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Gynoecious Sex Expression and Parthenocarpy in Cucumber: Genetic Basis and Breeding Implications

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Abstract: -

Gynoecy and parthenocarpy are pivotal reproductive traits underpinning modern cucumber (Cucumis sativus L.) improvement, particularly for hybrid production under protected cultivation. Gynoecy, primarily regulated by the dominant, dosage-dependent Femaleness (F) locus, enhances the proportion of fruit-bearing nodes by promoting pistillate flower development, whereas parthenocarpy enables fruit set without pollination, offering distinct advantages under pollinator-limited greenhouse and poly-net house conditions. This review synthesizes current understanding of the genetic and molecular regulation of these traits, encompassing the copy-number variation and ethylene-mediated function of the F locus and the complex polygenic and hormonal architecture of parthenocarpy, including major loci such as Parth2.1 and Parth6.1. The breeding significance of combining gynoecy and parthenocarpy is examined through evidence from line × tester and diallel analyses demonstrating favourable combining ability and heterosis in derived hybrids. Key constraints, including environmentally and epigenetically responsive gynoecious expression and potential yield–quality trade-offs, are also considered. Recent advances in genome-wide association studies and functional genomics are highlighted for their potential to refine allele discovery and accelerate the development of stable, high-yielding, quality-oriented parthenocarpic-gynoecious cucumber hybrids for protected cultivation.

Keywords: *Cucumis sativus; gynoecy; Femaleness (F) locus; parthenocarpy; hybrid breeding; combining ability etc.*

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Introduction:

Cucumber (*Cucumis sativus* L.) is an economically important cucurbit characterized by its short growing cycle, broad adaptability, and suitability for both open-field and protected cultivation. Improvement in yield and fruit quality has been facilitated by exploiting key reproductive traits, particularly gynoecy and parthenocarpy, which are highly valuable for hybrid seed production and stable fruit set under protected conditions.

Sex expression in cucumber is governed by a well-defined genetic and hormonal system. Wild, semi-wild, and most landrace accessions are generally monoecious, whereas gynoecious genotypes produce predominantly or exclusively female flowers. Gynoecy is primarily controlled by the dominant, dosage-dependent *Femaleness* (*F*) locus (Dhall *et al.*, 2023). Molecular studies have shown that this locus involves a copy-number variation of the ACC synthase gene *CsACS1G*, whose increased copy number relative to the ancestral *CsACS1* enhances ethylene biosynthesis and promotes pistillate flower development (Li *et al.*, 2020). The locus comprises tandemly repeated units of approximately 30.2 kb, while instability of gynoecy and the occasional appearance of monoecious plants have been linked to unequal crossing-over between these repeats during meiosis (Li *et al.*, 2020). Closely linked SSR markers, including SSR13251 and UW020605, have been developed for marker-assisted selection of gynoecy (Devi *et al.*, 2022).

Parthenocarpy, the development of fruit without pollination or fertilization, is particularly valuable in protected cultivation, where inadequate pollination can restrict fruit set. It enables more reliable fruit production and is also associated with reduced seed development and desirable fruit texture (Wu *et al.*, 2016). Unlike gynoecy, parthenocarpy has a complex genetic basis involving coordinated auxin, gibberellin, cytokinin, and ethylene signalling. Several QTLs associated with

parthenocarpic fruit development have been identified, including the major-effect loci *Parth2.1* and *Parth6.1* (Wu *et al.*, 2016; Devi *et al.*, 2022), providing useful genomic resources for breeding cucumber cultivars suited to protected production.

Understanding Sex Expression in Cucumber

Sex expression in cucumber is a well-established genetic and physiological system regulated by the interaction of the major loci *F*, *M*, and *A*, which collectively account for the diverse floral phenotypes ranging from monoecious and gynoecious to androecious, andromonoecious, and hermaphroditic forms (Dhall *et al.*, 2023). The common monoecious condition produces staminate and pistillate flowers separately on the same plant, with staminate flowers typically predominating at the lower nodes and appearing earlier in development, thereby reducing the proportion of nodes available for fruit production. The dominant *F* allele enhances the initiation of pistillate flowers, whereas its recessive state favours monoecious sex expression (Dhall *et al.*, 2023). At the molecular level, the *F* locus is associated with a tandem duplication of the ACC synthase gene *CsACS1G* within an approximately 30.2-kb repeat unit. Increased *CsACS1G* dosage promotes ethylene biosynthesis, which favours carpel development and inhibits stamen formation (Li *et al.*, 2020; Dhall *et al.*, 2023). The dosage sensitivity of this locus also contributes to variation in the degree of gynoecy among genotypes.

