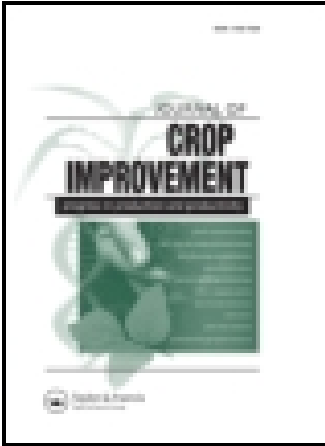


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Biological Factors Affecting Seed Production in East African Highland Bananas

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ABSTRACT. Seed production from hybridizations involving the East African Highland bananas (*Musa* spp., AAA group) is low due to high levels of sterility. This is a major impediment for the development of hybrids with disease and pest resistance and superior agronomic traits. The objective of this study was to examine the effect of inflorescence and

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stigma developmental stages on seed production in East African Highland bananas. Five female-fertile cultivars were pollinated daily with *Musa acuminata* spp. *burmannicoides* 'Calcutta 4' as the male parent. The level of female bract opening, distribution of the stigma development stages, and seed production per hand of a bunch were recorded. Means and standard deviations were computed for the ratings given to levels of bract opening. A Chi-square test was used to determine whether hand position affects the distribution of stigma classes. Correlation coefficients were calculated to determine the relationship of seed set to stigma development stages. At the time of pollination it was observed that the bracts of the upper hands were narrowly open, the bracts on the lower hands widely open and those in the middle hands were intermediate between the two extremes. Stigma development stages I and II were common in the upper hands, III in the middle hands, while lower hands were in stage IV. More seeds were obtained from the middle than from the upper and lower hands in a bunch. Stage III stigmas were highly receptive, stages I and II were not yet receptive while stage IV stigmas had lost receptivity. Pollinating hands with stage III stigmas could improve seed production in the East African Highland bananas. [Article copies available for a fee from The Haworth Document Delivery Service: 1-800-HAWORTH. E-mail address: <docdelivery@haworthpress.com> Website: <<http://www.HaworthPress.com>> © 2006 by The Haworth Press, Inc. All rights reserved.]

KEYWORDS. East African Highland banana, fertility, seed production, stigma receptivity

INTRODUCTION

The East African Highland banana (*Musa* spp., AAA group) is a staple food crop for millions of people in the highlands of East Africa, especially Uganda, Rwanda, western Kenya, north-western Tanzania and Eastern Democratic Republic of Congo (DRC). The average per capita consumption of banana in the region is high and in Uganda it is approximately 250 kg/year. However, production of the East African Highland banana has declined during the last 20 years due to pests and diseases that account for major yield losses in the crop. The major diseases include black Sigatoka (*Mycosphaerella fijiensis*), banana bunchy top and banana streak, while the most important pests include a complex of nematodes (*Radopholus similis*, *Pratylenchus goodeyi* and *Helicotylenchus multicinctus*) and the banana weevil (*Cosmopolites sordidus*).

A new wilt disease caused by the bacterium *Xanthomonas campestris* pv *muscaearum* has been destroying banana fields in Uganda, Eastern DRC and northern western Rwanda.

Bananas are mostly grown and sold by resource-poor small-scale farmers who cannot afford pesticides and other inputs. Therefore development and deployment of pest and disease-resistant varieties is considered the most economical and feasible means of overcoming losses due to pests and diseases. One of the major constraints in banana breeding is the low female fertility. Several investigators have reported large variation in seed set in crosses of *Musa* cultivars (Swennen et al., 1991; Vuylsteke, 1993; Ortiz and Vuylsteke, 1995). This variation in hybrid seed production is, perhaps, influenced by several factors. Stigma receptivity has been reported to limit fruit set in several crops, for example, pear (Herrero, 1983), cherry (Stosser and Anvari, 1982), apricot (Egea and Burgos, 1992) and kiwifruit (Gonzalez and Coque, 1995).

Knowledge of the factors affecting stigma receptivity is essential for understanding seed set and seed production in bananas and there have been no published studies for East African Highland bananas. Therefore the objective of this study was to determine the influence of biological factors, such as bract opening and stigma developmental stages, on seed set in East African Highland bananas in Uganda.

