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Research Article

Structure and Stability of Cocoa Flowers and Their Response to Pollination

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This study investigated the position of staminodes around the style of cocoa flowers and the stability of cocoa flowers relative to pollination and seasonality. Cocoa flowers were categorized into converging, ≤1.20 mm; parallel, 1.21–2.40 mm, and splay ≥2.41 mm, depending on the distance between the staminode and style. Some flowers were hand pollinated while others were not and were excluded from insect visitors. Proportions of flowers of converging (56.0%), parallel (37.5%), and splay (6.5%) remained similar along the vertical plane of cocoa trees. Although pollination rates of flowers with splay staminodes were the lowest, the overall pollination success of cocoa trees was not significantly affected because of the small proportion of splay flowers.The stability of the cocoa flowers depended on both the season and pollination. During the dry season, unpollinated flowers of cocoa trees showed a flower-stability ratio of 72% on the second day, while the flower-stability ratio was 94% in the wet season. Pollinated (senescent) flowers had a stability ratio of 95% after 5 days during the wet season, but all pollinated flowers dropped after 5 days in the dry season, indicating that seasonal factors, such as water stress, can have dramatic effects on cocoa yields.

1. Introduction

Very low fruit set of cocoa relative to the numerous flowers the tree produces has been reported by several researchers (e.g., [1, 2]). This implies that there is obviously a delicate balance between crop success and failure. Factors identified include scarcity of the main pollinators (ceratopogonid midges), especially in the dry season [3–5]. Some authors [6, 7] argued that the spatial arrangement of staminodes around the style of the cocoa flower affects pollination success and hence may limit fruit set. Others [8–10] also believed that cocoa flowers are nectarless and odourless. Young et al. [11] have demonstrated the presence of microscopic nectaries on the pedicels, sepals, and guide lines of the petals and staminodes that produce odour. These characteristics of the cocoa flower seem to make it unattractive to many potential pollinators, and therefore only insects that have evolved with the plant will successfully pollinate it. The morphological and behavioural characteristics of ceratopogonid midges, however, make them effective pollinators of cocoa [3, 12, 13].

According to [7] midges are attracted to the vertically oriented staminodes and use it for landing. The dorsal part of the thorax of the midges brushes against the style, thereby smearing the style with pollen grains as the midge probes and descends toward the base of the staminodes, after landing on the inner surface of a staminode. The fact that style pollination generally results in more fruit set than stigma pollination makes the ceratopogonid midges efficient pollinating candidates [14]. The insect may then proceed into the petal hood along the purple coloured guide lines where curved bristles on the thorax press against the anther, thereby picking up pollen grains. Kaufmann [7] argued that staminodes which splay away from the style are not efficiently pollinated due to the widened staminode-style gap. There is however no empirical evidence as to what staminode-style distance reduces pollination efficiency of cocoa flowers. "Achieving

(a) Converging (b) Parallel (c) Splay

Figure 1: Cocoa flowers showing different staminode (arrowed) arrangement.

maximum pollination is necessary for optimum yield" [15]. It is therefore essential to acquire sound knowledge of the pollination ecology of cocoa, which has been largely ignored over the years [16, 17]. Winder and Silva [18] have observed that in order to enhance knowledge on natural pollination and hence the crop yield, the characteristics of the cocoa tree and its flowers must be considered. This calls for some studies of floral phenology of cocoa trees, as well as flower persistence and stability.

This study therefore evaluated the staminode-style distance in relation to fruit set of cocoa and the distribution of the different types of staminode-style arrangements along the vertical plane of the cocoa tree. In addition, the stability of the cocoa flowers under the dry and wet seasons was assessed to determine their response to pollination.

2. Methodology

2.1. Study Site. The study was conducted from 2009 to 2010 in two cocoa farms (N05°19.410′ W001°24.211′ and N05°19.516′ W001°24.107′) at Abrafo in the Twifo Hemang Lower Denkyira of the Central Region of Ghana, together with ten cocoa farms (6°40′36.4s N and 1°21′44.5s W) located at various distances to the Bobiri Forest Reserve at Kubease in the Ejisu-Juaben District, Ashanti Region. All the farms had mixtures of hybrid and Upper Amazon varieties of 15–25-year-old trees. Each farm was divided into 4 quadrants (plots), each measuring 1.2 ± 0.2SD acres.

