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REVIEW ARTICLE

A comprehensive review on role of recessive alleles in the genetic improvement of plantation crops

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Abstract

Recessive alleles play a significant role in the genetic improvement of plantation crops such as examples: oilseed (coconut, oil palm), beverage (coffee, tea, cocoa), nut (arecanut), etc. These alleles contribute to agronomically important including disease resistance, stress tolerance, yield enhancement and quality improvement. Unlike dominant alleles, recessive traits require a homozygous state for expression, making their deployment in breeding programs more challenging, yet often rewarding due to their unique genetic advantages. Recent advancements in marker-assisted selection (MAS), genomic sequencing and genome editing (CRISPR-Cas9) have facilitated the identification and application of beneficial recessive alleles in crop breeding. Examples include low-caffeine coffee, coconut varieties enriched in lauric acid and high-yield oil palms. Additionally, recessive mutations contribute to pathogen resistance (e.g., lethal yellowing in coconut, leaf rust in coffee and *Phytophthora* resistance in cocoa). Despite their benefits, challenges such as low allele frequency, inbreeding depression and linkage with undesirable traits require strategic breeding approaches. Advances in genomics and biotechnological tools are accelerating the deployment of recessive alleles in commercial cultivars, ensuring sustainable and climate-resilient crop production. This review underscores the pivotal role of recessive alleles in plantation crop breeding and emphasizes the transformative potential of modern genomics and biotechnology to harness these traits for sustainable agriculture.

Keywords: disease resistance; genome editing; marker-assisted selection; pink pigmentation; recessive alleles; stress tolerance

Introduction

In plant genetics, alleles are different versions of a gene that influence traits such as flower color, seed shape and disease resistance. Recessive alleles express their associated traits only in homozygous condition, where both gene copies are recessive. This concept was first systematically studied by Mendel in the 19th century, leading to the foundation of modern genetics (1). Understanding recessive alleles is crucial for plant breeding, as they often carry hidden traits that can be advantageous in specific environmental conditions or agricultural settings (2). In particular, recessive alleles are of great importance in breeding programs targeting genetic improvement of plantation crops. In plant breeding, including marker assisted selection and genome sequencing have allowed to identify and utilize beneficial recessive alleles for crop improvement. Genome editing, particularly through CRISPR/Cas9 technology, has emerged as a transformative tool in the improvement of plantation crops. Traditional breeding methods often fall short due to the long generation times and complex genetics of these species. Genome editing offers precise, efficient and rapid alternatives to address these challenges (3). Recessive alleles in coconut contribute to dwarfism and compact growth forms, which enhance harvest efficiency by facilitating earlier flowering and easier management of plantations. These alleles also play a role in conferring disease resistance, providing natural protection against fungal, bacterial and viral pathogens (4). Genetic traits related to drought and salinity tolerance improve water-use efficiency and survival in challenging environments by modulating various stress response pathways. Additionally, breeding efforts in related crops like oil palm focus on increasing oil yield, while in tea, enhancement of alkaloid content improves product quality and health benefits (5). For instance studies on pink husk coloration in coconut using SSR markers suggest that such phenotypic traits may recessive inheritance, although molecular evidence is still evolving (6). This review explores the multifaceted role of recessive alleles across a range of plantation crops and highlights how modern genetic tools are transforming their identification and use in crop improvement.

Scope of recessive alleles in the genetic improvement of plantation crops

Recessive alleles contribute essential traits like disease resistance, stress tolerance, yield enhancement and quality improvement in plantation crops, making them valuable for developing robust and high-yielding varieties. This genetic potential aids in sustainable and improved plantation crop production. Recessive alleles in the genetic improvement of plantation crops are listed in Fig. 1.

Role of recessive alleles in plantation crops

Coffee

Recessive alleles play a significant role in improving various important traits in plantation crops, particularly in coffee. These alleles contribute broadly to disease resistance, cup quality and flavor, caffeine content, abiotic stress tolerance and the development of hybrid varieties (7).

