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Chapter

The Ecophysiology of Abiotic and Biotic Stress on the Pollination and Fertilization of Cacao (*Theobroma cacao* L.; formerly Sterculiaceae family)

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Abstract

The cocoa crop growth is highly influenced by environmental conditions, viz. temperature, which influence the phenological stages of flowering, fruiting, and pod growth. The plant produces caulescent flowers that are hermaphrodite and pollinated by insects, mainly *Forcipomyia* sp. (Diptera: Ceratopogonidae), but flowers setting to pods are very low. The efficiency of pollination depends on the degree of pollen compatibility and the number of pollen grains deposited on the stigma. It is assumed that midge population can be a limiting factor in the pollination of cocoa in addition to the environmental conditions. However, populations of insect pollinators are often severely disturbed by hurricanes through flooding of essential habitat and the widespread loss of existing flowers. This chapter will explore the role of midges [biotic] and the effect of climate [abiotic] variables. Understanding these ecological dynamics can lead to ways of conserving midge populations, mitigating the effects of global climate change and extreme climatic events.

Keywords: phenological, *Forcipomyia* sp., insect pollinators, *Theobroma cacao* L.

1. Introduction

Cacao [*Theobroma cacao* L. (formerly Sterculiaceae family)] is a perennial crop in chocolate confectionary industry [1]. There are three main groups of cacao varieties, viz. Criollo (*T. cacao* var. *cacao*), Forastero (*T. cacao* var. *sphaerocarpum*), and Trinitario (hybrids of Criollo and Forastero) [2, 3]. The Criollo fruits are oblong to ovoid in shape with yellowish-white seeds. The Forastero are ellipsoid to round with a smooth surface. The Trinitario hybrid fruits are highly variable when the plants are grown by seeds. Breeding improvements have led to the "fine or flavour" cocoa beans which have high yield and quality as the Trinidad Selected Hybrids (TSH) [4].

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1.1 Cacao stress

Cacao cultivation is challenged by multiple abiotic and biotic stress factors [5], as they sessile to physical environment interactions with pest and pathogens [6], evapotranspiration [7], soil salinization [8], and climate change [9]. They developed a multitude of defence mechanisms to adapt and survive stress conditions [10] and harmful microorganisms [11].

1.2 Cacao agroecology

The agroecological zones [AEZ] relate to soil fertility cycling and weed, pest, and watershed management. The cacao crop growth is specific to the AEZ, viz. temperature [12], flooding [13], and water stress [14]. The bimodal seasons influence the phenological stages of flowering, fruiting, and pod growth [15]. Water stress inhibits leaf development and pod setting and induces leaf abscission and photosynthetic rate (PR) [16].

1.3 Scope of stress pollination and fertilization

The ecophysiology of abiotic and biotic stress on the pollination and fertilization of cacao is specific to four (4) main stages in the crop reproductive cycle, viz. prepollination, pollination fertilization, and postfertilization. This treatise processes from pollen germination to ovary fusion to the young pod development or cherelle [4].

The scope of the treatise is limited to the author's research and critical review of the biotic or the internal factors that influence flower and fruit set in cacao. The abiotic factors are light intensity, relative humidity (RH), flooding, water stress, and cultural practices as shade, intercropping, and crop nutrition. The resilience of the pollinator to adapt to climatic changes and crop residue manipulation to increase the population dynamics of the cacao midges is examined, as well as advances in the area of olfactory sensitivity and cacao pollen odour [17].

2. Botany

2.1 Vegetative stage

Cacao can be propagated by seedling, cuttings, or terminal grafts, reach maturity at 12–18 months [4], and develop juvenile vertical shoot which produces lateral branches or "jorquette/chupons". It is an evergreen understory tree (20–25 m) but is shorter under cultivation (3–5 m) [18] and exhibits a flushing-type growth pattern, with 2–4 flushes/year. The fruit is a drupe but is referred to as a pod as it is fleshy and indehiscent, with internal seeds.

