SELF- AND CROSS-INCOMPATIBILITY IN COCOA (*THEOBROMA CACAO* L.): A CONCISE REVIEW

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ABSTRACT - *Reproductive incompatibility is a critical yet often underestimated contributor to the Theobroma cacao L. yield gap, and the only major constraint to be fixed at planting. This review examines the literature from 1927 to 2026 to establish the factors contributing to this reaction, yield costs, and strategies that could be taken to overcome the problem. It is reported that, in a late-acting system, while pollen germination and tube growth are indistinguishable from compatible matings, gametic fusion fails within the embryo sac. Genetically, this multi-allelic S-locus system prevents closely related clones from sharing alleles by pollinating one another. As a result, monoclonal or poorly designed polyclonal blocks may suffer low pod yield despite abundant flowering and pollinator activities. The retention indices reported across studies vary from 0% to 87.5% across parental combinations. Incompatibility, pollen limitation, and resource constraints are found to act multiplicatively rather than additively. Thus, field diagnosis, verified compatible clonal arrangements, and side-grafting are reported to be the cost-effective interventions that must precede pollination and nutrition inputs.*

Keywords: Cocoa, cross-incompatibility, polyclonal plot design, self-incompatibility, *Theobroma cacao*

INTRODUCTION

Cocoa is a primary income crop for four to six million tropical smallholder households, supporting a global industry valued at over US$100 billion annually (Lander *et al*., 2025). However, financial sustainability remains hard to achieve. Van Vliet *et al*. (2021) reported that in West Africa, about 73% to 90% of producers fall short of living income benchmarks. This economic instability is mirrored by supply instability. According to International Cocoa Organization (ICCO, 2025) data, a huge 489,000-tonne deficit in the 2023/24 season drove a surge in global prices, escalating the need to increase yields on existing farmland rather than expanding via deforestation.

From Malaysia's perspective, reviving the upstream cocoa sector is equally important. Annual GDP reports from 2019 to 2023 show a steady contribution from the agricultural sector with an average rate of 7.2% (Ministry of Finance Malaysia, 2023). With cocoa exports rising to RM8.2 billion in 2023, maximizing productivity per hectare becomes a national priority.

The reproductive biology of *Theobroma cacao* L. presents a paradox that bears directly on this objective. Although a mature tree may produce up to 100,000 flowers annually, only 0.5% to 5% of these flowers are pollinated and proceed to the initial fruit set (Bartley, 2005). Successive losses through incompatibility, cherelle wilt, and competition for maternal resources reduce this fraction further, so that a tree carrying 30 mature pods converts only about 0.03% of its floral effort into harvestable pod yield. The two values therefore describe different points along the same developmental funnel rather than a single conversion rate. While agronomic stresses and lack of pollinators are the common explanations (Van de Sande *et al*., 2026; Ríos-Moyano *et al*., 2025; Groeneveld *et al*., 2010; McKelvie, 1960), plant breeders are beginning to acknowledge self-incompatibility as a primary genetic driver. This self-incompatibility occurrence creates a reproductive bottleneck that prevents the initial fertilisation required to prevent fruit abscission (Cope, 1962, Lanaud *et al*., 2017).

Much of the literature reports compatibility and agronomy as separate disciplines. Genetic accounts are rarely addressed in field application (Muñoz-Sanz *et al*., 2020), while agronomic studies often treat compatibility as a fixed background variable (Toledo-Hernández *et al*., 2017; Dani & Rokhmah, 2022). This review aims to bridge that gap. We propose that incompatibility, pollen limitation, and resource constraints act multiplicatively rather than additively. Therefore, compatibility must be treated as a first-order design parameter diagnosed before intervention and corrected at establishment.

CYTOLOGICAL MECHANISMS & SYSTEMS COMPARISON

The reproductive biology of *T. cacao* L. presents a developmental bottleneck. Out of 100,000 flowers opened annually by a mature tree, only a small proportion of 0.5% to 5% converts into initial fruit set, and fewer still persist as harvestable mature pods (Alvim, 1984; Bartley, 2005; Lachenaud & Mossu, 1985). This yield loss is driven by a series of reproductive, environmental, and physiological filters (Figure 1). While lack of pollinators and cherelle wilt account for significant macro-level losses along this developmental funnel (Van de Sande *et al*., 2026; Ríos-Moyano *et al*., 2025; Groeneveld *et al*., 2010; McKelvie, 1960; Melnick, 2016), plant breeders identify late-acting self-incompatibility (LSI) as the foundational genetic driver of early flower drop (Cope, 1939, 1958).