In terms of disease resistance, recessive alleles have been linked to enhanced resilience against major fungal pathogens such as coffee leaf rust (CLR), caused by *Hemileia vastatrix* and coffee berry disease (CBD), caused by *Colletotrichum kahawae* (8, 9). These alleles are utilized in breeding programs to develop cultivars that can better withstand these diseases, improving crop stability and yield (10).

Regarding cup quality and aroma, recessive alleles affect the biosynthesis of flavor-related compounds in *Coffea Arabica* (11). Notably, the *Sucrose Synthase* gene, under recessive inheritance, influences sugar content in coffee beans, enhancing desirable taste profiles (12). Additionally, recessive alleles govern caffeine content; for example, the recessive b allele is associated with reduced bitterness, facilitating the breeding of naturally low-caffeine coffee varieties with improved flavour (13).

Abiotic stress tolerance is another critical area impacted by recessive alleles. These alleles regulate traits such as water-use efficiency and root architecture, contributing to drought resistance (14). Recessive genes also provide cold tolerance, enabling coffee cultivation in high-altitude and diverse climatic conditions (11).

Finally, recessive alleles are pivotal in hybrid breeding programs. Controlled crosses incorporating these alleles have led to the development of notable hybrid varieties like *Catimor* and *Sarchimor*, which combine disease resistance with high yield and adaptability (15). This strategic use of recessive alleles enhances genetic diversity and supports sustainable coffee production (9). Main factors for using recessive alleles in plantation crops are represented in Table 1.

Tea

Cold tolerance

Cold tolerance in tea plants include osmoprotectant-related genes such as those involved in sugar signaling and proline