2.2 Cacao floral and fruit phenology

Cacao flowers prolifically (800–1000 caulescent flowers/tree) with 40 flower cushions [4]. The flowers dehisce in the afternoon and release pollen to a receptive stigma (**Figure 1**). The non-pollinated flowers abscise 24–36 h after anthesis. The flower setting to pods or cherelle is very low (0.5–5%) [19], hermaphrodite, and pollinated by insects, mainly *Forcipomyia* sp. (Diptera: Ceratopogonidae) [20]. The position of staminodes is around the style of cocoa flowers, and the stability of cocoa flowers is relative to pollination and seasonality [21]. The overall cacao pollination is low and is not significantly affected due to the small number of splay staminodes.



Figure 1.
BBCH of cacao flower from first visible observation to fully open. (a) BBCH 60: flowers open (30-31 FBV), (b) BBCH 62: 10% of flower open, (c) BBCH 65: 50% of flower open and (d) BBCH 69: 90% of flower open.

2.3 Cacao BBCH scale

The BBCH scale was used to differentiate the growth stages of cocoa steps, as it provides an insight of the floral phenology [4, 17, 22, 23]. The inflorescence emergence visible sign (Stage 5) shows flowering, that the buds primordia are 150 μm wide at the first bud visible (FBV). This continued over 30 FBV days and terminated at stage BBCH 59, when the flower bud growth is completed, but the bud is still closed. Usually, the individual flower cushion can produce many flowers at different stages of development over this growth stage (**Figure 2a–d**).

2.4 Cocoa reproductive anatomy and physiology

The cocoa flowers emerge as small cushions on the mature branches. The petal curves into a tiny hood that fits down around the style. The male flower consists of five double stamens, with each stamen consisting of up to four anthers. The female flower consists of five united carpels, each containing 4–12 locules (cavities). Due to this anatomical structure, a large insect like a honeybee in search of nectar could be a difficult venture, and only small insect as biting midge (subfamily Forcipomyiinae) would be able to pollinate the crop [4, 17]. The flower does not produce nectar, but the midges are attracted to red spikes on the flowers as the flower opens at dawn to facilitate the pollen release, and the stigma is only receptive to pollination for a period less than 12 hours. Unpollinated flowers drop off the next day with <10% successful pollination and 2% fruit development [4, 17].



Figure 2.
Cocoa cherelle wilt.

2.5 Crop ecophysiology

Cacao is a specific physiotype occupying a limited and defined ecophysiological sphere based on the crop comparative morphology and anatomy, physiology, biochemistry, biophysics, and molecular biology [24, 25]. The crop has its own set of complete phenotypical traits generated by a genotype in the morphological domain as a morphotype and in the physiological domain as a physiotype.

The crop physiotypical traits basically provide a good explanation of the occurrence of plants in their habitats and their relations between the environment and the morphological traits. The ecophysiology is influenced by both biotic and abiotic factors that affect vegetative growth and subsequent pollination and fertilization. The ecophysiology of cacao is measured by the actual behaviour of plants under natural environmental conditions, especially photosynthesis and transpiration.

2.6 Crop yield determinant

The cacao pod yield is influenced by photosynthesis and partition of photoassimilate [26]. The most important parameters for determinants of cacao yield are related to light interception and photosynthesis and photoassimilate distribution. These chains of events are modified by abiotic factors particularly during the floral phenology of the crop and influence the yield of cocoa. Yields of this crop depend upon successful transfer of pollen between flowers. Pollinator availability and efficacy can influence fruit set [27]. Recent studies have shown significant pollination limitation in several regions due to ineffective pollinators [28, 29].

3. Pollination and fertilization

Cocoa flowers are hard to pollinate due its complicated reproductive structure [29], and pollination and pod set depend on *the* degree of pollen compatibility, quality [30], and germination [31]. Pollination is the result from the visit of the single pollinator [32], and fertilization is influenced by a combination of plant morphological traits (biotic) and climatic variables (abiotic).

