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Inheritance Patterns and Heterosis in F_1 Cowpea Hybrids: Implications for Breeding Resilient Cultivars

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Abstract

Cowpea (*Vigna unguiculata* L. Walp) is an important grain legume in the tropical and sub-tropical regions, particularly in Africa and Asia. However, in spite of its relevance, as a consequence of its narrow genetic base, its productivity is limited due to its susceptibility to several biotic and abiotic stresses. This review describes the inheritance patterns of key phenotypic traits among cowpea F_1 hybrids derived from hybridization, showing consistent heterosis for yield component traits (such as the number of pods, number of seeds, and seed weight), phenological traits (such as the number of days to flowering and maturity), biotic and abiotic stressors, and qualitative traits like seed coat colour, governed by additive gene action, dominance, epistasis, and maternal effects. Empirical studies across diverse crosses highlight strategic parental selection's role in exploiting non-additive gene effects, while molecular tools such as quantitative trait loci (QTL) mapping and markers-assisted selection (MAS) enable precise trait introgression from wild relatives. These insights guide efficient breeding for resilient, high-yielding cultivars, enhancing cowpea's nutritional and economic value amid climate challenges.

Keywords: Cowpea; Dominance; F_1 Hybrids; Heterosis; Hybridization

Abbreviations: CABMV: Cowpea Aphid-Borne Mosaic Virus; QTL: Quantitative Trait Loci; MAS: Markers-Assisted Selection

Introduction

Cowpea *(Vigna unguiculata L. Walp)* is an important grain legume in the tropical and sub-tropical regions, particularly in Africa and Asia. It is both a vital nutritional and income source for many resource-poor people of these regions, contributing to food security and alleviating poverty [1]. Cowpea is adapted to a wide range of agroecologies, has a high nutritional status, and possesses a tremendous ability to fix atmospheric nitrogen into the soil; these attributes make it a suitable crop candidate for the tropical and subtropical climates [2,3]. However, in spite of its relevance, cowpea productivity is limited due to its susceptibility to several biotic and abiotic stresses as a consequence of its narrow genetic base. The narrow genetic base of the crop hinders its potential for improvement and deepens its susceptibility to biotic and abiotic constraints [4]. This narrow genetic variability among the cultivated genotypes hinders the improvement of important traits for withstanding factors such as disease, drought stress, salinity, and other soil toxicity, as well as improvement of nutritional quality, which contribute to low productivity and increased susceptibility of the crop to pests and other environmental constraints [5].

Hybridization provides an avenue to overcoming these challenges through the recombination of genes that can enhance yield, stress tolerance, and other important agronomic traits. It provides breeders with the opportunity to incorporate desirable genes for combating biotic and abiotic stresses and enhancing other characteristics influencing consumer preference and market values into new varieties. Therefore, understanding the patterns of inheritance of phenotypic traits among F_1 cowpea hybrids as well as the genetic compatibility among individuals of its species is critical for the timely development of superior genotypes [6]. A successful cowpea breeding strategy is hinged on the selection of parental lines of wide variation with the possession of complementary traits. Individuals adapted to specific ecological constraints serve as valuable sources of important genes. The extensive genetic variation for critical traits in the tropical regions provides breeders with credible genetic resources that can be explored to develop hybrids targeted at specific production constraints. As traits such as drought tolerance, disease, and pest resistance are multigenically driven, understanding their patterns in F_1 hybrids is crucial for developing improved cultivars [5]. Understanding the inheritance of phenotypic traits in F_1 hybrids provides breeders with critical insights needed to predict trait transmission, stabilize desirable characteristics, and develop resilient, high-yielding cowpea varieties. This knowledge strengthens breeding decisions and supports efforts toward enhanced agricultural sustainability and food security [7].

Many studies have revealed that cowpea possesses a wide genetic variability for critical quantitative traits influencing yield, coupled with high heritability and genetic advance that can be exploited reliably in selection [6,8]. Combining such traits in individuals through hybridization is crucial for expressing heterosis at the F_1 generation. Regarding abiotic stress tolerance in the context of climate change consequences limiting crop productivity, such as drought, aluminum stress under acidic conditions, and salinity, the high genetic diversity among cowpea for such critical production constraints and the magnitude of important traits that are positively correlated with grain yield are critical to developing F_1 individuals with superior inherited traits [9-11]. In light of the foregoing, this review examines the current evidence of the inheritance patterns of key phenotypic traits and provides critical insights into the expression of heterosis in F_1 cowpea hybrids.

Hybridization and Breeding in Cowpea and Other Crop Species

Cowpea hybridization and breeding are important procedures driving the improvement of the crop to enhance resilience and yield, and improve quality. Cross ability, the capacity of different genotypes to interbreed and consequently produce viable offspring, is fundamental here. Exchange of genes among diverse, contrasting, and complementary individuals is crucial for introducing diversity into breeding strategies, which allows the development of hybrid genotypes exhibiting improved traits [12]. Expanding genetic diversity through cross ability-driven hybridization improves adaptability to variable environmental conditions, enhances resistance to pests and diseases, and ultimately improves yield [13]. The importance of hybridization in improving cowpea genotypes cannot be overemphasized. This is critical due to its narrow genetic base, which is a consequence of its being self-pollinating, limiting its genetic variation. The principal cause of the narrow genetic base of cowpea can be linked to limited exchange of genes between the wild genotypes and cultivated varieties, and can also be attributed to its advancement from a limited wild germplasm [14].

Breeding strategy of the crop for improved traits can be frustrated by its narrow genetic base, making it difficult to improve such traits as resistance to diseases and pests, tolerance to drought and other soil toxicity, and yield stability under varying environmental conditions. Combating these limitations requires backcrossing to either wild relatives or other species to introduce desirable traits [15]. Identification of cross-compatible wild relatives to fast-track this strategy is now made easy by the recent advancements in molecular markers, making the broadening of the crop genetic base possible [16]. Advancement of molecular tools helps breeders in the effective incorporation of new combinations of genes from wild relatives into new varieties to enhance their resilience against biotic and abiotic stresses [17]. One of the important ways to combine desirable traits from parental genotypes is the development of F_1 hybrids. Genetically distinct parents are utilized in producing these hybrids, as this strategy is known to drive heterosis and quality. Offspring exhibiting heterosis in important traits from their parents benefit from such superior traits. Hence, the advantage of F_1 hybrid breeding lies in allowing breeders to exploit superior traits effectively [12].