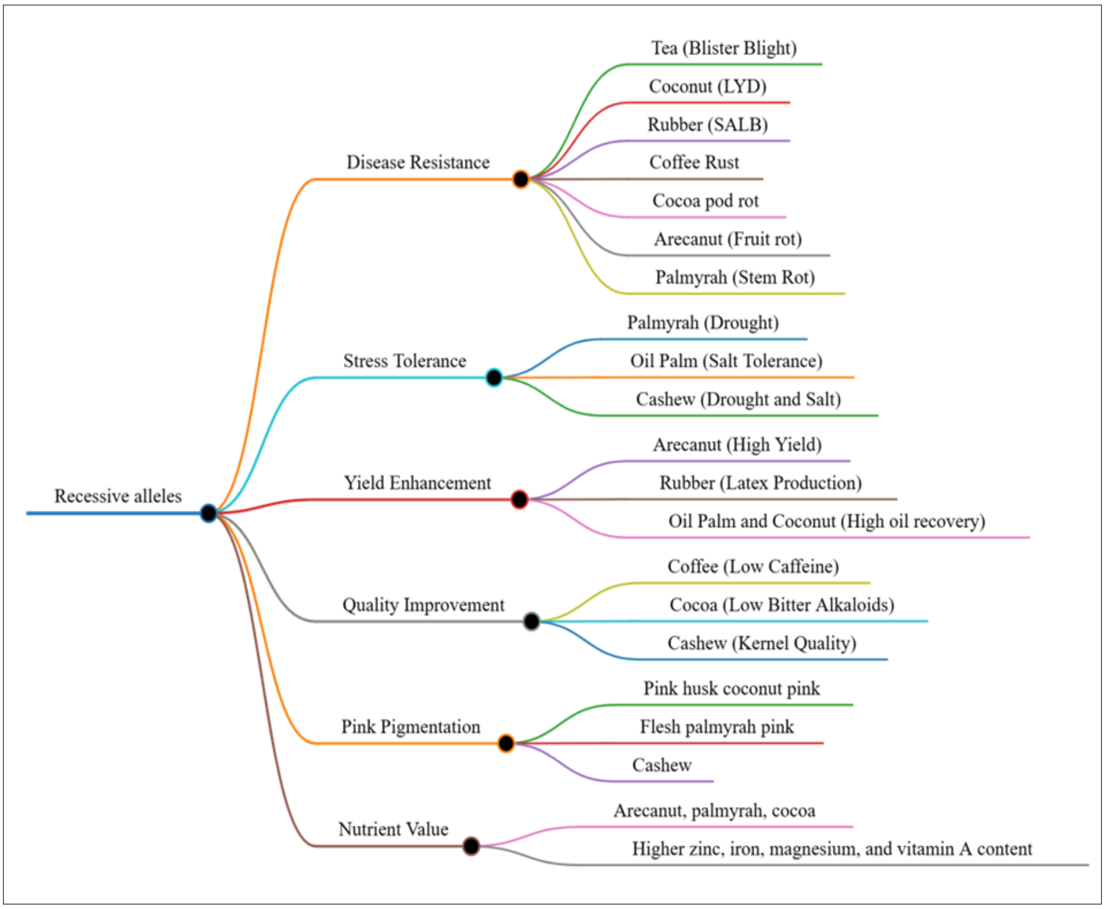

Fig. 1. Scope of recessive alleles in genetic improvement.

Table 1. Main factors for using recessive alleles in plantation crops

Factor	Importance	Example in Crops	Reference
Mode of Inheritance	Recessive traits show if two copies	Coconut yellowing resistance	(126)
Breeding Strategies	Needs careful molecular breeding or tools	Powdery mildew (rubber) Blister blight resistance (tea)	(127) (128)
Genetic Linkage	May link to undesirable traits	Disease resistance linked to low yield (cashew) Caffeine-free trait (coffee)	(129) (130)
Environmental Influence	Trait stability varies by environment	*Phytophthora* resistance (arecanut)	(131)
Genetic Diversity	Risk of losing diversity and increasing vulnerability	Wild coconut varieties used for resistance	(132)
Breeding Cost & Time	Takes longer than dominant allele breeding	Ganoderma resistance (oil palm)	(133)
Biotechnology Use	Genome editing speeds process	CRISPR-Cas9 (rubber) CRISPR-based disease resistance (cocoa)	(134) (135)

biosynthesis, including CsP5CS (pyrroline-5-carboxylate synthase), which enhance freezing resistance through osmotic regulation and sugar transport (16). Geographically, tea cultivation ranges in tropical to subtropical areas but cold stress limits tea growth especially at higher latitudes and elevations (17). Recessive alleles involved in osmoprotectant production help protect tea plants from frost damage (18). Breeding efforts aiming to enhance cold tolerance focus on leveraging these genetic variants, including recessive alleles, to produce cultivars capable of thriving in diverse elevations and geographies (19).

Recessive alleles significantly contribute to enhancing tea quality traits by influencing the production of key biochemical compounds responsible for aroma and flavor development. These alleles regulate the biosynthesis of catechins and theaflavins, which are essential polyphenols that define tea's astringency and health benefits (20). Additionally, they affect the synthesis of volatile aromatic compounds, such as monoterpenoids and sesquiterpenoids, that provide the distinctive fragrance in tea, particularly in oolong varieties. The modulation of these biochemical pathways by recessive alleles plays a critical role in shaping the overall sensory profile of tea (19).

In terms of taste, recessive genes help reduce bitterness by controlling the accumulation of caffeine and tannins (21). Caffeine interacts with bitter taste receptors, while tannins contribute to both bitterness and astringency (22). By regulating the levels of these compounds, recessive alleles enable the production of tea with a more balanced and pleasing flavour (23). This regulatory effect is important in developing tea cultivars that meet consumer preferences for milder bitterness without compromising health benefits (24).

Disease resistance

Regarding disease resistance, blister blight caused by the fungus *Exobasidium vexans* is one of the most devastating foliar diseases affecting tea plantations worldwide. Recessive alleles have been found to be linked with natural resistance mechanisms against blister blight, enabling some tea varieties to survive and maintain productivity under high disease pressure (25).

Root rot diseases, often caused by fungal pathogens such as *Phellinus noxius*, are another major threat to tea health and yield. Research has identified recessive genetic factors that contribute to tolerance against root rot, helping plants limit pathogen invasion and sustain growth in affected soils (26). These recessive alleles may affect the plant's immune response or root structure, thereby improving resilience (27). Integrating these genetic traits into breeding programs will be essential for developing high-quality, disease-resistant tea cultivars that can thrive in diver (28). Recessive alleles are essential in hybridization programs aimed at improving stress tolerance and quality traits in tea. For example, breeding programs in China and India have utilized recessive genetic variations to develop high-yielding and stress-resistant cultivars (29).