3.1 Cacao pollination

The main pollinators are midges (Diptera: Ceratopogonidae) and other small Diptera (Cecidomyiidae) [33–35]. The flowers are minute, so only a few taxa can be effective pollinators (**Figure 3**). The Ceratopogonidae are effective pollen carriers as

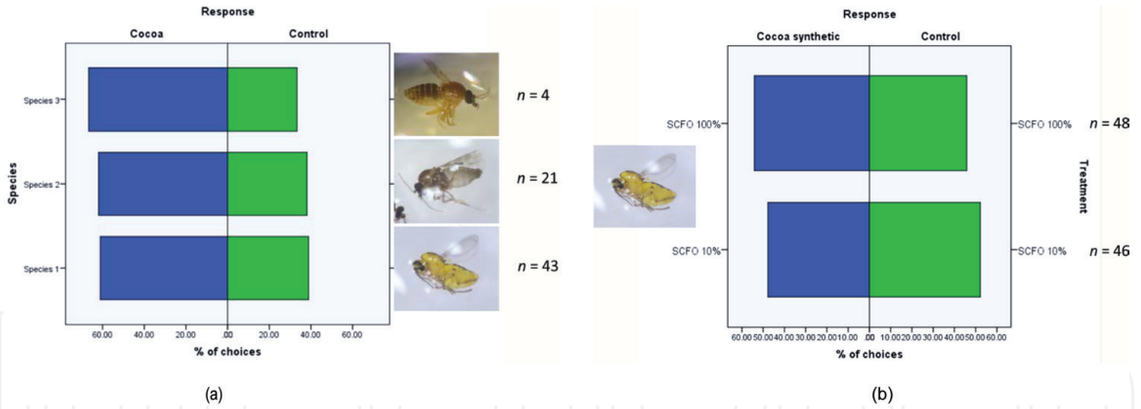


Figure 3.
(a) Response of midges to natural cocoa flower odour and (b) response of midges to synthetic blend mimicking cocoa flower odour.

the flower produces no nectar for the midges to collect, and it is suggested that they may be attracted to an odour or pheromone [36].

3.2 Pollinator dynamics

Midge population are threatened by tropical hurricanes and flooding. These small poor-flight insects are easily swept away by high winds [4, 17]. Midges would normally thrive in moist humid environment [37, 38], but excessive rain or drought could decimate the natural population. Bridgemohan et al. [4] examined the relationship between the midge population, flower pollination, and selected weather variables in several different Caribbean cocoa-producing islands. They recommended the manipulation of cocoa and banana residues as habitat for the adult midges to complete their reproductive cycle. This has improved crop yield through improved pollination and enhanced fertilization (**Table 1**).

3.3 Pollination intensity

There is a relationship between pollination intensity, fruit survival, and cocoa seed production [39]. The pollen/seed ratio increased with increased pollination intensities and seed yield.

3.4 Pollen germination and fertilization

Cacao genotypes are self-compatible and self-incompatible [19]. The pollen germination and fruit set will not occur after self-pollination of an incompatible

Months	Cacao leaf litter	Cocoa pods	Banana pseudostems	$\bar{x}$ [SE]
March	4.75	4.25	4.75	4.6±[0.17]
April	5	4.25	2.75	4.0±[0.66]
May	3.5	3.25	1.5	2.8±[0.63]
June	2.75	1.75	2	2.2±[0.30]
July	5	8.25	7	6.8±[0.95]
August	11.5	9.5	11.75	10.9±[0.71]
$\bar{x}$ [SE]	5.4 ±[1.27]	5.2±[1.23]	5.0±[1.59]	

Table 1.
Population of midges harvested from the Centeno [Trinidad] location.

genotype. Pollen germination improves (95%) with enclosed pollination due accumulation of CO_2, but fruit set can be low (45%) and seeds produced from self-pollinations are high (95%) compared to the cross-pollination (100%). The ovary 48 h after showed that the self-pollination varieties had the majority of ovules with a zygote, but some ovules contained unfused male and female gametes and polar nuclei.

3.5 Compatibility

Compatibility is highly variable in cacao. Self-incompatibility is higher in Criollo and Trinitario types, but Forastero cultivar is self-compatible with a high degree of cross-pollination [40]. Pods in self-compatible trees (50%) are cross-fertilized. It was inconclusive that all pods were the result of cross-fertilization. The fertilization of different flowers by different male parents or by mixed pollen was evident.