Hybridization and Hybrid Vigor (Heterosis) in Cowpea and Other Crops

Hybrid vigour, universally referred to as heterosis, is a significant occurrence observed in hybrids developed through wide hybridization, especially at the F_1 generation. Offspring exhibiting superior performance and qualities, such as improved growth rates, higher yields, and greater overall vigour, are common outcomes. Expression of heterosis, which can lead to a significant improvement in crop performance under variable environmental conditions, is considered very valuable in agricultural systems [17]. The mechanisms governing heterosis are complex, multigenic, and physiological factors that may be explained by either the dominance or overdominance hypothesis. The dominance hypothesis hinges its argument on the premise that hybrids' superior performances are a consequence of masking deleterious alleles domiciled in the parental lines [18]. Overdominance suggests that favorable expression of certain traits in hybrids is a consequence of the interaction of different alleles leading to improved performance [19].

An effective breeding strategy is wide hybridization, which involves crossing genetically distinct individuals. This is essential in crop breeding programs as it introduces genetic variability for enhanced resilience to climate change and its other consequences [17]. In cowpea breeding, hybridization plays a crucial role in widening genetic diversity by developing F_1 hybrids that combine favorable traits from different genetic backgrounds, a valuable approach in improving overall productivity, resilience, and stability of yield for varied environments [12]. Studies have shown that F_1 hybrids have the capacity to significantly outperform their parent lines for grain yield and resistance to insect pests [20,21]. Furthermore, application of hybridization has successfully produced dual-purpose cowpea varieties combining higher grain yields with nutritious fodder for livestock, and these varieties have gained popularity among farmers for their economic benefits [22]. Research on heterosis exploitation in crop species has produced

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significant findings about F_1 hybrid performance. The combination of genes between domesticated eggplant varieties and their wild relatives through hybridization produced F_1 populations that demonstrated improved drought resistance [23].

The F_1 hybrids demonstrated superior drought tolerance to their parental lines because they maintained better vegetative development and flower stability, which indicated heterosis and showed that both parents contributed beneficial traits. The research indicates that hybridization presents an effective method for developing eggplant cultivars that resist drought. The research results showed that hybridization presents an effective method to develop eggplant cultivars that can tolerate drought conditions. The study by [24]. Found that Moringa F_1 hybrids displayed their highest heterosis values for seedling vegetative characteristics, chlorophyll content, and protein and fiber content. The study results showed that these traits follow genetic patterns instead of environmental factors. The research by [25]. evaluated rice heterosis under different phosphorus conditions, which revealed that hybrid plants produced more spikelet's per panicle and grains than lines and testers. Multiple hybrid lines produced significant grain yield increases when tested under different phosphorus conditions. The research findings demonstrate that heterosis effects depend on both the measured characteristic and the parents used in crossing and the surrounding environment. Scientists can use specific hybrid combinations to boost crop yields and productivity according to these research results.

Phenotypic Traits Driving Productivity in Cowpea

In the cowpea breeding program, a number of phenotypic characteristics are crucial for enhancing resilience, production, and nutritional value. With an emphasis on yield-related characteristics including the number of pods per plant, number of seeds per pod, number of seeds per plant, seed yield per plant, and total biomass, numerous studies have investigated the yield potential of numerous cowpea varieties across a variety of agroecologies and farm techniques. According to [2], these investigations have revealed cowpea varieties with greater production potential, offering useful information for cowpea improvement efforts. Pods contain several seeds; the number of pods per plant is an important factor in grain yield in cowpea. Thus, yield-related qualities are critical for increasing overall crop productivity. Various studies have demonstrated that some genotypes produce more pods per plant, which is directly related to greater seed yield per plant [6]. Furthermore, seed weight influences market value, customer preferences, and nutritional quality, as larger seeds command higher prices and contain more nutrients [15]. Total biomass is another crucial trait that reflects the overall health and vigour of the plant. Research indicates that accessions with greater biomass not only yield more but also demonstrate better adaptability to varying environmental conditions [26].

In addition to nutritional traits, cowpea is characterized by important morphological and phenological characteristics, such as but not limited to plant height, canopy spread, pod length, shape, number of leaves, and number of days to flowering, number of days to maturity, seed coat colour, and plant pigmentation. Cowpea exhibits significant variability for these traits across different genotypes, with leaf morphology variation and canopy spread particularly important for light interception, photosynthetic efficiency, and adaptability to varied ecological zones [27,28]. The overall agronomic performance and adaptability of cowpea are driven by these traits; for instance, early-maturing varieties are particularly useful in regions with short growing seasons or where drought is common [29]. Other phenotypic traits in cowpea include inherent resistance and tolerance to specific biotic stresses like pests and diseases, and abiotic stresses such as drought, heat, and low soil nutrient status. Comparative studies on different varieties of cowpea have confirmed the existence of significant tolerance and resistance to aphids and Striga [26]. Fusarium wilt, mosaic viruses, and Maruca pod borer [30]. This resilience makes it a suitable crop for cultivation in challenging environments where other crops may fail [17].

Inheritance Patterns of Phenotypic Traits in Cowpea

The inheritance patterns of various phenotypic traits in plant species are controlled by Mendelian principles, including dominance, segregations, and independent assortment. When gametes form, to ensure an independent inheritance of traits controlled by genes located on different chromosomes, there is a separation of dominant and recessive alleles [31]. It is pertinent in genetics to distinguish between quantitative and qualitative traits for a proper understanding of the inheritance of parental characters among offspring. One or a small number of genes control qualitative traits with a clear discontinuous variation, as found in seed coat and flower colours that are influenced by dominant and recessive alleles [32]. The quantitative traits, on the other hand, are polygenic in nature with continuous variation controlled by multiple genes that contribute a small additive effect individually [33,34]. All metric traits and those involving tolerance to biotic and abiotic factors are included in this class. Among these are plant height, seed weight, seed yield, disease resistance, and physiological traits [4,35]. The ultimate concept in quantitative genetics is the heritability of the quantitative traits. Heritability indicates the proportion of the total phenotypic variation of individuals in a population that is controlled by the genetic factor. Heritability is important to breeders because it helps to estimate the effectiveness of specific traits' selection in breeding programs [29,10].