MATERIALS AND METHODS

Number of Seeds Produced per Hand

This study was conducted across three years at two locations in Uganda. The physical and climatic characteristics of the two sites are shown in Table 1. Both sites lie in the moist sub-humid zone with a bi-modal rainfall pattern and with most of the rain falling from March to May and from September to November.

Three cultivars 'Bitambi', 'Enzirabahima' and 'Nfuuka' from the *Nfuuka* clone set and two cultivars 'Kazirakwe' and 'Nakayonga' from the *Nakabululu* clone set were used to determine the number of seeds produced per hand in a bunch. These cultivars were selected on the basis of their seed-producing ability (Ssebuliba et al., 2005). 'Enzirabahima' is a high seed producer; 'Kazirakwe' and 'Nakayonga' are medium seed producers, while 'Nfuuka' and 'Bitambi' are relatively low seed producers. The female flowers of each cultivar were hand pollinated daily between 0630 and 0730 hours with pollen from *Musa acuminata* spp

TABLE 1. Physical characteristics of the two sites where these experiments were conducted.

Site	Location	Elevation (masl)	Average Daily Temperature		Relative Humidity	Mean Annual Rainfall (mm)	Soils	Soil pH Range
			Min	Max	%			
Kawanda	32°32'E, 0°25'N	1177	15.3	27.3	76.3	1250	Sandy loam (deep fer- rallitic clay type)	5.5 to 6.0
Namulonge	32°35'E, 0°32'N	1150	16	30	80	1000	Sandy-clay loam	5.2 to 6.0

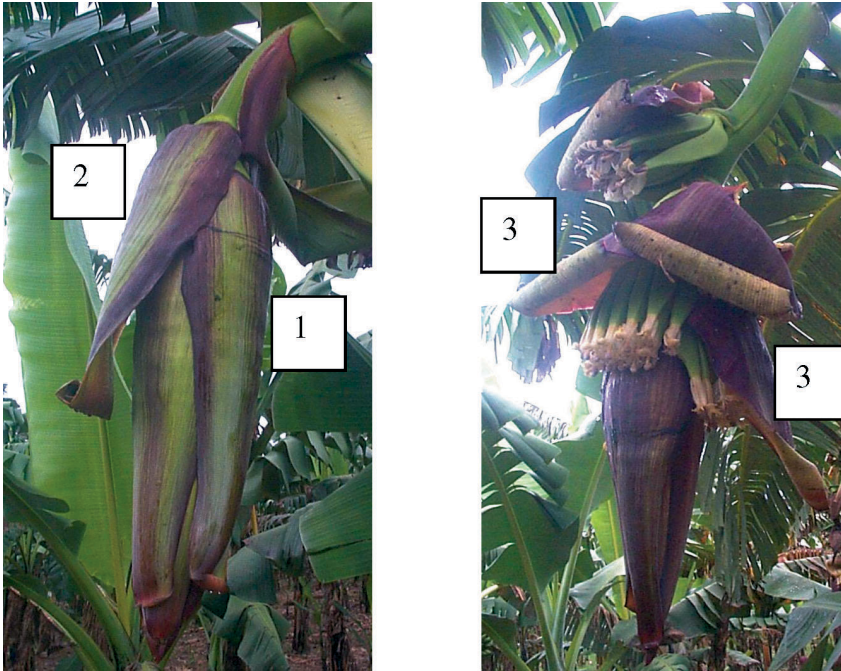
burmannicoides 'Calcutta 4' following procedures described by Ssebuliba et al. (2005). At maturity, bunches were harvested and ripened at room temperature in a closed room. Seeds were extracted manually from the fingers of each nodal cluster (hand), washed, air-dried, counted and the number of seeds obtained per hand for each bunch at both locations were recorded. For each location, seed-set data were subjected to cube-root transformation (Emerson and Stoto, 1983) prior to separation of means using the GLM procedure of SAS (SAS, 1998) to assess differences due to hand position within a cultivar.

Bract Opening and Stigma Development Stages

Bract opening and stigma developmental stages were recorded only at Namulonge. Bract opening was recorded as the angular distance of the tip of the bract from the rachis. A score of 1 was assigned when the angle was less than 45° with concealed pistils. A score of 2 was assigned when the bract tip had reached an angle of about 45° from the rachis exposing the stigmas. A score of 3 was assigned when the bract had fully opened exposing both stigmas and styles (Plate 1). Mean ratings for the level of bract opening in the different hands and standard deviations were computed.