The repetitive structure of the *F* locus can introduce genetic instability, as unequal crossing-over during meiosis may modify *CsACS1G* copy number and occasionally result in the reversion of gynoecious plants towards monoecious sex expression (Li *et al.*, 2020). This phenomenon is particularly relevant to hybrid breeding because the stability and genetic purity of gynoecious parental lines must be maintained over successive generations.

Sex expression is further modified by additional genetic loci. The recessive *m* allele at the *M* locus is associated with andromonoecy, while the *A* locus contributes to the regulation of other sex phenotypes, including androecy (Dhall *et al.*, 2023). An alternative mechanism for stable gynoecy involves the *gy* locus, which is associated with mutation of the WIP-family transcription factor *CsWIP1* and functions through the ethylene-associated gene *CsPSTK1*. These distinct genetic mechanisms indicate that gynoecy may be established either through enhanced ethylene production mediated by *CsACS1G* or through modification of ethylene signalling involving *CsWIP1*. Overall, ethylene biosynthesis and signalling constitute

the principal physiological framework underlying cucumber sex determination, while the diversity of genetic mechanisms provides useful opportunities for developing stable gynoecious lines for high-yielding and intensive production systems.

Gynoecism: A Breeding Advantage

The commercial significance of gynoecy in cucumber arises from its ability to increase the proportion of fruit-bearing nodes and thereby enhance earliness and productivity. In monoecious genotypes, early nodes are often dominated by staminate flowers, delaying fruit set, whereas gynoecious plants produce predominantly pistillate flowers from early developmental stages, resulting in earlier harvest and greater cumulative fruit production (Dhall *et al.*, 2023). Consequently, gynoecy has become a key component of modern cucumber hybrid breeding. Gynoecious inbred lines offer major advantages as maternal parents because the absence of staminate flowers eliminates the need for laborious emasculation and facilitates efficient large-scale F1 seed production. Moreover, the greater proportion of fruit-bearing nodes provides a favourable background for exploiting heterosis for earliness, fruit number, and yield (Dhall *et al.*, 2023). Breeding evaluations under Indian protected-cultivation conditions have reported superior mean performance, general combining ability, and heterosis for fruit number and yield in gynoecious lines and their hybrids, supporting their value as parental resources for hybrid development (Singathiya *et al.*, 2025).

Despite these advantages, gynoecy can be influenced by environmental conditions, particularly temperature and photoperiod, with high temperatures potentially reducing the stability of female expression in protected environments (Dhall *et al.*, 2023). Together with the structural instability of the *F* locus (Li *et al.*, 2020), this necessitates careful phenotypic and, where available, marker-assisted monitoring during parental-line maintenance. These considerations are particularly important when gynoecy is combined with parthenocarpy to develop cucumber hybrids suited to protected cultivation.

Parthenocarpy: Fruit Set Without Pollination

Parthenocarpy, the formation of fruit without pollination or fertilization, is an important breeding trait in cucumber, particularly for protected cultivation where inadequate pollination can compromise fruit set (Wu *et al.*, 2016; Singathiya *et al.*, 2025). Besides ensuring stable fruit production, parthenocarpy produces seedless fruits with desirable firmness and uniformity, enhancing market value (Wu *et al.*, 2016). Its genetic

control is complex and involves coordinated hormonal regulation, with auxin initiating ovary growth and gibberellin and cytokinin promoting fruit development, while ethylene and abscisic acid modulate the process. Genes associated with these pathways include *CsTIR1*, *CsAFB2*, *CsARF10*, and *CsNPF1*. Major-effect genomic regions include *Parth2.1*, associated with candidate genes such as *CsARF19*, *CsWD40*, and *CsEIN1*, and *Parth6.1*, identified in Pusa Parthenocarpic Cucumber-6 and reported to show a major incompletely dominant effect (Wu *et al.*, 2016; Devi *et al.*, 2022). Functional studies have additionally implicated *CsWIP1*, *CsACO2*, and *CsFUL1*, although several candidate genes require further validation. For breeding, combining parthenocarpy with stable gynoecy is particularly advantageous: gynoecy reduces unwanted pollination, while parthenocarpy ensures fruit set without fertilization. This combination supports reliable, seedless fruit production and improved productivity under protected cultivation (Devi *et al.*, 2022).