Several studies on the inheritance patterns of phenotypic traits in cowpea have revealed findings with complex interpretations. Qualitative traits such as flower colour, leaf pigmentation, immature pod colour, seed coat colour, seed eye pattern, and colour have been reported to be governed by a single gene or a few genes in cowpea, following Mendelian patterns of segregation. Lachyan et al. [36] reported. that growth habit, flower colour, and seed coat patterns followed the Mendelian patterns of 3:1 while the seed coat colour showed a more complex segregation ratio with dominant epistasis (12:3:1). However, studies have shown that seed coat colour inheritance in cowpea may be of multigenic nature similar to those of the quantitative traits. [2,5,37] reported that the seed coat colour in cowpea followed that of the traditional interpretation of quantitative trait inheritance involving multiple genes, aligning with earlier findings by [38], who noted the complexity of seed coat pigmentation inheritance as a trait not yet fully understood. Recent advancements in genomics have facilitated mapping studies that identify specific loci associated with seed coat colour. For example, three loci, C (colour factor), W (Watson), and H (Holstein), have been linked to genes involved in the flavonoid biosynthesis pathway [39]. The seed coat traits in cowpea, such as seed coat patterns, colour, and texture, determine its consumer preferences and market values, with preferences varying across Africa. While the previous studies confirmed the Mendelian factors controlling the pigmentation patterns [37,39], recent QTL mapping in recombinant inbred lines (RILs) has revealed that the traits may be of polygenic control [40].

Many quantitative traits in cowpea and its crosses among contrasting parents have revealed various gene effects and magnitudes among individuals with additive, dominance, and epistasis playing cogent roles. Consistent contributions of additive, dominance, and epistatic gene actions in phenotypic variation for important traits have been observed in cowpea genotypes and their hybrid lines; consequently, providing valuable guidance for parental selection and breeding strategies aimed at yield improvement and adaptation based on hybrid performance, heterosis, and estimates of heritability [41- 43]. The following studies highlight how gene effects, heritability, and hybrid vigour influence key traits such as pod length, grain yield, plant architecture, and flowering behavior in cowpea improvement programs [44]. Investigated the gene effects for pod length and yield-related traits in crosses between two cowpea lines and yard-long bean. In one cross, F_1 pod length matched the mid-parent values, indicating an additive gene action, while they showed heterosis for the number of peduncles per plant and seeds per plant, exceeding that of the better parent. The second cross also displayed a similar partial dominance in the F_1 for pod length and the number of pods per plant, with the seed yield surpassing both parents' values. The data revealed predominantly additive gene effects for pod length, alongside dominant effects for yield components like the number of branches and number of pods, surpassing hybrid vigour in F_1 generations. These patterns suggest affective allele transfer for longer pods in F_1, ideal for initial selection in cowpea improvement.

In a study on heritability and expression of yield and related components in cowpea by [43], to identify promising parents. High broad-sense was observed for most traits measured, except pod width, with grain yield heritability ranging from 43% to 61%, indicating a moderate genetic control. Traits such as plant height, the number of days to flowering, and seed weight showed very high heritability up to 99%. Six hybrids outperformed their parents for grain yield, with certain parent combinations driving the vigour in F_1s. The study demonstrates that hybridization among diverse cowpea can unlock yield potential with high heritability traits, ensuring effective selection and hybrid breeding, offering a path to improved cultivars. The moderate heritability for grain yield observed in the study among the F_1s indicates that yield is influenced by both genetics and environments. Several F_1s showed heterosis in grain yield exceeding the parents' averages, while certain hybrids involving specific parental contributions consistently outperformed others, suggesting strong general combining ability.

Imposing reciprocal crosses among two cowpea genotypes [45] observed high heritability coupled with high genetic advance in traits such as seed yield, seed weight, and number of days to flowering, and pod length, indicating that these traits are controlled by additive genetic effects with less environmental effects, which make them reliable for direct selection. The number of leaves, leaf area, and plant height also displayed high heritability. Hence, exploring these traits as key selection criteria in breeding programs will provide a positive outcome. Since shorter growth cycles might reduce the risk of crop failure, early maturity among F_1 hybrids relative to parental lines can be investigated for targeted breeding in areas affected by moisture deficit. The significance of parental choice in hybridization programs is evident in the various impacts that reciprocal crosses have on hybrids. Heterosis and yield potential can be maximized by using genetically different parents. Cowpea has been reported to exhibit diverse responses to biotic stresses such as pests and diseases. Studies have identified several dominant genes responsible for resistance to aphids (*Aphis craccivora*) and cowpea aphid-borne mosaic virus (CABMV) in cowpea. However, some of the dominant genes reported to confer aphid resistance in cowpea have become ineffective against emerging populations of pests with time [46,47].

Specific genetic studies of parental lines and F1 hybrids

While these foundational principles govern phenotypic trait inheritance in cowpea, empirical studies using specific parental crosses and their F_1 hybrids provide deeper insights into dominance, maternal effects, heterosis, and epistasis, often revealing deviations from simple Mendelian expectations. Specific genetic studies of parental lines and F_1 hybrids, such as those examining seed coat colour and yield components, illustrate these dynamics in practice.

Inheritance of Seed Coat Color and other Qualitative Traits

Crosses among cowpea genotypes with white and brown seed coat colours revealed among the F_1 that brown and white seed coats were observed when the female parents were brown

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seeded and white seeded, respectively, suggesting that maternal influence is involved in the inheritance of seed coat colour of Ife Brown × IT-95K-193-12 populations, where the genotype of the mother determines the phenotype of the progenies [48]. However, this was in contrast to the findings of [6], which support some of the findings of [37] on maternal influence on the seed coat colour inheritance among F_1 cowpea hybrids. The findings of [48] emphasize the importance of maternal influence in determining the seed coat colour in F_1 generations, and therefore, using varieties with preferred seed coat colour as female parents in crosses will significantly improve the market values of the progeny, as supported by the findings of [49] in green gram vs. black gram.