3.6 Climatic effects

The impact on pollinator distribution and abundance in tropical agricultural system areas are more likely to be affected by climate change with reduced crop yields [41, 42]. When rainfall and humidify cannot be managed, it will interfere with the efficacy of pollination and fertilization [37].

4. Effects of abiotic factors

Abiotic stresses affect the internal metabolic processes of plant and reduce their efficiency in dry matter production, accumulation, and partitioning [43]. There is an interaction between climatic variables, crop management, cacao pollination, and adult midge pollinators [37].

4.1 Light intensity

Cacao is limited by light interception and photosynthesis due to external and internal shade (self-shading) and light extinction inside the canopy [44, 45]. Heavy shade reduces seed yield because of low photosynthate production and partitioning [46, 47] and increases the incidence of diseases. Cacao is a shade-tolerant plant, and appropriate levels of shading could improve photosynthesis and seed yield [4] and reduce excessive evapotranspiration [48] and can tolerate decreased humidity and high temperature stresses during the dry season [21].

4.2 Relative humidity (RH)

Humidity is predictor of insect abundance, but it is difficult to predict its impact on pollination in cocoa [37]. Stomatal opening is related to relative humidity [49] but does not show high stomatal resistance under water stress or low RH [50]. Some genotypes are more sensitive to low RH which can be a limiting growth factor [49] and result in a reduction of net photosynthesis and low water-use efficiency [46, 50].

4.3 Rainfall

The stability of the cocoa flowers depends on the season and % pollination [51]. In the dry season, unpollinated flowers showed a low flower stability (72%)

compared to the wet season (94%). This improvement indicated that seasonal factors (water stress) have drastic effects on yields. The crop requires a high rainfall (1200–2500 mm/yr), and the rainfall over the previous month is a significant predictor of cocoa midge abundance, as the larvae require moist, decomposing vegetation (cocoa pods and leaf litter) that is more abundant in the wet season [52, 53].

4.4 Flooding

The tropics have a distinct dry and a wet season with hurricanes, excessive rainfall, and flooding [4, 47]. Flooding affects the initial crop growth when the total rainfall exceeds evapotranspiration. The hypoxic conditions in the hydromorphic soil [13] result in decreased vegetative growth, photosynthesis, flowering, and pod production [13, 24, 54, 55].

4.5 Water stress

Almeida et al. [14] found that drought resistance occurred through osmotic adjustment in most cacao genotypes and that many maintained relative water content (90%) and leaf water potential (Y_w = −1.0 MPa) are gradually decreasing (55% at −3.5 MPa). They found that there was a significant increase in leaf [K and P] during the dehydration process of some genotypes (Y_w = −1.5 MPa). Water stress affects internal water availability, translocation of assimilates, sink-source relationship, and flower set and cacao bean development [45, 47].

4.6 Shade

As a shade crop, cacao bean yields are considerably low due to shade-intercrop competition for water, nutrients, and light [56]. Traditionally, it was assumed that shade was critical regardless of yield [46, 57]. However, the cacao can tolerate full sunlight and produce more pods than under shade [58]. Under fundamental cultural practices, increased in crop density, aeration, and sunlight penetration seed production are enhanced [59, 60]. Moderate shade hardly affects bean yield, compared to heavy shading (>60%) which reduces yields by 30% [61].

4.7 Intercropping

Intercropping manipulates the agroecological conditions and enhances yield by promoting effective mutualism between species. In pure stand/shade tree-cocoa systems, there is inconclusive evidence on species interactions and competition under two separate shade species (*Terminalia superba* and *Newbouldia laevis*) [62]. Intercropping had no effect on cocoa biomass production in comparison to monoculture cocoa. Shading induced foliage and root formation both with and without fertilization. Light affects growth in the absence of underground competition. Intercropping can suppress K uptake in cocoa foliage (25%), due to interspecific competition.