Four developmental stages (I-IV) (Plate 2) of the stigma have been distinguished and reported in plantains (IITA, 1993). These stages differ in color, shape and composition of the mucilaginous mass on the stigma. Stage I is characterized by a smooth stigmatic surface with a distinctive ridge and yellow- to bone-white mucilaginous mass. In stage II, the stigma is more or less rounded and creamy and the surface is cor-

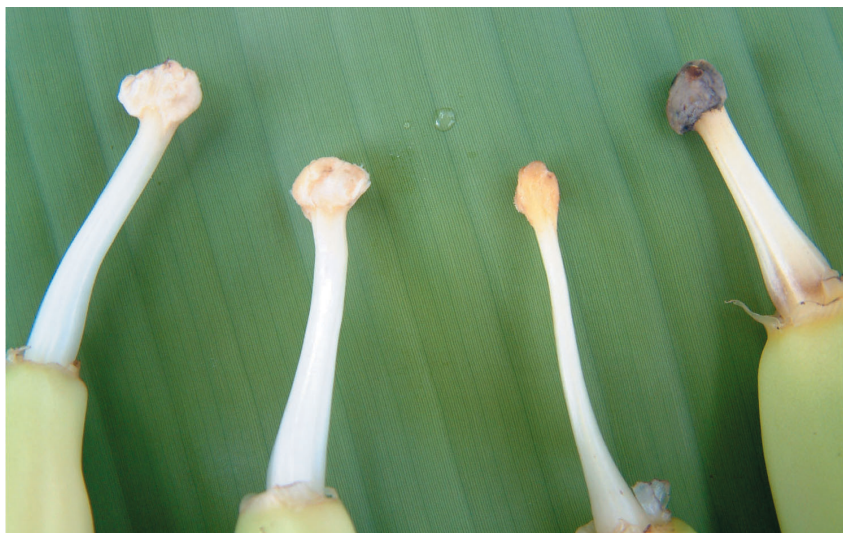
PLATE 1. Female inflorescence showing different levels of bract opening



- 1 = Narrow, bract just loose or open at a very narrow angle of less than 45° from the rachis with concealed pistils.
 2 = Medium, bract tip open at an angle of about 45° from the rachis, exposing the stigmas.
 2 = Wide, bract fully open exposing both stigmas and styles.

rugated due to the abundance of mucilage. Stage III resembles stage II, but differs in that the stigma is dark brown with several black patches and the mucilage is drier. In stage IV, the stigma is almost completely black with a few brown patches and the mucilaginous mass is dry. Stages II and III were found to be the most receptive in two plantain cultivars—‘Obino l’Ewai’ and ‘Bobby Tannap’ (IITA, 1993). The number of stigmas belonging to the various stigma development stages was recorded for each hand. Data were subjected to a Chi-square test to determine the variations in frequency of stigma classes per hand, variation in frequency of a given stigma class across hands and the effect of hand position on the distribution of stigma classes. Pearson’s correlation coefficients were calculated to determine the relationships of seed set per hand with stigma development stages.