Maternal effects on cross ability were emphasized by [5] in their study investigating the inheritance of seed coat colours and cross ability in F_1 cowpea hybrids. Even though cross ability among accessions was highly influenced by maternal effects, they did not influence the inheritance of seed coat colour. All F_1 hybrids exhibited black seed coat colour regardless of the direction of crossing (for both direct and reciprocal). Black seed coat colour was dominant over brown, suggesting heterosis and epistasis aligning with the findings of [50]. Here, brown-seeded plant × green-seeded plant produced F_1s that were black, a phenotype not matching either parent, indicating that black seed coat colour is dominant and that two interacting genes condition seed coat colour expression in the F_1 population. Similarly, as reported by [51], crosses black × white, brown × white, and brown × black all produced F_1 seeds that uniformly expressed the dominant parental colour class: black over white, brown over white, and black over brown. However, F_1 seed coat colours often differed from simple dominance expectations in the findings of [37] involving the inheritance of seed coat colour in cowpea, indicating a complex inheritance for several parental combinations. First, black eye was dominant over solid white; solid brown × white with black eye produced F_1s with solid black coat, not matching either parent, suggesting interaction of brown and eye-colour genes to produce enhanced pigmentation. Second, solid white × solid brown individuals produced F_1s that were solid black, implying epistasis or quantitative effects rather than simple brown dominance over white. Third, solid white × solid brown produced solid black F_{1S}, and black eye × dark mottled produced black F_1, consistent with the strong dominance of black pigment derived from black eye over the mottled pattern.

Beyond seed coat colour inheritance in cowpea, several researchers have also highlighted the importance of maternal influence on the inheritance of several phenotypic traits among cowpea F_1 hybrids and other closely related legumes [49,52,53]. In a study by [52], cowpea hybrid lines were evaluated by reciprocal crosses among wild accessions and cultivated varieties. Phenotypic traits such as pod colour and seed coat texture were strongly influenced by maternal effects among the F_1 hybrids, although other vegetative and reproductive traits showed strong wild-parent dominance [53]. Evaluated F_1 hybrids derived from reciprocal crosses between two cowpeas with contrasting traits: one (kidney-shaped mottled red seeds, curved pod, photoperiod sensitive, purple flowers, and large seeds) and the other (rhomboid seeds, straight pods, photoperiod neutral, white flowers, and small seeds) cowpea. F_1 phenotypes showed strong maternal effects for seed coat colour, seed and pod shapes, and photoperiod sensitivity, while flower colour exhibited purple dominance regardless of the direction of cross, indicating dominant monogenic inheritance.

Confirming the monogenic control of seed coat and flower colour traits in cowpea, [36] examined the inheritance patterns for flower, seed coat colour, and growth patterns. All F_1 hybrids showed dominant traits for erect growth pattern, light violet standard and violet wing flower colours, brown seed coat, and Watson seed coat patterns. All traits followed monogenic dominance inheritance patterns, and no maternal influence was detected on the inheritance patterns of the traits among the F_1 hybrids. This lack of maternal effects makes cowpea breeding more direct, reliable, and efficient, allowing breeders to focus on genetic recombination and selection rather than maternal inheritance complexities. Similar findings were reported by [50] while investigating the genetics of seed-related attributes in cowpea crosses. The F_1 plants consistently showed dominance effects for all the seed and pod-related traits. In all three F_1 crosses evaluated, plants produced violet flowers, matching the violet-flowered parent and not the white-flowered parent, indicating that violet flower colour is controlled by a single dominant gene over white in F_1. In all crosses, F_1 seeds were uniformly smooth, making the smooth dominant over the rough trait. Red pod beak and red calyx pigmentation were also dominant over green colour. Black pods showed dominance over red while yellow pods showed dominance over black pods at maturity among F_{1S}, indicating epistasis interaction.

Similar patterns of inheritance were reported for leaf shape, pod shape, and colour in cowpea F_1 hybrids [51]. All F_1 plants showed clear dominance of specific traits, confirming simple inheritance patterns. Leaf shape was lanceolate among F_1 hybrids, indicating that lanceolate leaf shape is controlled by a single dominant gene over ovoid in the F_1. Crosses between a straight podded parent and a coiled-podded parent also produced F_1 plants that were all coiled, indicating coiled pod shape is therefore dominant over straight in F_1. Purple pods were also dominant over brown. In a similar vein, most F_1 combinations showed mostly the characteristics of the wild parent for growth pattern and habit, leaf traits, flower and pod colour, indicating the dominance of the wild type characteristics.

These findings have several implications for breeding cowpea, especially for market value traits. The dominant traits expressed consistently, such as black seed coat colour over brown and white seed coat, violet over white flower colour, smooth over rough seed texture, and coiled over straight pod shape, indicate that simple dominant genes control the expression of phenotypic traits in cowpea. Hence, selection in early generations is simplified

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because desirable dominant genes can be fixed rapidly through hybridization and selection. However, crosses controlled by maternal effects, especially in seed coat colour and expression of pod traits, indicate that expression of traits may be influenced by hybridization direction among F_1 hybrids, and should therefore be a consideration for selection of parental lines. Therefore, breeders should prioritize using the preferred genotypes as maternal parents in cases where maternal influence has been demonstrated if the objective of the breeder is to develop varieties expressing a specific market-preferred seed coat colour. Additionally, expression of heterosis and epistasis observed in some instances points to the importance of screening segregating generations to fully understand gene interaction stabilizing lines.