Combining Gynoecism and Parthenocarpy in Hybrid Breeding

The integration of gynoecy and parthenocarpy in a single genetic background is a key breeding objective for protected-cultivation cucumber, as the two traits are functionally complementary. Parthenocarpic plants that retain monoecious or unstable gynoecious expression may undergo incidental self-pollination, resulting in misshapen and non-marketable fruits, whereas gynoecious but non-parthenocarpic plants remain dependent on external pollination, which is often unreliable under greenhouse and poly-net house conditions (Devi *et al.*, 2022). Consequently, parthenocarpic-gynoecious inbred lines have become important parental resources for developing hybrids suited to protected production, particularly Beit Alpha and slicing cucumber types (Singathiya *et al.*, 2025).

In India, Punjab Agricultural University, Ludhiana, has contributed substantially to the development and exploitation of combined parthenocarpic-gynoecious germplasm, including the poly-net house cultivar 'Punjab Kheera-1', derived from the line PBRK-4. Subsequent line × tester and diallel studies involving such germplasm have demonstrated significant genotype, environment, and genotype × environment effects for several yield and quality traits. Evaluation of eleven parthenocarpic-gynoecious Beit Alpha parents and their 28 F_1 hybrids identified parents with superior general combining ability and cross combinations with stable performance and favourable specific combining ability for fruit yield and fruit number across winter and summer environments (Singathiya *et al.*,

2025). These findings highlight the breeding value of integrating both traits within the parental background.

The relative contribution of parental components also varies among traits, with some studies indicating a greater influence of testers on specific yield attributes, emphasizing the importance of tester selection in trait-oriented crossing programmes (Singathiya *et al.,* 2025). Earlier diallel evaluations likewise reported favourable heterobeltiosis for yield-related traits in selected parthenocarpic-gynoecious combinations, supporting the exploitation of heterosis in this genetic background. Nevertheless, combined gynoecy and parthenocarpy remain environmentally sensitive. Elevated temperatures in protected structures can reduce gynoecious stability, leading to staminate flower formation and renewed risks of incidental pollination and fruit deformation. Therefore, maintaining both traits requires consistent phenotypic evaluation supplemented by marker-assisted verification, where available, across successive generations of parental-line development and maintenance.

Breeding Strategies and Selection Methods

The genetic knowledge underlying gynoecy and parthenocarpy can be translated into breeding gains through two complementary strategies**:** phenotypic selection using structured mating designs and molecular marker-assisted selection (MAS) targeting their associated loci. Phenotypic improvement primarily employs line × tester and diallel designs to evaluate parthenocarpic-gynoecious inbred lines and their F_1 hybrids for yield, earliness, and fruit quality, while estimating general and specific combining ability (Singathiya *et al.,* 2025). These designs enable partitioning of additive and non-additive genetic effects, facilitating the identification of superior combiners and heterotic cross combinations. However, maintenance of parental purity requires repeated phenotypic screening because gynoecious expression is environmentally sensitive and unstable sex expression may increase the risk of unwanted pollination.

MAS provides greater precision and early-stage selection, particularly for gynoecy, where phenotype alone may not reliably distinguish *F*-locus genotypes. A co-dominant marker within the *BCAT* gene, closely linked to the *F* locus on chromosome 6, enabled approximately 90% genotype classification in diverse cucumber inbred lines and permitted early identification of gynoecious zygosity (Win *et al.,* 2015). SSR markers such as SSR13251 and UW020605, located approximately 1.0 and 4.5 cM from the *F* locus, respectively, have also been validated for marker-assisted introgression of gynoecy (Devi *et al.,* 2022). For parthenocarpy, marker

development has largely relied on QTL mapping, reflecting its polygenic and hormonally regulated inheritance. Markers linked to the major-effect *Parth6.1* locus and sequence variation associated with *Parth6.1* and *Parth2.1* provide useful tools for introgressing parthenocarpy into elite germplasm through marker-assisted backcrossing (Wu *et al.*, 2016; Devi *et al.*, 2022).

Thus, integrating mating-design-based phenotypic evaluation with molecular verification provides an efficient framework for developing and maintaining stable parthenocarpic-gynoecious cucumber parents and hybrids, combining field-level assessment with greater precision in trait selection.