Figure 1. Demographic funnel from flower to harvested pod in T. cacao. Intermediate values for compatible pollen receipt, ovule fertilisation, and cherelle set are illustrative, derived from the reported natural pollination rate and retention ranges rather than measured in a single study.

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Unlike common incompatibility systems that reject pollen pre-ovarianly, the mechanical failure in cocoa occurs at the ultimate stage of reproduction. Cytological evaluations demonstrate that pollen germination, pollen tube kinetics, and embryo sac penetration occur identically in both compatible and incompatible matings (Bouharmont, 1960; Cheesman, 1927; Cope, 1958, 1962). Rejection occurs exclusively during gametic fusion within the embryo sac, where the released sperm nuclei either fail to migrate or fail to execute membrane fusion with the egg cell and central nuclei (Figure 2) (Ford & Wilkinson, 2012).

This post-zygotic site of action distinguishes *T. cacao* from the S-RNase-mediated gametophytic (de Nettancourt, 1997; McClure, 2008) and Brassicaceae-type sporophytic systems (Table 1) (Schopfer *et al*., 1999; Stein *et al*., 1991; Takayama & Isogai, 2005). Crucially, because full pollen tube growth and initial ovarian expansion precede expression of the reaction, cocoa incurs an exceptionally high metabolic maternal resource cost compared to pre-ovarian rejection systems.

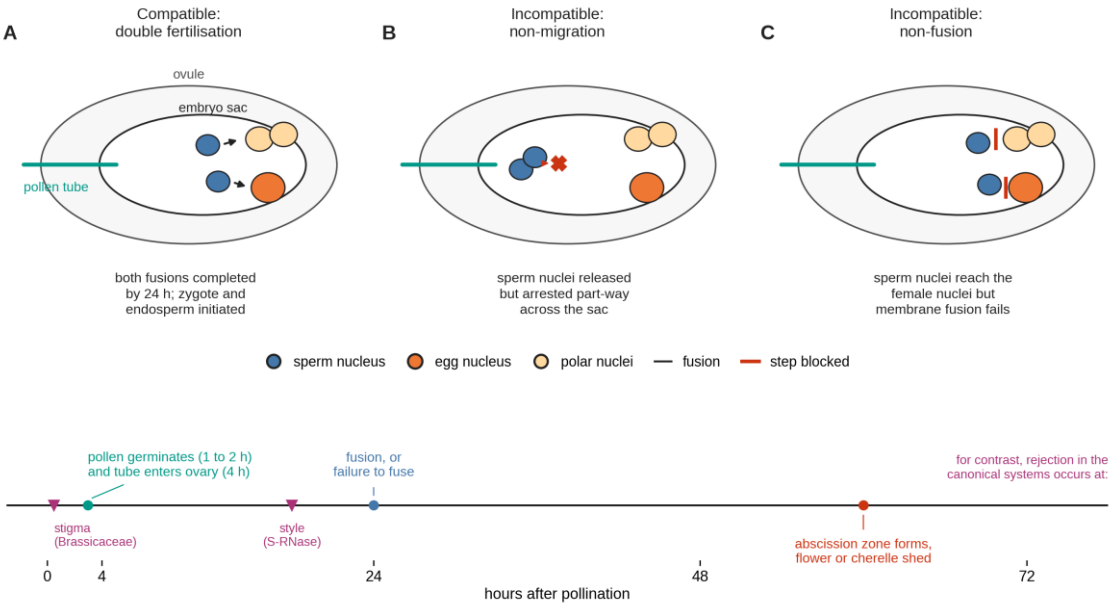


Figure 2: Cytological basis of late-acting self-incompatibility. Panels show a single embryo sac 24 hours after pollination: (A) compatible, with syngamy and triple fusion completed; (B) incompatible, with sperm nuclei released but arrested part-way across the sac; (C) incompatible, with sperm nuclei reaching the female nuclei but membrane fusion failing. The timeline below marks pollen germination, ovary entry, fusion or its failure, and abscission-zone formation, with the stigmatic and stylar arrest points of the two canonical incompatibility systems marked for contrast.

Table 1: Comparison of self-incompatibility systems in angiosperms and the position of *T. cacao*.