Inheritance of Disease and Pest Resistance

The inheritance of brown blotch disease resistance in cowpea F_1s was governed by maternal influence, with 100% resistance expressed only when the resistant parent served as the female. However, in crosses in the other direction, resistance was observed in 35 individuals against susceptibility, which was 45 these results imply that using resistant varieties as female parents during hybridization significantly improves disease resistance in the progeny. In a similar study exploring interspecific hybridization between Mungbean (*Vigna radiata*) and black gram (*Vigna mungo*) for Mungbean Yellow Mosaic Virus (MYMV) resistance and broaden variability, [49] observed that all F_1 plants were free from MYMV infection, which suggests that the resistance trait from V. mungo was expressed in the heterozygous state consistent with dominant inheritance. However, sterility in most F_1s complicates the interpretation of results, as sterility from wide crosses can be a result of chromosomal incompatibility and not necessarily gene dominance. F_1 plants also showed mixed trait expression, especially in leaf shape from green gram, seed coat colour from black gram, suggesting maternal influence on leaf shape as well as determining whether viable hybrids would emerge.

Flower bud thrips (*Megalurothrips sjostedti* Trybom) is a pest of many legumes with a complicated management strategy. The inadequacy of several cultural practices recommended to manage its infestation has refocused research on exploring genetic diversity for resistance mechanisms existing in some cowpea genotypes [54], two crosses were evaluated in cowpea to explore the resistance trait for flower thrips in the genotype Sanzi (resistant) against the susceptible Lori and VYA cowpea genotypes. F_1 plants displayed nearly identical levels of resistance to that of the resistant parent and intermediate between resistant and susceptible parents for thrips damage scores. The number of thrips per flower was also lower among F_1s compared to susceptible parents, but slightly higher than the resistant parent, indicating a partial dominance for thrips resistance traits among the F_1 hybrids. These results present several implications for breeding. First, the close to resistant parents' resistance levels showed by the F_1 plants, especially in thrips damage scores, although not totally additive, but more of dominance and epistasis, can be exploited by breeders in the later generations when resistance has stabilized. Second, heterosis for yield traits linked to resistance can be exploited by breeders for yield advantage.

In the cases where maternal influence governs the expression of disease and pest resistance, the breeding implications of these imply that resistance should be introgressed, prioritizing the use of the resistant genotypes as female parents, because the likelihood of transmitting the effective resistance would be maximized in this direction. Definitely, resistance can be incorporated rapidly into breeding lines through breeding, taking into cognizance of the dominant expression of resistance observed among the interspecific hybrids, bearing in mind that the sterility barriers accompanying wide crosses need careful management strategies. Commencement of selection for thrips-resistant phenotypes is recommended to be done in the early segregating generations, for the partial dominance of thrips resistance observed in F_1s. Additionally, the strong expression of resistance exhibited by the F_1 hybrids provides opportunities for the exploitation of heterosis in cases where resistance and superior agronomic performance are genetically linked, leading to a simultaneous broadening of the genetic base and improvement of resistance stability.

Inheritance of Phenology Traits

Phenology traits such as the number of days to flowering and maturity are crucial in breeding programs of cowpea as one of the traits to be considered in parental choice, especially when breeding for drought tolerance. In a tester × lines cross in cowpea employing four cross combinations [55], most F_1 hybrids were observed to flower slightly later than the tester parent, but all flowered earlier than line parents, indicating heterosis for flowering. Similarly, [56] observed early maturity among F_1 hybrids compared to parental lines in a line × tester design study for heterosis in cowpea. However, [49] observed dominance of the maternal parent for days to flowering and an intermediate value for days to maturity among the F_1 population. Negative heterosis observed among F_1s of reciprocal crosses in a full diallel scheme for earlier flowering and maturity indicates the superiority of the hybrids for earliness [57]. This earliness was also found to be controlled by maternal effects. Consequently, these consistent heterosis for early flowering and maturity among F_1 hybrids, together with the involvement of maternal effects, indicate that these hybrids can be strategically exploited by breeders for their vigour and maternal parent selection for developing early maturing varieties. It is impossible to overstate the benefits and significance of early flowering and maturity in drought-prone areas or short-season environments for cowpeas and other crops because they enable plants to finish their life cycle before experiencing extreme stress. Hence, prioritizing the adoption of earlier-flowering genotypes as maternal parents in crossing schemes with aiming hybrids displaying negative heterosis for phenological features may speed the progress toward generating drought-tolerant, early-maturing

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cowpea cultivars.

Inheritance of Yield-Component and Yield Traits

The knowledge regarding genetic variability and the inheritance of morphological, yield-component, and yield traits in cowpea is crucial to the improvement of the crop through hybridization [6,55]. Highlighted the importance of yield components of cowpea, such as the pod length, the number of seeds per pod, seed weight, and the seed yield per plant, to its productivity. In their F_1 hybrids generated through tester × line crosses, all F_1 hybrids were observed to show longer pods, compared to their line and tester. F_1s produced more seeds per pod consistently than their parental lines, and showed intermediate values for seed weight between parents, outperforming parents in seed yield. In a study for unravelling heterosis and combining ability for improving yield and its component traits in cowpea [56], generating 24 F_1 crosses using 3 lines × 8 testers, and by evaluating them with 11 parents and a standard check, three F1s showed strong specific combining ability (SCA) effects for yield traits. Five showed standard heterosis for seed yield, ranging from 63.54 to 26.68%, with three exhibiting superior performance for SCA effects in yield components such as the number of pods per plant (19.60), number of clusters per plant (3.15), number of seeds per pod (1.3), and pod length (1.69). These superior performances indicate that F_1 hybrids demonstrated heterosis in most traits examined, confirming the effectiveness of line × tester design in cowpea improvement.

Similarly, [54] observed a higher number of pods per plant and higher pod weight among F_1 hybrid cowpea compared to the mid-parent values and the values for both parents, suggesting overdominance in yield traits. These values observed for the components of yield among the F_1 hybrids exceeding the mid-parent's values indicate heterosis that could be explored by breeders for yield improvement. In a similar scenario, [34] observed heterosis among F_1hybrid cowpea for yield component traits such as the number of pods per plant, and seed weight that was superior to parental lines or one of the parents, but showed intermediate response for pod length, number of seeds per pod, indicating a potential for selection. These results are in accordance with many findings [49,53,56]. where F_1s exhibited an intermediate expression of many yield and yield component traits.