PLATE 2. Stigma development stages



I

II

III

IV

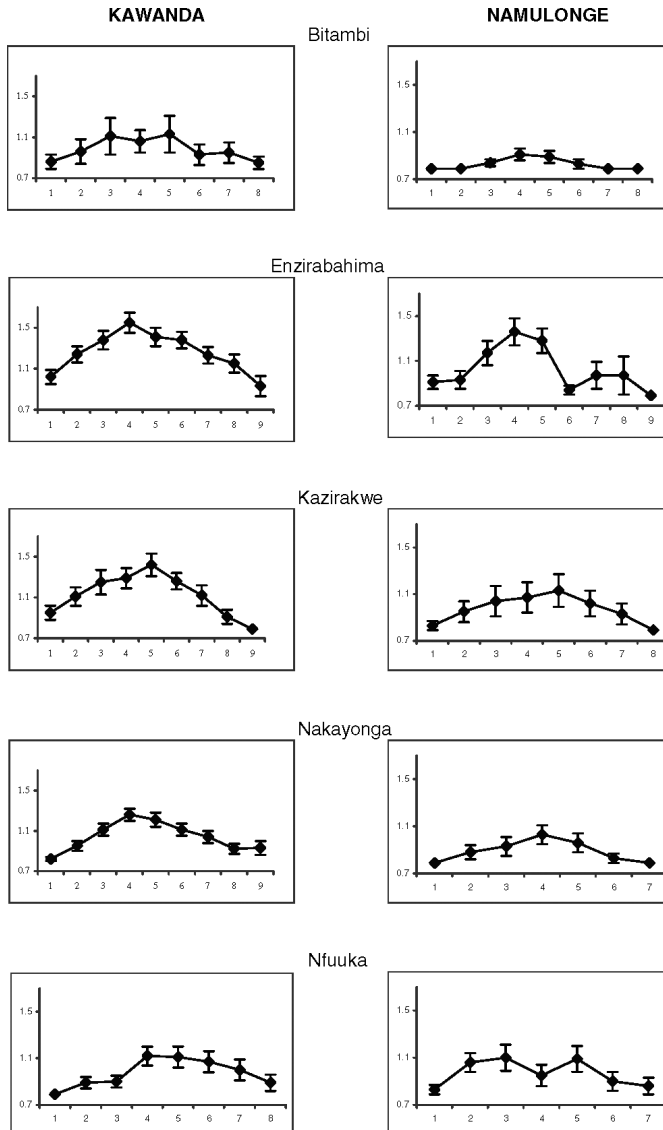
- I: Stigma is ridge shaped, smooth, with creamy mass.
 II: Stigma is round, rough, with abundant creamy mass.
 III: Stigma is light brown, with drier mass.
 IV: Stigma has several black patches, with dried up mass.

RESULTS AND DISCUSSION

Seed Production per Hand

Significant ($P \leq 0.001$) differences were obtained in seed set among hand positions within cultivars at the two sites (Figure 1). Generally, more seeds were produced in the middle hands than in the upper (proximal) and basal (distal) hands. The highest seed set was recorded in the 4th or 5th hand at both locations. This was true for all cultivars irrespective of their seed production rates. These results are consistent with those obtained in the West African plantain cultivar 'Bobby Tannap' (Swennen and Vuylsteke, 1990) and in two Indian cultivars 'Palayankodan' and 'Nendran' (Krishnakumar et al., 1990; Karmacharya et al., 1992). On the contrary, Shepherd (1954) obtained more than half of the seeds in a bunch from the two basal hands in 'Gros Michel', while

FIGURE 1. Seed set per hand (LSMeans of cube roots of actual seed set values) in selected clones of highland bananas



in 'Bluggoe', the two proximal hands were the most fertile. Thus, no general pattern for seed set per hand appears to apply to all *Musa* cultivars. Seed set per hand appears to be cultivar-specific. This study provides useful information for crossing programs in East African Highland bananas.

Bract Opening at the Time of Pollination

The level of bract opening in the different hands varied significantly ($P < 0.05$) among cultivars and with respect to the day and hour of pollination (Table 2). Generally, bract opening among all cultivars increased from the proximal to the distal hands. Thus, bracts of distal hands were widely open at the time of pollination (between 0630 and 0730 hours) compared with the proximal bracts.

Stigma Development Stages at the Time of Pollination

Four stigma development classes were recognized in the East African Highland bananas (Plate 2). Results of the Chi-square test revealed significant variations in the frequency of stigma development stages within and among hands (Tables 3-7). Hand position significantly influenced the frequency distribution of stigma development stages. Cultivars 'Bitambi',

TABLE 2. Bract opening scores in five genotypes of East African highland bananas.

Hand	Bitambi		Enzirabahima		Kazirakwe		Nakayonga		Nfuuka	
	N	Score	N	Score	N	Score	N	Score	N	Score
1	16	1.50	13	1.54	9	1.67	15	1.87	11	1.60
2	16	1.50	13	1.96	9	1.78	15	1.67	11	2.00
3	16	2.13	13	2.23	9	2.00	15	2.40	11	2.55
4	16	2.38	13	2.38	9	2.44	15	2.33	11	2.91
5	16	2.75	13	2.38	9	2.44	15	2.53	11	2.73
6	16	2.63	13	2.62	9	2.78	15	2.87	10	2.90
7	13	2.62	13	2.77	8	2.75	12	2.50	5	2.60
8	5	3.00	8	2.50	3	2.67	3	3.00	—	—
Mean	—	2.24	—	2.25	—	2.26	—	2.33	—	2.46
SD	—	0.76	—	0.71	—	0.66	—	0.69	—	0.67

1 = Narrow, bract just loose at a very narrow angle of less than 45° from the rachis with concealed pistils.