5. Effects of biotic factors

Biotic stress affects pathogens, and there is an interaction between abiotic and biotic factor stresses (osmotic, ionic, or exogenous) [63, 64]. These biotic stress factors can affect pollination and fertilization through its physiology, nutrition, pest and disease, hormones, and pollinators and predators.

5.1 Physiological

Environmental factors affect cacao growth (morphology and physiology) in the orthotropic phase especially light intensity, photosynthetic capacity, and chlorophyll content [48, 63, 65–67]. Shaded leaves exhibit greater variability than full sunlight [68]. Leaf blade thickens with the increased light intensity regardless of NO_3 concentration, but under shade with high [N] there is a reduction [69]. Under full sunlight, rates of leaf expansion are low due to excessive transpiration and fewer stomata per unit leaf [58]. Cacao exhibits increased rates of net photosynthesis (400–750 μmol m^{-2} s^{-1}), which reflects 20–30% of PAR at full sunlight, compared to shaded (3–4%) [70]. Once the nutritional demands of the crop are met, the yield is dependent mainly on solar radiation [71]. Partial pruning of cacao reduces the fine root production resulting in a reduction photoassimilation and internal competition between vegetative flushing and root formation [72].

5.2 Crop nutrition

Mineral deficiencies or surpluses can lead to poor growth and development or toxicity to physiological processes, inclusive of pollination and fertilization. In cocoa under shade, N, P, and K uptake can be increased by 54, 112, and 71%, respectively. Intercropping with shade trees may not increase cocoa biomass; however, nutrient uptake is sustained for N and P due to low interspecific competition [62]. The crop utilizes 700 kg K/ha to produce 1000 kg/year of seeds including biomass. There is an inverse relationship between leaf transpiration and K doses [72]. Cacao trees well supplied with K are more tolerant to adverse water stress [73]. Regardless of the source of K, it induced low stomatal conductance and transpiration rate and improved WUE but without affecting shoot dry biomass [73].

5.3 Plant growth regulators

Plant hormones in cacao facilitate the adaptation to changing environments through mediating nutrient allocation and source/sink transitions [17]. ABA controls abscission, and ethylene accelerates it in the presence of ABA, but naphthalene acetic can prevent it without inducing fruit set. Cytokinins and auxins effects could be either synergetic or antagonistic depending on the interactions to other abiotic stresses. Unpollinated cacao flowers (90%) abscised immediately after anthesis due to increased ABA levels [19]. Fluridone inhibits ABA production, abscission zone layer, and senescence of the flowers, while ethylene production increases only after anthesis. Aminoethoxyvinylglycine (AVG) application can delay abscission compared to NAA + AVG.

5.4 Pollinators and predators

The key pollinator of cacao is the midge (Diptera: *Ceratopogonidae*) *in* which the plant receives self or outcross pollen and/or exports pollen to a conspecific plant [74]. This can be interfered by disturbances to the insect natural habitat and use pesticide [4, 47], resulting in low fruit set [75]. Conservation of the pollinator improves crop yield by removing practices that alleviate the negative impacts on the insect's habitat [37]. Discarded cacao pod increased the number of fruits/tree (**Table** 1) indicating a promotion of the pollinator in the ecosystem [4, 17]. Cacao pod residue increases the population of the two predators to the midges, viz. spiders and skinks, but these predators do not inhibit pollination. Improvements to midge habitat increased the availability of alternative habitat and food resources for both the pollinators [38]. Biological conservation and good agricultural practices improved pollinator efficacy and species conservation [75].

5.5 Diseases

Cacao is adapted to areas with high humidity climates but is pre-disposed to the risk of fungal diseases. In some areas, the cocoa crop is affected by various diseases (30–40%) which attack their vegetative parts and fruits. The crop is most susceptible at the fruiting cycle regardless of the genotype [76, 77]. Adomako [78, 79] found that cocoa experienced high yield loss due to unusable pods (10%), black pods (64%), immature ripe pods (30%), rodent damage (4%), and other damages (1.3%) which is close to 98 kg ha^{-1} yr^{-1} of dry beans. The four major diseases are witches' broom disease, frosty pod rot, *Phytophthora* pod rot, and vascular-streak dieback (VSD).