In the study of the inheritance of pod length and other yield components in cowpea and yard-long bean crosses [42] involving cowpea lines TVu2280 or TVu2027 and yard-long bean TVu6642 (long pods) under field conditions. The crosses TVu2280 × yard-long produced F1s with pod length (25.20 cm) close to the mid-parents (27.40 cm), indicating an additive gene, with heterosis for peduncle per plant (39.60 vs. 29.30 max parent), seed weight (2.00 g superior), and seed yield (84.70 g, 69 – 130% better parent heterosis). On the other hand, TVu2027 × yard-long bean F_1s exhibited dominance toward TVu6642 for pod length, pod weight, and heterosis for the number of pods per plant, and seed yield per plant. The F_1 heterosis for yield traits supports the use of these hybrids for introgression long-pod genes for enhancing cowpea yield. Reciprocal crosses of [57] produced F_1 hybrids that consistently outperformed the parental lines across multiple traits, especially pod yield, number of branches, and protein content.

The consistent expression of heterosis for yield and important yield component traits in F_1 cowpea hybrids shows that hybridization is an effective strategy for yield improvement. The frequent experience of better-parent and standard heterosis, along with SCA effects, indicates that non-additive gene action (dominance and overdominance) plays an important role in the inheritance of many yield traits. Breeders can identify superior cross combinations by strategically selecting parents and using line-by-line testing. However, the finding of intermediate expression for several traits emphasizes the importance of additive gene effects, which supports the prospect of obtaining genetic improvements through selection in subsequent segregating generations. The successful introgression of long-pod and desirable features from varied parents emphasizes the importance of expanding the genetic base with exotic or specialized germplasm.

Overall, existing data support the continued use of hybridization, combining ability analysis, and heterosis breeding as key techniques in cowpea improvement projects aimed at yield increase and trait introgression.

Inheritance of Drought Tolerance

Despite the importance of cowpea and related legumes in tropical and subtropical regions, drought poses a significant threat that limits their productivity, which can sometimes result in complete crop failure [4]. Although adopting an irrigation option exists that can be explored to mitigate the effect of drought on crop productivity, this is expensive to deploy [23], and the most cost-effective option is to develop tolerant genotypes. Hence, developing drought-tolerant high-yielding genotypes of cowpea and other legumes is crucial for sustainable agricultural productivity. Heterosis breeding is one way in which balanced gene combinations that are useful in agriculture for their resilience and adaptability to varied environmental conditions can be obtained in crop species [58,59]. Achieving heterosis requires crosses between genetically distinct individuals to develop F_1 hybrids that exhibit enhanced or decreased vigour compared to their parental lines. Cowpea, being a self-pollinating crop, requires heterosis breeding as the most appropriate way of obtaining genetic variability in legumes. Heterosis breeding has been explored in different crop species to develop hybrids with enhanced productivity and resilience, especially in regions prone to moisture deficit [60].

Exploitation of heterosis for drought tolerance in snake bean

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(*Vigna unguiculata* subsp Sesquipedalis) crosses for identifying suitable parents and crosses for developing drought-tolerant, high-yielding varieties revealed several interesting findings among F_1 hybrids and their parental lines [58]. Several F_1 hybrids were identified with significant heterosis for drought tolerance and yield traits. Out of 21 F_1 hybrids of snake bean, 18 showed significant positive average heterosis for yield, 9 showed significant standard heterosis, and 12 demonstrated positive and significant heterobeltiosis for yield under drought stress. [61] evaluated cowpea varieties and hybrids for drought tolerance and the vegetative and reproductive phases. The tolerant parents generally maintained higher chlorophyll and proline content under stress, while the sensitive parents showed reduced yield and chlorophyll content. Similar to tolerant parents, three F_1 hybrids displayed improved photosynthetic efficiency and chlorophyll stability compared to the sensitive parents. Two hybrids were similar to the sensitive parents with weaker physiological responses. Two hybrids outperformed the sensitive parents for seed yield and seed weight, implying heterosis, while two also showed poor yield performances similar to the sensitive parents under stress. Two hybrids delayed flowering and maturity, resembling tolerant parents, while others matured quickly like the sensitive parents.

These findings showcase the importance of heterosis breeding as a practical approach for developing drought-tolerant, high-yielding cowpea and related legume crops. An indication that a sufficient genetic diversity exists among the parental lines useful for effective hybrid development was displayed as the consistent expression of positive heterosis for yield and important physiological traits across several F_1 hybrids. A careful parental selection that is based on complementary traits is recommended rather than yield alone, because of the contrasting responses among hybrids for important traits. Physiological parameters such as chlorophyll content, accumulation of proline, and delayed phenology under stress were shown to be useful secondary selection criteria for drought tolerance and should be incorporated into breeding programs alongside agronomic traits. Overall, exploiting heterosis combined with physiological parameters in multiple environment evaluations provides a strong direction to speed up genetic gains for drought tolerance, with improvement of yield potential in cowpea and related legumes.

Molecular Markers and QTL Mapping for Phenotypic Trait Inheritance in Cowpea

In this procedure, molecular markers such as Single Nucleotide Polymorphisms (SNPs) and Simple Sequence Repeats (SSRs), sometimes referred to as microsatellites and characterized by repeating DNA sequences consisting of two to six base pairs, are indispensable. They are great markers for genetic research because they are widely distributed throughout the genome and highly polymorphic. Conversely, single-base pair changes in the DNA sequence that arise at particular locations in the genome are known as SNPs. By detecting genetic differences associated with particular phenotypes, these markers aid in tracking gene inheritance in F_1 hybrids [62]. For instance, in a study on cowpea, in which SSR markers were deployed to create a genetic linkage map, the identification of quantitative trait loci (QTL) linked to significant agronomic traits was made easier [63]. Particularly in crops like cowpea, QTL mapping is an effective method for locating genetic areas linked to phenotypic features. In order to help breeders comprehend the genetic architecture of complex qualities like yield and stress tolerance, QTL mapping uses statistical analysis to associate genetic markers with observable traits [63].