Feature	**Gametophytic (S-RNase)**	**Sporophytic (Brassicaceae)**	**Late-acting (*T. cacao*)**
Representative families	Solanaceae, Rosaceae, Plantaginaceae	Brassicaceae	Malvaceae (*Theobroma*)
Female determinant	S-RNase	SRK receptor kinase	Not validated; LRR-RLK candidates
Male determinant	SFB or SLF F-box protein	SP11/SCR pollen-coat protein	Not validated
Site of rejection	Style, pollen tube arrest	Stigma surface	Embryo sac, gamete non-fusion
Timing after pollination	12h to 48 h	Under 1 h	24 to 72 h
Pollen phenotype determined by	Haploid pollen genotype	Diploid parental genotype	Both, gameto-sporophytic
Resource cost to maternal plant	Low	Very low	High
Genetic architecture	Single multi-allelic S locus	Single multi-allelic S locus	Two loci plus polygenic background

Note: LRR-RLK =leucine-rich repeat receptor-like kinase; SFB = S haplotype-specific F-box protein; SLF = S-locus F-box protein; SP11/SCR = S-locus protein 11 / S-locus cysteine-rich protein; SRK = S-locus receptor kinase.

CLONAL PERFORMANCE & REGIONAL SURVEYS

Comparable surveys corroborate these reproductive patterns while introducing critical caveats. In Côte d'Ivoire, a half-diallel analysis of ten elite clones identified six self-compatible lines. Their self-pollination success ranged from 3% to 53%, while inter-pollination success spanned 9% to 24% (N'Zi *et al*., 2017). Notably, the control clone C8, which was previously classified as self-incompatible, exhibited a 33% success rate under selfing, which the authors attributed to environmental modulation (N'Zi *et al*., 2017).

Regional evaluations in Latin America further highlight this geographic compatibility. A study of 46 clones across five geographic groups revealed high inter-compatibility, with optimal combinations exceeding an 80% fruit set (López *et al*., 2021). Similarly, cross-pollination with locally adapted native genotypes has been shown to improve both fruit set and bean quality in Peruvian cocoa (Vansynghel *et al*., 2023). A Colombian trial also illustrated the highly asymmetrical distribution of these reproductive traits within specific clone pairings. Clone FSV 1 demonstrated balanced success, returning 60% self-compatibility and 60% bidirectional inter-compatibility. In contrast, clone ICS 60 exhibited only 11% self-compatibility but achieved 60% success rate as a pollen donor (Coronado-Aleans *et al*., 2025). Consequently, both genotypes remain highly viable for polyclonal systems, provided they are strategically deployed according to their specific functional roles.

Cross-incompatibility systematically emerges when elite breeding programs heavily recycle a limited pool of high-value founders. When two genotypes share identical alleles, the failure is phenotypically invisible; orchards exhibit healthy vegetative growth, abundant flowering, and active midge populations, yet fail to set fruit. Controlled pollination trials reveal that flower retention indices vary broadly from 0% to 87.5% depending entirely on the specific parental combination (Table 2) (Branco *et al*., 2018; N'Zi *et al*., 2017).

For instance, highly self-compatible clones like CCN-51 and Catongo maintain retention rates exceeding 54%, whereas elite lines such as TSH-516 and IMC-119 exhibit complete reproductive failure (0% retention) under selfing (Branco *et al*., 2018). Cross-pollination can radically alter these outcomes; crossing the self-incompatible lines TSH-565 and TSH-1188 yields the highest recorded success at 87.5% retention, whereas crossing EB-1017 with TSH-1188 results in absolute cross-incompatibility (Table 2) (Branco *et al*., 2018).

Table 2: Some examples of flower retention index 10-15 days after controlled pollination, illustrating the amplitude of the trait. All values are percentages of pollinated flowers retained (Branco *et al.*, 2018; N'Zi *et al.*, 2017).

Genotype or Combination	Retention index	Classification	Reference
CCN-51, self-pollinated	55.1	Self-compatible	Branco *et al.* (2018)
Catongo, self-pollinated	54.8	Self-compatible	Branco *et al.* (2018)
CCN-10, self-pollinated	50.0	Self-compatible	Branco *et al.* (2018)
TSH-516, self-pollinated	0.0	Self-incompatible	Branco *et al.* (2018)
IMC-119, self-pollinated	0.0	Self-incompatible	Branco *et al.* (2018)
TSH-565 crossed with TSH-1188	87.5	Highly cross-compatible	Branco *et al.* (2018)
EB-1017 crossed with TSH-1188	0.0	Cross-incompatible	Branco *et al.* (2018)
IMC-119 crossed with TSH-1188	7.3	Cross-incompatible	Branco *et al.* (2018)
Mean of 22 self-pollinations	15.6	Not applicable	Branco *et al.* (2018)
Mean of 16 crosses with TSH-1188	53.6	Not applicable	Branco *et al.* (2018)
C9, self-pollinated	53.0	Self-compatible	N'Zi *et al.* (2017)
C9, inter-pollinated	24.0	Cross-compatible	N'Zi *et al.* (2017)

Note: A retention index above 80% indicates a highly cross-compatible combination.