Witches' broom disease (*Moniliophthora perniciosa*) attacks growing tissue causing cocoa trees to produce branches with no fruit and ineffective leaves. The epidemiology is synchronized with the crop phenology, and the spread and reproduction of the fungus depend on the availability of water. Basidiospores are released at night with high humidity (80%) and temperatures (20–30°C) but have a short viability period and are sensitive to light and drying. The pathogen is also spread by infected seeds or budwood. Host resistance is the best option for control, such as the Trinidad selected hybrids, and treatments of fungicides and phytosanitary pruning have proven to be effective [77, 80, 81].

Frosty pod rot (basidiomycete: *Moniliophthora roreri*) infects young pods (1–3 months) with a white fungal mat on the pod surface. The dry powdery form of spores can be dislodged by water, wind, or physical disturbance of the pod and is spread easily. Disease incidence varies with the cultivar, pod age, and high rainfall. Application of systemic copper fungicides is essential when the crop is to be propagated by seeds or budwood. All cocoa species are susceptible to this disease, but fungicides (Flutolanil) and quarantine of infected fields can be effective [77, 80, 81].

Pod rot or black pod is caused by the fungus *Phytophthora* spp. (*P. palmivora*, *P. megakarya*, and *P. capsici*.) resulting in high yield loss (20–30%) and tree deaths (10%) (**Figure 4**). *P. megakarya* is the most important pathogen in cocoa in Africa and *P. capsici* in Central and South America, causing significant rotting or necrosis of pod losses especially in favourable environments [77, 80, 81]. Infestation can occur at any stage of development with the initial symptoms appearing as small, hard, and dark spots on the pod. Internal tissues and the beans are colonized and leaving a shrivelled pod.

Pod infected with *P. palmivora* produces up to 4 million sporangia which are disseminated by rain, ants, flying insects, rodents, and bats, including contaminated pruned branches. *P. megakarya* sporulation is usually more abundant with a soil borne phase which causes root infection and maintains a reservoir of inoculum in the soil surface water.

Treatment with systemic copper fungicides (metalaxyl) is frequently recommended together with injections of inorganic salt and potassium phosphonate,



Figure 4.
(a) Banana psuedostem as used as breeding site for midges and (b) cacao pod used as breeding site for midges.

which have proven to be effective against *P. palmivora*. Farm management practices which optimize shade and aeration can reduce surface wetness effectively. The complete harvesting, sanitation, and disposal of infected pods and husks can reduce the disease [77, 80, 81].

This disease is caused by *Oncobasidium theobromae* with its characteristic symptoms of chlorosis of the leaf. The fungus spreads internally within the plant resulting in death. Infected leaf litter in the rainy season is the main source of basidiospore discharge and spreads mainly at night and by wind or high humidity [77, 80, 81]. The spores have short lifespan. Protective fungicides, open canopy, and control of shading which increases aeration and insolation of the foliage are effective.

5.6 Insect pests

Insect pests are less destructive to the cacao floral and reproductive organs compared to rodents, birds/parrots, and monkeys. They are classed in three groups, viz. cause primary damage, transmit disease, or rise to pest status due to tolerance to insecticides. The two major pests are the mirids and the cocoa pod borer (CPB).

Mirids (capsids) are the major cacao insect pests (*Distantiella theobroma*, *Sahlbergella singulari*, *Helopeltis* spp., and Monalonion spp.) which reduce yields (75%) by feeding on the stem, shoots, and pods producing necrotic lesion causing dieback. Female mirids lay up to 60 eggs inside the pod husk, thus spoiling the beans. The insect is more attracted to trees in full sunlight but feeds and inhabits on the shady areas of trees [27, 82].

The organochlorine insecticides and Imidacloprid (Actellic/Talstar and Promecarb) are effective, but reduced insecticide is recommended to allow the natural enemies to increase for biological control. Integrated pest management (IPM) can control mirid using black ant (*Dolichoderus thoracicus*) and weaver ant (*Oecophylla smaragdina*).