Similar to this, QTL studies have pinpointed regions for drought tolerance (e.g., seedling QTLs via restriction site polymorphisms), root-knot nematode resistance (major QTL at Rk locus), and Fusarium wilt. These support F_1 hybrid selection for agronomic traits [64]. Similarly, the identification of genomic regions linked to drought tolerance in cowpea has been made possible by Genome-Wide Association Study (GWAS) mapping. For instance, a GWAS for drought tolerance in cowpea seedlings was carried out by [65], who found the SNP markers and potential genes for drought tolerance. Marker-Assisted Selection (MAS) is a technique that allows breeders to select for specific traits in F_1 hybrids by using molecular markers linked to desirable alleles. MAS accelerates the breeding process by enabling the early identification of hybrids with superior genetic potential. This method reduces the time and resources needed for traditional breeding by focusing on plants that carry the desired genetic markers, thus improving the efficiency and effectiveness of breeding programs. According to [66], MAS has revolutionized plant breeding by significantly shortening the time required to develop new crop varieties, especially for enhanced yield, stress tolerance, and disease resistance [67]. Also highlight the importance of MAS in modern plant breeding, emphasizing its potential to combine beneficial genes from diverse backgrounds without genetic drag from poor donor individuals. Although pinpointing several challenges, combining MAS with genomics enables efficient and cost-effective transfer of useful alleles into elite genotypes for improved resilience and yield.

For important characteristics like stress tolerance and disease resistance, MAS supports cowpea breeding initiatives. Prior research by [68] created sequence characterized amplified regions (SCARs) markers from amplified fragment length polymorphism (AFLP) loci for Striga resistance, a parasitic weed that causes significant yield losses. This allowed for early selection of resistant F_1 plants and accelerated variety development, as reviewed in [17]. In a similar vein, MAS has enabled seedling-stage selection to expedite breeding by facilitating bacterial blight resistance by marker introgression into elite lines like C-152 using linked SNPs. Although integration with genomic selection is becoming more popular for complicated yield variables, these applications show the effectiveness of MAS in cowpea.Building on the efficiency of MAS for traits like Striga and bacterial blight resistance, accurate hybrid production is equally critical in cowpea breeding to maximize genetic gains from crosses. Cowpea is a self-pollinated

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crop, just like many legume crops, making hybridization difficult because flowers naturally avoid outcrossing. Manual crossing often results in low success rates (10–20%) due to flower abscission and escapes (self-pollinated plants instead of true hybrids). Without early detection, false F_1 plants waste time and resources in breeding programs.

Ensuring true hybridity and genetic diversity among parents is critical for effective cultivar development. Without any quick detection technique, these escapes would not be easily detectable, constituting potential wasted time and resources that would be carried forward in the breeding program [62,69].

Quality control (QC) in breeding programs is essential to eliminate false hybrids early and optimize genetic gain. Molecular tools like SNP markers, kompetitive allele specific PCR (KASP) assays, and SSR provide reliable, high-throughput, and cost-effective methods for parental fingerprinting, hybridity authentication, and early detection of selfed plants. Efficient and optimized breeding programs include routine QC to eliminate the false F_1 plants early enough to make the most impact with the resources available [6269]. In this context, [61] studied the genetic relationships among cowpea parental lines and determined the hybridity of resultant putative F_1 progenies for further advancement in the program using a KASP-based SNP assay. The study confirmed parental diversity and authenticated the hybridity of F_1, demonstrating that KASP-based SNP assays are highly effective for molecular fingerprinting and hybridity authentication in cowpea breeding programs. Similar studies in chickpea using SSR markers confirmed true hybrids and separated them from impure plants, making SSRs superior to both biochemical and morphological markers, and offering clear, reproducible DNA fingerprints for purity testing and hybrid identification [69].

Conclusively, understanding the inheritance patterns of phenotypic traits in F_1 cowpea hybrids is enhanced by tools that combine QTL mapping with molecular markers. These tools facilitate the detection of genomic regions driving critical traits in cowpea, such as grain yield, drought tolerance, and disease resistance, helping breeders to accelerate breeding schemes. MAS further accelerates breeding, saving time and resources in contrast to conventional techniques. By ensuring hybridity authentication and removing fake hybrids, QC techniques like SSR fingerprinting and KASP assays maximize genetic gains. When molecular markers, QTL mapping, and MAS are combined, cowpea breeding programs are strengthened, and cultivar development is more resilient and efficient.

Challenges in Studying the Inheritance of Phenotypic Traits in F_1 Cowpea

There are few direct discussions of the difficulty in deciphering inheritance patterns in F_1 cowpea hybrids, but several studies subtly point to significant obstacles related to genetic complexity, environmental impacts, and trait-specific gene action. When taken as a whole, these studies show that inheritance in the F_1 generation is frequently non-uniform, trait-dependent, and heavily impacted by non-additive genetic factors, rendering prediction based on parental performance unreliable. Several studies have demonstrated that mixed gene action-comprising additive, dominance, and epistatic effects-complicates the interpretation of F_1 inheritance. [70] reported trait-specific gene control in cowpea, with additive effects governing seed weight, dominance influencing sphericity, and combined effects affecting porosity and surface area. Moreover, the direction of dominance varied among traits, being negative for most but positive for surface area, further obscuring general conclusions. High broad-sense heritability coupled with low narrow-sense heritability in F_1 hybrids suggests a strong role of dominance and other non-additive effects, reducing the predictability of F_1 performance based on parental values. The occurrence of both positive and negative heterosis across traits reinforces the absence of a consistent inheritance pattern at the F_1 level.

Inheritance studies are further complicated by genotype × environment interactions (GEI) and environmental variables. According to [71], both additive (general combining ability, GCA) and non-additive (specific combining ability, SCA) gene effects were observed in cowpea under drought stress. In the study, traits such as plant height, chlorophyll and proline contents, and seed weight showed strong responses to stress, while yield-related traits were either weak or inconsistent. Notably, the inconsistencies in gene action and heritability estimates across varied stress levels significantly limit conclusions regarding inheritance patterns of traits.