FIELD LAYOUTS & SPATIAL DYNAMICS

Because ceratopogonid midges are weak fliers with foraging ranges constrained to a few meters, a tree's functional pollen pool is determined strictly by its immediate neighbors (Toledo-Hernández *et al*., 2021). Segregating clones into large monoclonal patches functions as a structural barrier to reproduction, driving expected fruit set to 0% (Figure 3A, 3B). Even when different clones are interdigitated, selecting a

cross-incompatible pairing will result in total crop failure (Figure 3C). Maximizing productivity requires a spatial arrangement in which four mutually cross-compatible clones are finely interdigitated within rows, ensuring that every individual flower rests within a functional, highly compatible pollen web (Figure 3D)
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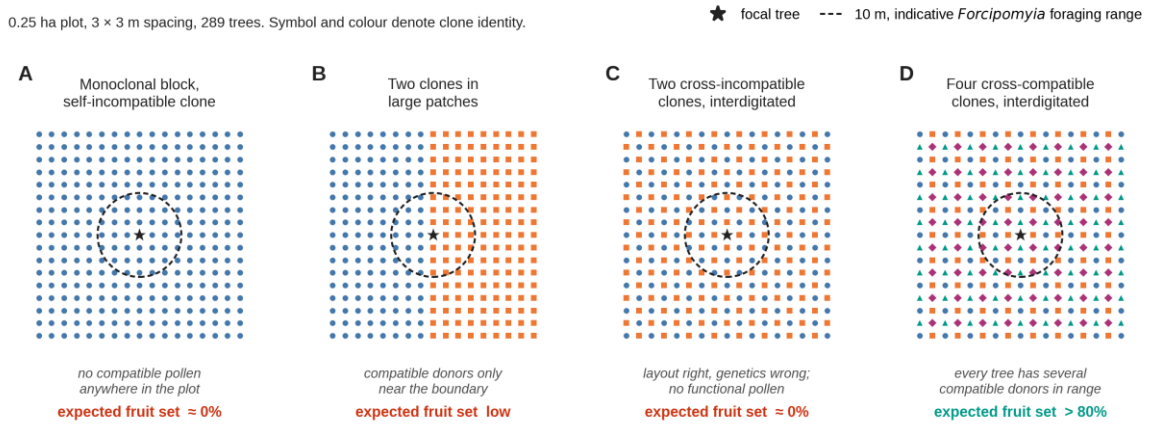


Figure 3: Compatibility-informed planting design, shown as a plan view of a 0.25 ha plot with 3 by 3 m spacing carrying 289 trees. Symbols and colours denote clone identity: (A) monoclonal block of a self-incompatible clone; (B) two clones in large monoclonal patches; (C) two cross-incompatible clones finely interdigitated; (D) four mutually cross-compatible clones interdigitated within rows. The dashed circle indicates an indicative 10 m foraging neighbourhood of ceratopogonid midge pollinators around a focal tree.

Table 3: Field interventions to overcome incompatibility, compared by time to effect, cost structure, and dependency.

Intervention	**Time to effect**	**Cost structure**	**Implementing level**	**Dependency**
Bag-and-pollinate diagnosis	15 days	Negligible; bags and labour	Extension or lead farmer	Trained operator
Verified compatible clone set at establishment	Immediate	One-off; near-zero marginal cost	Nursery and distribution	Compatibility data
Fine-scale interdigitation	Immediate	One-off; design only	Nursery and farmer	Compatibility data
Inclusion of self-compatible clones	Immediate	One-off	Nursery and farmer	Acceptance of lower heterozygosity
Side-grafting to a compatible donor	2 to 3 years	One-off, moderate labour	Farmer and extension	Diagnosis; scion supply
Interplanting or gap-filling with donors	3 to 4 years	Low, staged	Farmer	Scion or seedling supply
Marker-assisted prediction of compatibility	One season for screening	Laboratory capital; low per sample	Breeding programme	Marker validation
Pollinator habitat management	1 to 2 seasons	Low, recurring	Farmer	Compatibility-sound planting
Targeted partial hand pollination	Same season	High, recurring labour	Farmer	Verified compatible pollen
Matching nutrition and water to increased set	1 to 2 seasons	Moderate recurring	Farmer	Increased set achieved

For existing, low-yielding orchards, corrective field-level interventions must be systematically appraised against their time-to-effect and economic constraints (Table 3). In this review, side-grafting refers to

grafting scions of a verified compatible donor onto a proportion of the primary stem of an established tree, so that a compatible pollen source is introduced within the canopy while the remainder of the crown continues to bear; where growers instead practise side-grafting onto the trunk or chupons, the same compatibility principle applies. While long-term structural changes like side-grafting or donor interplanting require two to four years to manifest, short-term agronomic support such as pollinator habitat enrichment and targeted hand pollination can stabilize yields within one to two seasons, provided the background genetic layout is fundamentally sound (Van de Sande *et al*., 2026; Ríos-Moyano *et al*., 2025; Asante *et al*., 2023; Frimpong *et al*., 2011; Toledo-Hernández *et al*., 2021).