The cocoa pod borer (*Conopomorpha cramerella*) causes losses in both young and mature cocoa pods. The main symptom of infested pods is premature ripening resulting in poor bean quality. Contact pyrethroid or carbamate insecticides on the undersides of lower branches can keep economic damage levels to a minimum. The fungus *Beauveria bassiana* can infect larvae and pupae. Traps with synthetic pheromones or female pod borer moths are used to reduce male's population.

5.7 Olfactory sensitivity and cacao pollen odour

The cocoa flowers appear to have no discernible odour like citrus, and it is only the pollen and nectar that are the pollinator's attractants. However, Erickson et al. [83] found floral fragrance in cultivated *T. cacao* consisted of 78 components which are mainly saturated and unsaturated hydrocarbons, with 1-pentadecene or *n*—pentadecane. Arnold et al. [37] *found that* three species of cocoa midge were attracted to the natural odours of cocoa flowers. *Dasyhelea* cf. *borgmeieri* was not attracted to a synthetic cocoa flower odour suggesting that it is the minor component of the cocoa flower's odour that attracts midges.

6. Cherelle wilt and fruit abortion

Young pods or cherelles are lost to physiological thinning known as cherelle wilt [84, 85]. Many of the cherelles die later with cherelle wilt as a natural event or become infected by fungi or bacteria. The first cherelle wilt occurs at 7 weeks after pollination (WAP) with a second wilt later (10 WAP) and has larger embryos and

smaller pod stalk pods. Young fruit abortion is high (10%) with a reduction in bean weight (3–10%) [86]. Pollination and assimilate limitation cause low fruit: flower ratios in cacao [27]. The "wilting phase" exhibits many changes in the anatomical structure including swelling of the pod, enlarged vascular, and lignification of the middle pericarp [85]. The xylem of the fruit of cherelle wilt was caused by occlusions in the xylem vessels of the fruit-stalk, which is associated with the oxidative activity of a cambial or meristematic tissue [86].

6.1 Biotic effects on cherelle wilt and fruit abortion

It is postulated that both types of wilt arise as a result of biotic and abiotic factors. Lachenaud [87] examined the stages between pollen germination and ovule fusion and found incomplete pod filling occurred mainly after physiological heritage wilt. The amount of fallen flowers with set ovary is insignificant (0.5%), suggesting that flowers pollinated with sparse pollen grains fell without setting. When fruit setting occurred at the same time on the same trees, wilted cherelles contained significantly more fertilized ovules than pods with beans.

The lack of hormones produced by the endosperm causes a decrease in the uptake of water and minerals, thereby inducing wilt. Wilted pods contained less cytokinin-like substances than healthy pods [88]. Auxin accumulates in deficient tissues may be responsible for incomplete filling and parthenocarpy [84]. Wilt is associated with increased levels of tricarboxylic acid cycle intermediaries and decreased levels of major metabolites in the biosynthetic pathways and regulation of abscisic acid and cytokinin levels [24].

There is inverse relationship between the wilt index and endogenous growth compounds in cacao [85, 86], with more polyphenol oxidase activity in the inner and outer pericarps of pods [84]. The pericarp and seed development are largely independent processes except for the inception of fruit growth and the changeover from the wilting to the non-wilting phase.

Despite the abundant flowering in cacao, a small number of cacao flowers (0.5–5%) become pollinated, and others become cherelles. Further to the low pod set of trees, few cherelles develop into mature pods with up to 75% of cherelles lost to the thinning condition. This may be due to lower level of assimilates available to the cherelle due to severe intra-plant competition [38, 89] and inefficient partitioning of photoassimilates [4]. Cherelles are attacked by insect (*stramenopile*) and fungi (*Phytophthora* and *perniciosa*) in early stages and frosty pod rot (*Moniliophthora roreri*), and *r*odents, squirrels, and parrots are common in mature pods. Pollination efficiency is negatively correlated with the number of flowers, and cherelles produced also varied between and within crosses [90]. Higher yielding trees were more efficient in converting flowers into pods mainly due to events that occur at the late cherelle stage.