2 = Medium, bract tip open at an angle of about 45° from the rachis, exposing the stigmas.

3 = Wide, bract fully open exposing both stigmas and styles.

TABLE 3. Distribution of stigma development stages (I-IV)* in 'Bitambi'.

Hand Position	I	II	III	IV	χ^2 (Ho 1)
1	7.19	8.69	3.00	0.00	2.11
2	4.31	9.88	2.31	1.13	2.32
3	1.38	6.94	7.00	1.75	1.61
4	0.19	2.31	13.00	0.69	6.68**
5	0.00	3.31	8.50	3.81	2.41*
6	0.25	3.13	6.88	4.56	1.68
7	0.62	2.00	8.23	5.38	2.14
8	0.00	0.00	3.20	12.00	6.68**
χ^2 (Ho 2)	15.96***	4.23	2.13	7.87*	27.49* (Ho 3)

TABLE 4. Distribution of stigma development stages in 'Enzirabahima'.

Hand Position	I	II	III	IV	χ^2 (Ho 1)
1	0.00	16.77	2.31	1.38	7.02**
2	0.00	11.31	5.62	1.38	3.70*
3	0.00	6.62	5.77	4.92	1.41
4	0.00	3.46	9.46	3.46	2.76*
5	0.00	3.38	9.77	2.69	3.27*
6	0.00	1.46	8.08	5.92	2.86*
7	0.00	3.85	7.69	5.31	1.76
8	0.00	3.25	6.38	5.88	1.71
χ^2 (Ho 2)		6.54	2.23	3.35	12.63 (Ho 3)

TABLE 5. Distribution of stigma development stages in 'Kazirakwe'.

Hand Position	I	II	III	IV	χ^2 (Ho 1)
1	9.00	6.78	1.11	1.89	1.98
2	3.78	6.44	6.22	0.00	1.59
3	0.78	6.11	9.44	0.00	3.63*
4	0.11	3.22	9.67	2.44	3.37*
5	0.44	2.89	9.44	1.44	3.90*
6	0.22	1.78	6.56	5.33	2.19
7	0.00	2.38	6.13	6.00	2.02
8	4.00	1.67	3.67	4.00	0.34
χ^2 (Ho 2)	11.40*	2.80	3.04	7.73*	24.06* (Ho 3)

TABLE 6. Distribution of stigma development stages in 'Nakayonga'.

Hand Position	I	II	III	IV	χ^2 (Ho 1)
1	6.27	6.67	2.33	2.40	0.87
2	1.87	9.47	5.73	0.00	2.92*
3	0.60	4.47	8.87	2.20	2.38*
4	0.00	1.53	10.33	2.40	5.03*
5	0.00	1.07	10.87	2.53	5.61*
6	0.00	1.40	7.40	5.33	2.82*
7	0.25	3.33	4.58	5.83	1.40
8	0.00	0.00	0.00	14.67	12.00***
χ^2 (Ho 2)	26.24***	5.99	2.64	7.37*	35.58*** (Ho 3)

TABLE 7. Distribution of stigma development stages in 'Nfuuka'.

Hand Position	I	II	III	IV	χ^2 (Ho 1)
1	1.20	11.70	2.00	0.00	6.26**
2	0.09	9.45	3.55	2.18	3.32*
3	0.00	3.18	7.18	4.45	1.94
4	0.27	2.36	6.27	4.82	1.79
5	0.00	1.27	5.64	6.82	2.78*
6	0.00	1.10	6.20	6.10	2.85*
7	0.00	3.00	1.60	5.60	2.60*
χ^2 (Ho 2)	23.52***	5.09	1.40	1.88	27.74 (Ho 3)

* I: Stigma is ridge shaped, smooth, with creamy mass.

II: Stigma is round, rough, with abundant creamy mass.

III: Stigma is light brown, with drier mass.

IV: Stigma has several black patches, with dried up mass.

Chi-square tests:

Ho 1: No evidence of variation in frequency of "stigma classes" per hand.

Ho 2: No evidence of variation in frequency of "stigma classes" across hands.

Ho 3: No evidence that hand position affects the frequency distribution of "stigma classes."