CONCLUSIONS

The primary cause of yield failure in cocoa is a late-acting genetic recognition system in which gametic fusion fails at the final stage within the embryo sac. Because this reaction is governed by shared alleles, incompatibility is fundamentally a property of the specific combination of trees rather than an isolated trait of an individual clone.

This review concludes that incompatibility, pollen limitations, and resource availability act multiplicatively rather than additively. Consequently, yield gaps cannot be resolved by single-factor interventions like fertilisation if the spatial genetic layout is fundamentally flawed. Sexual compatibility must be handled as a first-order design parameter fixed at orchard establishment.

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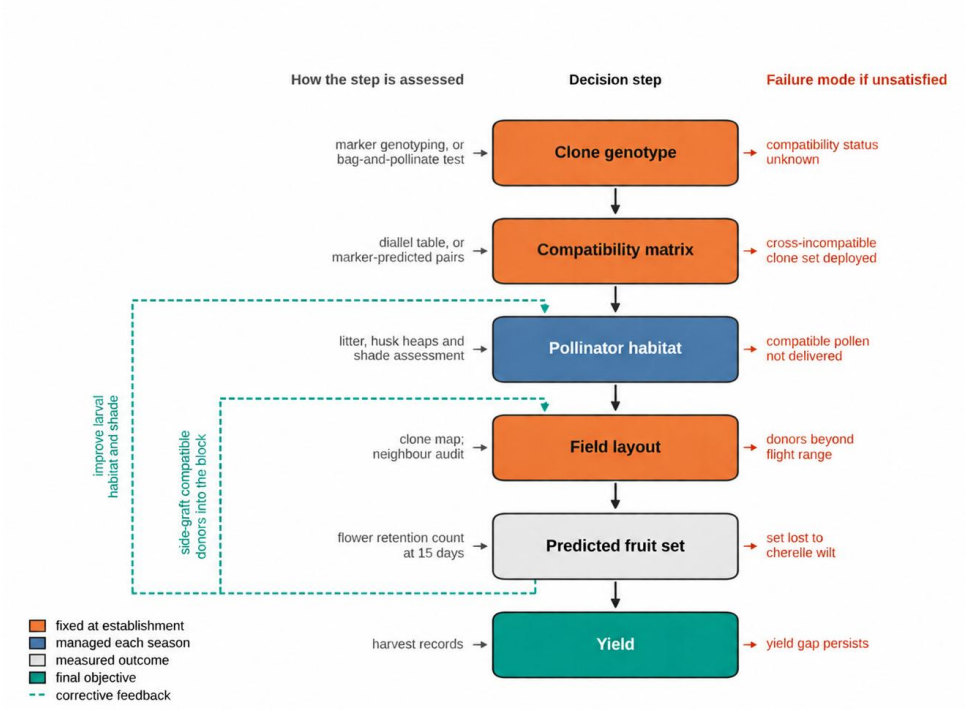


Figure 4: Decision pathway for overcoming incompatibility in the field. Each decision step is shown with the means of assessing it on the left and the failure mode arising if it is unsatisfied on the right. Steps are colour-coded according to whether they are fixed at establishment, managed each season, measured as an outcome, or the final objective. Dashed arrows indicate the points at which side-grafting and habitat management re-enter the sequence as corrective measures.

To recover the estimated 82% attainable yield gap without requiring expensive new technologies (Asante *et al*., 2022), four priorities should guide the global sector, as illustrated in Figure 4. The first is the establishment of a curated, open-access global compatibility database tied to standardised clone markers, so that the compatibility information accumulated by individual breeding programmes becomes usable at farm level. Building on this, multi-site agronomic evaluations are needed to stress-test the stability of clone classifications against environmental shifts, since a classification derived at a single location may not hold across contrasting climates.

Beyond characterisation, spatial explicit simulations of midge movement would allow candidate field layouts to be tested digitally before they are recommended to farmers, reducing the cost of trial arrangements in the field. Finally, full factorial field experiments crossing genetic compatibility, pollination intensity, and soil nutrition are required to map the multiplicative relationships among these factors definitively and so to convert the framework proposed here into quantitative planting recommendations.

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