6.2 Abiotic effects on cherelle wilt and fruit abortion

There are several environmental or abiotic factors that induce cherelle wilt, but these may have an interaction with the crop physiology. The cocoa tree allows as many cherelles to develop into mature pods based on nutrient availability, but those that do not fall become mummified and decayed [4]. There are significantly higher levels of nutrients (N and P) in soils under shaded than in un-shaded, corresponding with lower populations of wilts. Incomplete pod filling seems to be due to interactions between nutritional factors and genotypes [91].

Cherelle wilt is higher in un-shaded crop due to moisture stress, higher evapotranspiration, and lower nutrient available to support crop yield. There was a little

difference between the effects of the wet and dry conditions on flower production or setting or on cherelle wilt [92]. Cacao planted during the dry period developed few flowers, but initiation was apparently stimulated; in a subsequent wet or medium period, flowering was exceptionally heavy, but pod setting was poor and cherelle wilt was high [93].

Shaded cocoa has lower light intensity and interception but enhanced nutrient cycling and improved healthy pod development [4]. The level of overhead shade provided by the forest significantly influences litter fall, decomposition, and soil fertility and development of cocoa pods. Under un-shaded farms, litter fall is very high, but the rates of litter decomposition are very slow. Cacao fruit losses increase due to physiological wilt associated with higher temperatures, but differed between genotypes, reflecting genetic variation and also competition for assimilates between vegetative and reproductive stages [65].

6.3 Cherelle management

Cherelle wilt can be reduced by improving the health of cocoa trees through the *application of Fertilizers and mulches* and sunscald control. Ethephon application to the pedicel of young fruit resulted in morphological changes similar to natural wilt, suggesting that cherelle wilt could be reduced with indole butyric acid and gibberellic acid [94]. Cherelle wilt will increase due to high crop density and competition for nutrients, water, and light. Moist but well-drained soils and mulches will reduce cherelle. There is a balance between biotic and abiotic factors that determine the optimum number of cherelles that a tree can sustain, which is dictated by the demands of the "sinks" or developing beans within the surviving pods [4].

7. Conclusion

The interaction of environmental and plant genetic characteristics dictate the survival and reproductive efficacy of the cacao. Although the plant can produce its optimum yield of flowers, pollination and fertilization efficiency are under the influence of the equilibrium of the biotic and abiotic variables and their mutualistic interactions. The plant can only sustain a certain number of young pods or cherelles to full maturity. However, internally the number of beans/pods is still subjected to the partitioning of photoassimilates to ensure optimum bean filling. Regardless of the efficiency of pollination and fertilization, intra-plant competition for photoassimilates will result in a high number of beans/pod that will be incomplete or poorly filled and reduced bean weight and final yield.

The ecophysiology of pollination and fertilization of cacao beans is manageable by optimized agrocultural practices. Adequate midge breeding sites using cocoa pod and banana pseudostem can improve the insect population and subsequently increase pollination and fertilization [95]. This management practice is envisaged as the way to increase bean yield. The cocoa flowers are influenced by seasonality, weather conditions (abiotic) and pollination (biotic). The dynamics of cocoa pollination involves harmonization pollinator population cycle and the flower phenology. However, the numbers of cocoa-pollinating midges are lower in the dry season but increase in the wet season, but the natural habitat is pre-disposed to flooding, and insect flight is curtailed by high winds and rainfall.

Cocoa leaf litter and the pod husk constitute the bulk of ground material but dry up and become unsuitable in the dry season. Also, flower cushion is affected by water stress and high relative humidity and encourages flower abortion. In the favourable wet season, there could still be reduced pollination due to less

pollinators. The crop self manages it photoassimilate and its partitioning to avoid significant intra-plant competition, and to obtain functional balance, significant amount of flowers are abscised. A better understanding of the biotic and abiotic variables of pollination and fertilization processes and the midge biology and ecology has led to the development and validation of manipulation of the insect natural breeding site with an increase of insect population dynamics. This was amply demonstrated with increased pod yield and number of beans per pod.

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