Effective selection is further limited in F_1 populations by low genetic heterogeneity and considerable environmental influence. For the majority of characteristics in F_1 cowpea hybrids, [72] found usually low broad-sense heritability values (0.04–0.22), suggesting significant environmental masking of genetic influences. Similar findings by [73] noted that poor narrow-sense heritability prevents early selection and that non-additive gene action dominated in traits such as plant height, seed yield per plant, number of pods, and protein content. It was challenging to identify superior hybrids or draw consistent conclusions from F_1 data due to inconsistent expressions of heterosis and heterobeltiosis, as well as maternal effects seen in some crossings. Additional difficulties arise from complex inheritance patterns incorporating maternal influence and epistasis [5]. Reported the appearance of unexpected phenotypes, such as black seed coats in F_1 hybrids derived from non-black parents, indicating epistatic interactions among several loci, which show that cowpea seed coat colour does not always follow simple Mendelian inheritance. While seed coat colour showed a distinct inheritance pattern, maternal impacts were also shown to affect features like pod quantity, pod length, and maturation time. This inconsistency across traits further complicates F_1 interpretation.

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Traits influenced by post-harvest physiology and qualitative attributes also demonstrate complicated inheritance [74]. showed partial dominance and strong epistatic effects for storage-induced cooking time in cowpea, with F_1 means often intermediate between parental values. The F_1 generation's gene action was difficult to classify due to skewed trait distributions, deviations from normalcy, and considerable environmental sensitivity, suggesting that basic dominance–recessive models are inadequate. Population structure adds another level of complexity at a larger genetic level. According to [75], cowpea subpopulations with various origins exhibit significant genetic differentiation. Because of population stratification, linkage between loci, and the underrepresentation of uncommon alleles in genotyping investigations, crosses between genetically distant populations may show unexpected segregation patterns. Both genetic background and environment have an impact on traits, including flowering time, drought tolerance, and pigmentation, which frequently lead to intermediate or highly variable F_1 phenotypes that differ from traditional predictions.

Based on many studies, it is generally noted that the patterns of inheritance among F_1 cowpea hybrids are influenced by a combination of factors such as non-additive gene effect, epistasis, maternal effects, environmental variations, and population structure. Thus, for a liable selection or genetic interpretation, a breeding program must not rely solely on the performance of F_1. The evaluation of hybrids must be done across segregating generations like F_2 and F_3, since recombination can both clarify additive gene effects as well as impose stability of phenotypic traits. Therefore, breeding strategies must be trait-specific; direct selection should be imposed on additive traits, dominance-controlled traits must employ recurrent selection, and hybrid exploitation should be preferred in the case of stable heterosis. Also, multi-environment testing must be incorporated to ensure long-term genetic stability and improvement. An additional challenge is limited resources, leading to releases of improved cowpea varieties with variable yield stability [76]. Recent studies have advanced understanding of qualitative traits (pigmentation, flower colour, disease resistance) and quantitative traits (protein content, seed yield), yet funding shortages in cowpea-growing regions hinder extensive genetic research like inheritance patterns and mapping [2,29].

Future Directions in Cowpea Inheritance Studies

Cowpea genetic research is nevertheless hampered by persistent resource constraints, especially when it comes to investigations of phenotypic trait inheritance. Several focused tactics can be used to increase effectiveness while upholding scientific rigor in order to overcome these obstacles. Using already-existing germplasm collections, like the IITA cowpea core collection, which offers a variety of parental lines at little cost, is one successful strategy. Researchers can concentrate on traits with high heritability, such as seed coat colour and pod length, by focusing F_1 hybrid evaluations on a small number of crosses, usually four to six, thereby ensuring relevant results with little resources. As evidenced by recent genome-wide association studies (GWAS), collaborative networks with regional programs like the African Agricultural Technology Foundation (AATF) and the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) further improve efficiency by allowing joint field trials and access to genotyping-by-sequencing at lower rates [77]. Furthermore, putting phenotypic screening ahead of molecular analysis provides an economical route: F_1s can be produced by manual crosses, and basic Mendelian ratio tests, like Chi-square analyses, can be used to confirm maternal effects and dominance before investing in molecular markers.

Funding and infrastructure solutions are equally critical. Small-scale grants from initiatives such as Consultative Group on International Agricultural Research (CGIAR) challenge funds or national adaptation programs, including Nigeria's Agricultural Growth and Gender Integration Resource project (AGGIR) project, can provide budgets in the range of $50,000 to $100,000, sufficient to support two-year F_1 studies focused on drought tolerance and yield stability [78]. Citizen science and student-led projects also represent valuable contributions, with students trained in diallel crossing techniques using campus fields and data aggregated across institutions to enable meta-analyses of heterosis patterns [79,80]. The adoption of open-access computational tools, such as R packages for heritability estimation and mobile applications for trait scoring, further reduces costs by eliminating reliance on proprietary software [71].

A structured implementation timeline ensures that these strategies yield timely results. In the first three months, parental selection and F_1 crosses can generate over one hundred hybrids. This is followed by six months of field evaluation and segregation ratio testing, producing robust datasets on inheritance patterns. In order to produce reliable data, the last three months are devoted to statistical analysis and report preparation. When taken as a whole, this method offers a workable framework for generating dependable F_1 inheritance data within a year, even with limited funding, which advances our knowledge of cowpea genetics and aids in crop improvement initiatives. For newly developed genetic methods, these phenotypic datasets offer crucial validation targets. While CRISPR/Cas9 [81] provides functional testing of dominance/maternal effects found in field trials, the cowpea reference genome [82] allows accurate mapping of F_1 inheritance sites. Under budget limitations, this two-tiered strategy-low-cost phenotyping followed by targeted genomics-maximizes the impact of research.

Conclusion

The role of hybridization in expanding the narrow genetic base of cowpea and harnessing heterosis among F_1 hybrids for enhanced yield, stress tolerance, and market-valued traits, determined by dominance, maternal effects, epistasis, and additive gene actions, cannot be overemphasized. Specific trait

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selection and hybrid development for mitigating biotic and abiotic constraints have now been improved through molecular markers, QTL mapping, and MAS, thereby enhancing productivity in tropical agroecologies.

Ensuring further acceleration of breeding of resilient cowpea cultivars for sustained contribution to food security, nutrition, and livelihoods in resource-limited regions requires tactical parental selection, multi-environment validation, genomic selection, and integration of wild germplasm.

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