	Tannins
0 N	2.18±0.08b	-	58.56±1.00a	37.63±0.46a	6.63±0.50a	1.47±0.78a
P	1.12±0.10x	0.01±0.01y	57.56±1.00x	36.79±0.5x	5.87±0.78x	1.18±0.15x
25 N	2.38±0.18ab	-	57.42±1.34a	37.72±1.67a	7.01±1.56a	1.51±0.11a
P	1.40±0.37x	0.035±0.005x	58.39±0.85x	38.00±0.90x	4.60±0.53x	0.81±0.07x
50 N	2.62±0.21ab	-	55.23±0.21a	35.40±0.55a	5.44±0.26a	1.40±0.12a
P	0.73±0.08x	0.400±0.001x	53.80±6.00x	36.41±1.14x	4.20±0.34x	0.88±0.43x
75 N	2.90±0.09a	-	56.08±1.00a	36.58±0.12a	5.37±0.45a	1.50±0.58a
P	0.79±0.07x	0.038±0.003x	59.95±0.47x	37.21±0.13x	3.96±0.53x	1.07±0.09x

Legend: N-nitrogen fertilizer, P-phosphorus fertilizer, NDF-neutral detergent fibers, ADF-acid detergent f.

Table 5: Correlation between Fertilizer Treatments with Plant Tissue Constituents (*n* =12) and Number of Leafhoppers Settling on the Treated Plants (*n* =80)

Fertilizer treatment	Correlations, *r* (*p*),					
	With fertilizers (%)				With insect abundance	
	Nitrogen	Phosphorus	ADF	Lignin	After 1 day [a]	After 3 days [b]
Nitrogen	-0.712 (= 0.002)	-	0.333 (0.207)	0.362 (0.168)	-0.019 (0.945)	0.614 (= 0.011)
Phosphorus	0.428 (0.098)	0.734 (= 0.001)	-0.025 (0.927)	-0.560 (= 0.024)	-0.329 (0.019)	0.577 (= 0.019)

In bold are correlations significant at SNK, $p < 0.05$.

[a] Mean no. of leafhoppers per plant at 24 hours after insect release.

[b] Mean no. of leafhoppers per plant at 96 hours (nitrogen) and 72 hours (phosphorus) after insect release.

respectively), acid detergent fibers ($F = 1.422_{3,12}$; $p = 0.285$ and $F = 0.791_{3,12}$; $p = 0.522$ respectively), lignin ($F = 0.939_{3,12}$; $p = 0.452$ and $F = 2.271_{3,12}$; $p = 0.133$ respectively) and tannins ($F = 0.278_{3,12}$; $p = 0.840$ and $F = 3.282_{3,12}$; $p = 0.058$ respectively), were not significant (Table **4**).

Table **5** shows that plant tissue analysis had a negative correlation between nitrogen fertilizer treatment and levels of nitrogen in plants. Phosphorus fertilizer correlated positively with the level of phosphorus and negatively with lignin in plant tissues. On the other hand, both nitrogen and phosphorus fertilizer treatments correlated positively with abundance of leafhoppers on test plants.

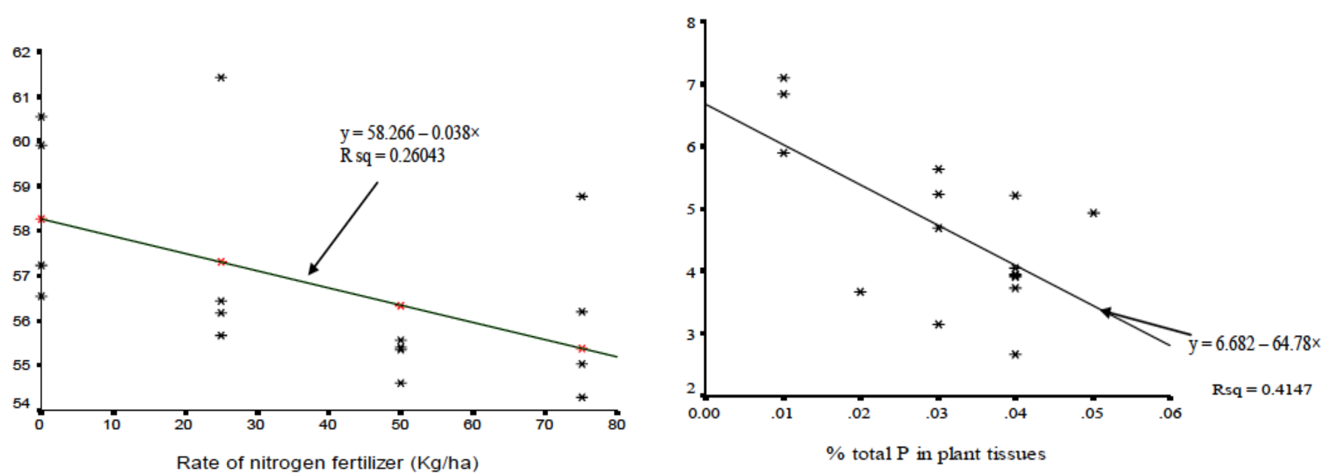
Regression analyses showed that percent neutral detergent fiber showed a significant negatively relationship with nitrogen fertilizer. Percent phosphorus showed a negative relationship with the level of lignin (Figures **4a** and **4b**).