2.2. Categorisation of Staminode-Style Distance. A total of 600 cocoa flowers (approximately 75 per plot) were randomly picked from the trees together with fresh flowers that had dropped to the ground. The flowers were put into glass jars with moistened cotton wool at the base, to prevent them from withering. Distances between the style and 2 randomly selected staminodes were measured in the laboratory, under a stereomicroscope, for each flower, and the mean (±SD) distance between the staminode and style was determined. Peaks and troughs of a distribution curve obtained by plotting mean staminode-style distance and their frequencies were used to determine intervals for various flower categories. Based on these, the flowers were categorized to three staminode types: converging, parallel, and splay (Table 1 and Figure 1).

Table 1: Categorized staminode-style distance and percent fruit set.

Type of staminode relative to style	Style-staminode distance (mm)	% Per staminode type	% Fruit set*
Converging	≤1.20	56.0	11.8[a]
Parallel	1.21–2.40	37.5	15.6[a]
Splay	≥2.41	6.5	0.5[b]

*The fruit set with the same letters is not significantly different.

2.3. Distribution of Staminode Types along the Vertical Plane of Cocoa Trees. Eight cocoa trees were randomly selected from each plot and 3 vertical sections of the trunk at heights 0.30–1.30 m, 1.31–2.30 m, and 2.31–3.30 m were marked with permanent marker. Thirty buds, which were due to open within the next 24 hours, within each marked trunk height were also marked for each plot. Matured buds about to open can be identified by the prominence of grooves along joined edges of sepals where they burst open. Buds that opened about 24 hours after marking were plucked and immediately put into glass jars with moistened cotton wool at the base. Flowers from each trunk section were put in different labeled jars. Flowers were carefully placed sideways (Figure 1) in the jars and were also spaced out to prevent the staminodes from tangling and subsequent altering of their spatial arrangement. Staminode-style distances were measured, as aforementioned, in the laboratory. This was repeated weekly for 6 weeks.

2.4. Relationship between Staminode-Style Distance and Pollination Success. The staminode type distribution experiment above was repeated but, in this case, marked flowers buds were inspected after 72 hours. All marked flowers that had dropped to the ground within the period were collected and their staminode-style distances measured as before. Unpollinated flowers usually drop off the tree after 48 hours [19] and thus flowers remaining on the tree after the 72-hour period were considered pollinated. Success of pollination of each staminode-style type was estimated indirectly based on the hypothesis that proportions of flowers that drop (unpollinated) should be comparable to that obtained in the earlier experiment, used to standardized staminode-style distance categories, if their efficiencies are similar.

2.5. Flower Stability and Pollination. A study was carried out during two dry (January–March) and wet (May–July) seasons to determine the floral stability of cocoa flowers (i.e., how long the flowers stayed when unpollinated or pollinated). By a simple random sampling approach, one hundred and eleven (111) cocoa trees were selected from ten (10) cocoa farms. A total of 555 (five flowers per tree) freshly opened cocoa flowers were randomly sampled from the selected trees for the study. These flowers were covered with muslin cloth to prevent contact with any insect. A second set of flowers were selected and manually pollinated following the standard manual cross-pollination of rubbing three anthers from flowers of three different trees against the subject flower's stigma, ensuring the likelihood of optimal pollination [20, 21]. A floral census was taken of both pollinated and unpollinated flowers from the second till the fifth day. The whole process was repeated for each season while observing all exogenous factors that could affect floral stability.

2.6. Data Analysis. Chi-square analyses of proportions of the three staminode-style types at different trunk heights were compared to the expected proportions (values obtained in the staminode type categorization experiment). This is to determine if the types are uniformly distributed along the vertical plane of the cocoa tree. Similarly, the proportions of marked flowers that dropped in the relationship between staminode type and success of pollination experiment were also compared to the expected values. Thus, a deviation in proportions between the obtained and expected results would mean that extent of pollination depends on the category of staminode-style distance.

The flower-stability ratio was then calculated as the percentage of the initial number of flowers. Means were given as ±1 standard error separated by Duncan's test. All analyses were considered at an overall significance level of $P = 0.05$.

3. Result

The staminode-style distances ranged between 0.05 mm and 3.25 mm and, based on these measurements, the three categories of staminode types were set out (Table 1). Most (56.0%) of the flowers had converging staminodes, whilst splay staminode constituted the least proportion (6.5%). Proportions of the three staminode types were independent of the two varieties; hence, the results were pooled together.