'Kazirakwe' and 'Nakayonga' had a higher frequency of stigmas in stage I in the upper two hands than in the other hands. The cultivar 'Nfuuka' had negligible frequency of stigmas in stage I, while stage I stigmas were not observed in cultivar 'Enzirabahima'. Generally, the frequency of stigma in stage II gradually decreased from the proximal to the distal end of the inflorescence. On the other hand, the frequency of stigmas in stage III was higher in the middle than in the upper and lower hands, while stage IV stigma frequencies were more prominent in the lower hands. Seed set was significantly positively correlated with number of stigmas in

stage III in all five cultivars used in this study (Table 8). The combined data also indicated a highly significant positive correlation coefficient between the frequency of stigmas in stage III and number of seeds obtained (Table 9). Furthermore, the combined data also indicated that seed set was significantly negatively correlated with the frequency of stigmas in stages I and II. These results suggest that a high number of stigmas in stage III favor high seed production. Stage III was the most receptive stigma development stage, while the rest of the stages were either less receptive or non-receptive. Stages II and III were reported to be quite receptive in the plantain cultivars ‘Bobby Tannap’ and ‘Obino l’Ewai’ (IITA, 1993), as opposed to the present study which identified only stage III to be superior to other stages in receptivity. Genetic differences may partly account for the observed difference in receptivity between highland bananas (AAA) and the plantain cultivars (AAB). Differences in location and therefore climatic conditions in which the two studies were conducted could also account for the differences in levels of stigma receptivity (Shepherd, 1954; Swennen et al., 1991; Ortiz and Vuylsteke, 1995).

TABLE 8. Correlation coefficients among seed set and stigma development stages in five genotypes of highland bananas.

Stage	‘Bitambi’	‘Enzirabahima’	‘Kazirakwe’	‘Nakayonga’	‘Nfuuka’
I	-0.141	–	-0.233	-0.141	0.060
II	-0.089	-0.187	-0.184	-0.202*	-0.151
III	0.212*	0.287**	0.321**	0.398***	0.386**
IV	-0.073	-0.094	-0.041	-0.186	-0.223

*, **, ***: Significant at 5%, 1% and 0.1% probability levels, respectively.

TABLE 9. Correlations among stigma development stages (I-IV) and seed set for the combined data of six highland banana cultivars.

Stage	Number of Seeds	Stage		
		I	II	III
I	-0.102*			
II	-0.191***	0.321***		
III	0.211***	-0.352***	-0.552***	
IV	-0.003	-0.206***	-0.464***	-0.357***

*, ***: Significant at 5% and 0.1% probability levels, respectively.

Relationship Among Bract Opening, Stigma Receptivity and Seed Set per Hand

The present study has revealed that bract opening among all cultivars increases from top to bottom. Thus bracts in the lower hands open faster than those in the upper and middle parts. This suggests that bract opening is a natural phenomenon that takes place in response to stigma receptivity. Bracts in the upper hands open slowly probably due to the fact that the stigmas are not yet receptive, while in the lower hands bracts open faster in order to expose the stigmas before they lose receptivity. Stigmas progressively change from stage I to stage IV and fewer seeds were obtained in the upper and lower hands than in the middle hands. The variation in the number of seeds among hands (upper, middle and lower) is probably due to differences in stigma receptivity. Similarly, the higher number of seeds obtained in the middle hands appears to be related to stage of stigma development. Shepherd (1960) noted that physiological immaturity of the stigma might prevent or delay the penetration of pollen tubes. Similarly, a tendency towards less penetrating pollen tubes for stage I than for stages II and III was observed in two plantain cultivars (IITA, 1993). In the middle hands, more seeds were obtained because pollinations were carried out when most of the stigmas were receptive. Few seeds were obtained from the lower hands because pollinations were carried out when most of the stigmas had lost receptivity. Studies in two plantain cultivars indicated that pollen germination failed or was incomplete on stage IV stigmas (IITA, 1993). Stigmas in bananas appear to be receptive just for a few hours as opposed to other crops where stigmas remain receptive for days after anthesis, for example, in kiwi fruit stigmas retain their receptivity up to the fourth day after anthesis (Gonzalez and Coque, 1995). Therefore, to increase seed production in East African highland bananas, pollination time should be adjusted to fit within the limited period of stigma receptivity.

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