4. DISCUSSION

Leafhoppers responded selectively to plants grown using different rates of nitrogen and phosphorus fertilizers, which indicates that insect-host plant interactions is important in determining the selection of host plants and possible transmission of MSV by *C. mbila*. This finding is consistent with previous studies, which observed that the settling behaviour of *C. mbila* is significant in regulating the efficiency of MSV transmission [5]. The preference of leafhoppers for plants grown under each of the higher rates of the two fertilizers supported the hypothesis that leafhoppers selectively settle on plants with appropriate nutrient content.

We also established that *C. mbila* required at least three days on high nitrogen, and four days on high phosphorus treated plants to successfully select and colonize the most suitable plants. Mesfin and Bosque-Pe´rez [11] gave a probable explanation for this relatively long delay in identifying a suitable host plant by the leafhopper. They reported that when leafhoppers encounter an unsuitable plant, the *C. mbila* would simply engage in non-probing activities such as walking or just resting. However, these intermittent insect behavioural process, which are associated with host selection such as frequent stylet probes, may increase the possibility of the leafhopper acquiring MSV, and not the transmission [5]. Successful inoculation of the virus can only occur when an infective leafhopper injects its saliva into the phloem tissues of a plant [12,13]. And therefore, the longer the viruliferous insects feed on healthy plants, the higher the possibility of viral transmission [2]. Therefore as the adult *C. mbila* populations undertake long flights particularly at the end of the wet season, an exponential increase of streak infection in crop fields can only be achieved if the rate of settling and colonization by the leafhopper is sufficiently high [2].

Many authors recognize the role of inorganic fertilizers in modifying the nutritive composition of plant tissues, and how fertilizers influence the selection and establishment of sap-sucking insects [14,15]. Our study showed that NO_3 (nitrogen) and P_2O_5 (phosphorus) levels in the plant tissues correlated positively with leafhopper abundance, which implied that an increase



(**a**) (**b**)

Figure 4: Relationship between nitrogen fertilizer and neutral detergent fibers. (**a**) Total phosphorus in plant tissues and percent lignin. (**b**) (*n = 12* for plants, *n* = 12 for soil analyses).

in the two compounds can facilitate leafhopper population build-up. The flying leafhopper thus faces the challenge of determining the appropriate sap composition of a host plant, particularly, in situations where a host plant contains 2% nitrogen against the 7% in the insect's body [7].

The conflicting benefits of fertilizers on yields as opposed to insect pest infestation suggests that although fertilizers increase crop yields, the consequential effects on pests might necessitate a pertinent compromise between acceptable yields and susceptibility of the fertilized crop to insect pests. Additional factors for further investigation include variation of the concentrations of secondary metabolites over the course of plant development, particularly in an MSV infected plant which is treated by different nutrient regimes. We deliberately used four - week old test plants in this study (based on the previous studies), because yield reduction in maize plants is a function of the age of plants at time of infection [2,16]. However, the low chemical concentrations of the various secondary metabolites in the young test plants used affected the sensitivity of the subsequent tissue analysis, which resulted in weakened demonstration of relationships between plant metabolites and leafhopper selection of host plants. We suggest further investigations to explore these relationships, preferably using methodologies that are more sensitive. It is however, possible that the lack of clear relationships between neutral and acid detergent fibers, lignin and tannins with leafhopper parameters is due to the interactive effects of a combination of several secondary metabolites in various concentrations. Kolehmainen *et al.* [17] made similar conclusions, which showed that insect responses are dependent on the concentrations of different types of lignin and tannins. Other relevant studies show that the altering of plant tissue constituents can promote the vulnerability of plants to insect attack [14,18].

Studies indicated that the levels of inorganic fertilizer elements in plant tissues determine the flight behaviour of insect vectors, and possible transmission of diseases [19-22]. We therefore, propose the design of comparative studies combining data of plant preference and long distance searching behaviour of leafhoppers to determine the true value of host nutrient composition. Such a study can be investigated at different levels of temperature, wind and precipitation. In summary, this study indicates that soil fertilizers can mediate the possible transmission of MSV disease by indirectly influencing the selection and colonization of maize plants by *C. mbila.* And therefore management programmes for MSV can exploit these antixenosis mechanisms to reduce the level of primary infection of MSV in maize fields.

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