The fruit set of 15.6% recorded for parallel staminodes was not significantly different from the 11.8% for flowers with converging staminodes but both were significantly higher ($P < 0.05$) than those with splay staminodes (Table 1). The distribution of the type of staminode was independent of the vertical section of the cocoa tree (Table 2). The proportions of the various staminode types per vertical section were also comparable to the results obtained in the experiment used to categorize staminode types.

The number and rate of unpollinated flowers that dropped were higher ($P = 0.04$) in the dry season than in the wet. During the dry season, 51.2 (±3.54) unpollinated flowers had a flower-stability ratio of 72%, but there were no unpollinated flowers on the tree after the third day (Table 3). On the other hand, unpollinated flowers in the wet season had a flower-stability ratio of 94% on the second day. This, however, was reduced to 45% by the third day. Daily observations of the mature buds during the studies indicated that mature buds were completely opened between 0500 and 0700 hrs.

Generally, the number of senescent flowers (i.e., pollinated flowers that remained stable on the trees) was significantly higher ($P = 0.001$) both during the dry and the wet seasons. Pollinated flowers had a 65% stability ratio on the third day in the dry season, whereas the ratio was 95% even on the fifth day in the wet season (Table 3). All the pollinated flowers were intact on the trees during the five days of observation in the wet season except a few flowers, that is, 15 (±2.5), while pollinated flowers dropped after 4 days in the dry season.

Table 2: Distribution of staminode types along the vertical plane of cocoa tree.

Trunk height above soil (m)	Type of staminode (%)		
	Converging	Parallel	Splay
0.3–1.3	56.6	37.5	5.9
1.3–2.3	57.0	36.0	7.0
2.3–3.3	55.9	38.0	6.1

4. Discussion

Two key factors that determine the success of fertilization of cocoa flowers after pollination are effective deposition of pollen balls (an aggregate or cluster of pollen grains) and pollen compatibility. Successful pollination of cocoa requires the smearing of pollen balls on the style and/or stigma of a receptive flower [9]. A minimum of 35 compatible pollen grains are required for successful fertilization [22, 23]. Ceratopogonid midges are generally deemed the major cocoa pollinators worldwide, but their efficiency depends on their body sizes, which generally ranges from <1 mm to >3 mm. Species <2 mm were inefficient because their thorax usually fails to touch the style as the insect crawls along the inner surface of the staminode [7, 24, 25]. Thus, no pollen may be deposited. However, when pollen is deposited, the quantities smeared on the style are inadequate to initiate fertilization. The efficiency of larger midges is also perceived to be influenced by the arrangement of the staminode relative to the style [7]. The results obtained in this study give credence to the perception. Earlier studies by [26] showed correlation between the population of ceratopogonid midges and fruit set of cocoa.

The cocoa tree was found to produce flowers with varying staminode-style distances ranging from 0.05 mm to 3.25 mm. Most of the flowers produced by the cocoa tree have staminodes separated from the style by less than 2.41 mm. Thus, converging and parallel staminode types of flowers form the majority and these two were also the most ideal staminode-style arrangements for effective pollination. The converging

Table 3: Floral stability of pollinated and unpollinated cocoa flowers during the dry and wet seasons.

Day	Dry season (January–March)				Wet season (May–July)			
	Pollinated Flower-stability		Unpollinated Flower-stability		Pollinated Flower-stability		Unpollinated Flower-stability	
	Ratio (%)	Total	Ratio (%)	Total	Ratio (%)	Total	Ratio (%)	Total
2	100	1110	72	800	100	1110	94	1043
3	65	721.5	0	0	100	1110	45	500
4	0	0	0	0	98	1088	5	0
5	0	0	0	0	95	1054	0	0

staminode flowers were expected to give higher fruit set compared to the parallel because the smaller staminode-style gap should offer a more intimate contact between pollinating midge and the style. Consequently, more pollen grains should be dislodged from the midge's thorax onto the style. On the contrary, parallel staminode flowers gave higher fruit set, though not statistically significant. It is therefore possible that midges prefer landing on parallel staminodes relative to converging ones, and further studies on landing preferences must be conducted.