Challenges in Breeding for These Traits

Despite their breeding value, gynoecy and parthenocarpy remain constrained by environmental plasticity, complex inheritance, genotype × environment interactions, and yield–quality trade-offs. Gynoecious expression is particularly sensitive to growing conditions; multi-year evaluation of cucumber germplasm revealed reduced female flower proportion under early-autumn compared with spring conditions, with high temperature and long photoperiod, especially temperature, being major determinants (Lai *et al.*, 2018). This instability involves both *F*-locus variation and environmentally responsive epigenetic regulation of sex-related genes, including *MADS-box* genes and *CsACO3* (Lai *et al.*, 2018). Temperature, photoperiod, and light intensity can likewise promote staminate flowering even in gynoecious lines, complicating trait stability under protected cultivation (Cantliffe, 1981).

Breakdown of gynoecy can compromise parthenocarpic performance by permitting incidental pollination and malformed fruit development, necessitating joint evaluation of both traits across environments. Significant genotype × environment effects reported for parthenocarpic-gynoecious hybrids further emphasize this requirement (Devi *et al.*, 2022; Singathiya *et al.*, 2025). Parthenocarpy is itself difficult to stabilize because of its polygenic, hormone-mediated control, while several associated candidate genes remain insufficiently validated for routine marker-assisted selection. In addition, high yield may not always coincide with desirable fruit attributes, with some superior hybrids exhibiting altered fruit dimensions that may reduce market acceptability (Singathiya *et al.*, 2025). Therefore, breeding must simultaneously target stable gynoecy, reliable parthenocarpy, high productivity, and market-preferred fruit quality across diverse production environments.

Future Outlook

Research on cucumber gynoecy and parthenocarpy is increasingly shifting from phenotype-based selection toward genome-informed and precision breeding, supported by high-resolution genomic and functional approaches. Recent GWAS of diverse cucumber germplasm have substantially expanded the genetic landscape of parthenocarpy. Deep resequencing of 236 accessions representing six ecotypes and evaluated across multiple seasons identified 34 associated loci, including several previously reported QTLs, and functionally validated *CsACA10*, *CsCaM*, and *CsERT2* as regulators of parthenocarpy (Zhu *et al.*, 2026). Another GWAS involving 201 lines from diverse ecotypes identified six loci for parthenocarpic fruit set and expansion, including the novel loci *Pfs1.1* and *Pfs4.1*, while identifying elite material with strong parthenocarpy, reduced first-fruit inhibition, and improved low-temperature performance.

These findings provide an expanded resource for marker-assisted and genomic selection**,** enabling the potential pyramiding of favourable alleles rather than dependence on individual major-effect loci. Concurrent advances in understanding environmentally responsive epigenetic regulation of gynoecy may further facilitate the development of female-stable genotypes better adapted to temperature and photoperiod fluctuations in protected cultivation. Future breeding will therefore increasingly emphasize the integration of validated parthenocarpy loci with stable, locally adapted gynoecious backgrounds, rather than maximizing either trait independently. Combining GWAS-derived loci, functionally validated genes, and established combining-ability approaches offers a promising framework for developing parthenocarpic-gynoecious cucumber hybrids with improved yield stability, fruit quality, and environmental resilience.

Conclusion

Gynoecy and parthenocarpy form the genetic cornerstone of modern hybrid cucumber breeding for protected cultivation. Gynoecy, primarily controlled by the dominant, copy-number-dependent *F* locus, increases the proportion of fruit-bearing nodes, while parthenocarpy ensures fruit set under pollinator-limited conditions and contributes seedlessness and desirable fruit quality. Their value is therefore complementary, with stable gynoecy essential for realizing the full benefit of parthenocarpy and minimizing pollination-induced fruit deformity. This combination underpins contemporary hybrid breeding programmes, supported by line × tester and diallel studies demonstrating useful combining ability and heterosis. However, stable expression remains challenging. Gynoecy is influenced by *F*-locus structural variation and

environmental regulation, whereas parthenocarpy has a complex polygenic and hormonal basis that is still being resolved through QTL and GWAS approaches. Integrating genomic resources, validated candidate genes, and conventional combining-ability breeding therefore offers a promising route to hybrids with more stable gynoecy and parthenocarpy, improved yield, fruit quality, and environmental adaptability under protected and off-season cultivation.

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