Although splay staminode flowers were less efficiently pollinated, they constituted very small proportions of the total flowers produced by the cocoa tree. This implies that a very small proportion of unpollinated splay staminode flowers did not influence significantly the proportion of successfully pollinated flowers. Moreover, aged flowers (about 48 hours old) tend to splay their staminodes, irrespective of the staminode type during the receptive phase of the flower [7]. It is therefore inferred that cocoa trees mostly produce the type of flowers that could be effectively pollinated by the right pollinators during the receptive phase of the flower. Cocoa flowers are produced at old axillary buds which tend to swell to form a "flower cushion" after repetitive flowering. These flower cushions are frequently injured through repeated pod harvesting, leading to reduced flower production at affected points. The even distribution of the three types of staminode flowers along the vertical plane of cocoa trees indicates that the age and nature of the flower cushion do not affect the type of staminode flowers they produce.

The results show that cocoa trees generally dropped their flowers when unpollinated, a confirmation of a widely reported phenomenon (e.g., [17, 27]). However, this study has demonstrated that the loss is greater in the dry seasons when humidity is low. Unpollinated flowers under the dry conditions could not be found after the second (2nd) day (Table 3). Flowers that dropped in the dry season appeared dry, pinkish, and reduced in size indicating some water stress [28]. The unpollinated flowers in the wet season were relatively more stable as they achieved 5% flower-stability ratio on the fourth (4th) day and some flowers were found even on the fifth (5th) day during the wet period. The 2 to 5 percent loss (flower-stability ratio: 98% and 95%) of pollinated flowers on the 4th and 5th days in the wet season could be explained in terms of flower abortion which is a common feature in angiosperms [1]. The observations imply that the stability of cocoa flowers may be influenced by two major factors: seasonal conditions (abiotic) and pollination (biotic).

Findings of this study could have bearing on the dynamics of cocoa pollination. Young [29] had noted that cocoa pollination involves harmonization between pollinator population cycle and the phenology of the flowering cocoa trees. This was further explained by [13] that indicated that the numbers of cocoa pollinating midges were reduced during the dry season, but increased in the wet season, and attributed it to the habit of the midges which live and breed in a cool and moist environment. During the dry season, cocoa leaves which constituted the bulk of ground mat dried up and thus became unsuitable for breeding of midges [13, 16]. Vaughton and Ramsey [30] have proposed two possible causes for the great loss through flower drops in the dry season: reduced rate of pollination resulting from low numbers of pollinators and reduced accessibility to nutrients and nutrients uptake. Their findings confirmed that the massive flower drops that occurred in the dry season could have been caused by a dwindling pollinator population during the dry season. It has long been known that tropical forest accumulates plant nutrients in the top few centimeters of soil. When such forest is cleared, the nutrients are rapidly released and give the soil a high fertility for a few years. The Amazon cocoa, which is a high yielding variety, depletes the soil of its nutrients at a faster rate [31]. Some authors have therefore suggested that the fastidious clearing of cocoa farms, as pertains in some cocoa areas, should be discouraged [15, 32]. The relatively higher stability of cocoa flowers in the wet season might be attributed to availability of requisite nutrients of cocoa, which need water for effective uptake and physiological cues inherent in the cocoa trees. During the dry season the reduced moisture in the soil might have affected the amount of nutrients for the cocoa plant. To obtain functional balance, flowers are abscised. The vast number of flowers that abscised might also result from a predisposition of cocoa to limit fruit development as explained above. Consequently, only under the best of circumstances may the necessary physiological signals be able to override the flower abortion signal. Hasenstein and Zavada [33] had attributed the abscission process in mature flower buds to reduced auxin levels. This seems to apply to cocoa flowers studied. Since flower production represents a considerable investment for the plant [1], the number of flowers could affect the allotment of auxin for each flower.

5. Conclusion

Flowers of varying staminode-style distances are produced by the cocoa tree and this has been categorized into converging, parallel, and splay staminode flowers. Splay staminode flowers were the least efficiently pollinated but were a small proportion of the total flowers; hence, they had an insignificant effect on overall pollination success of the cocoa trees. The stability of cocoa flowers is largely determined by pollination and seasons. Flowers stay longer during the wet period, and this may coincide with high pollinator abundance.

Conflict of Interests

The authors declare that there is no conflict of interests regarding the publication of this paper.

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