Cocoa

Disease resistance

Witches Broom Disease (WBD), caused by *Moniliophthora perniciosa*, reduces cocoa yield. Recessive alleles influencing hormonal pathways and lignin biosynthesis help suppress fungal colonization (29). WBD, caused by *M. perniciosa*, affects cocoa trees by inducing abnormal growth. Studies have identified recessive alleles associated with delayed symptom expression and enhanced tolerance (30). Black Pod Rot (*Phytophthora* spp.) is a major threat to cocoa. Some recessive mutations in defense-related genes enhance phenolic compound production, improving natural resistance (31). Recessive mutations in polyphenol biosynthesis genes increase resistance to *Phytophthora* spp. by enhancing natural antifungal compound production (32). The *Phytophthora* resistance gene in cocoa is controlled by a recessive allele. When plants inherit two copies of this recessive gene, they exhibit resistance to the devastating *Phytophthora* blight, which affects cocoa production worldwide (33).

Quality improvement (flavor and fat composition)

Recessive alleles can influence flavor, aroma and fat composition, which determine the quality of cocoa beans.

Flavor enhancement

Recessive alleles regulate the biosynthesis of volatile organic compounds (VOCs), leading to improved chocolate flavor (34).

Fat content and chocolate texture

The FAT gene, associated with cocoa butter composition, has recessive variants that alter the ratio of stearic, oleic and palmitic acids, influencing cocoa butter's melting properties (35). Low bitterness and astringency for recessive mutations in procyanidin biosynthesis genes reduce bitterness, improving flavor quality (36).

Dwarfing and high-yield varieties

Compact, high-yielding cocoa varieties are preferred for intensive cultivation.

Dwarf cocoa varieties

Recessive alleles control plant height, leading to shorter trees with increased pod production. These varieties improve harvesting efficiency and reduce vulnerability to wind damage (37). The dwarfing recessive allele (*dw*) reduces internode length, making trees compact (38).

Climate resilience (drought and heat tolerance)

With climate change affecting cocoa-growing regions, recessive alleles that enhance water-use efficiency and heat tolerance are valuable.

Drought resistance: Recessive mutations in stomatal regulation genes improve cocoa's ability to conserve water during dry periods. Recessive genes regulate stomatal conductance and deep root growth, enabling cocoa trees to survive prolonged drought (39).

Heat tolerance: Recessive alleles regulate the expression of heat shock proteins (HSPs), which help protect cocoa plants from extreme temperatures. Mutations in heat shock protein (HSP) genes allow cocoa plants to tolerate high temperatures without reduced bean quality (40). Heat tolerance in cocoa is associated with genes encoding heat shock proteins (HSP70) and heat shock transcription factors (HSFs), which protect cellular proteins from denaturation under high temperatures (41). Drought resilience involves genes regulating polyamine biosynthesis and reactive oxygen species (ROS) scavenging enzymes, enabling maintenance of photosynthesis and cellular integrity during water deficit (42).

Genetic variability in these traits includes recessive alleles that can modulate expression levels of stress-responsive genes, influencing tolerance (43). Physiological traits linked to drought tolerance, such as stomatal conductance and water use efficiency, correlate with specific allelic variants, including recessive ones exhibiting improved resilience. The integration of genotype-by-trait analysis facilitates selecting cocoa genotypes harboring recessive alleles that confer superior heat and drought tolerance (44).

Marker-assisted selection

Molecular markers facilitate the identification of recessive alleles, allowing breeders to select for high-yielding varieties more efficiently (45). The integration of SNP markers in breeding programs has shown promise in enhancing cacao yield through the selection of favorable alleles (46).

Oil palm

Shell thickness, yield and oil quality enhancement

Oil palm fruit types are determined by the SHELL gene, which controls shell thickness and oil content. There are three types:

1. Dura: Thick shell, lower oil content, dominant genotype (ShSh or ShSh*).
2. Tenera: Thin shell, higher oil content, heterozygous genotype (Shsh).
3. Pisifera: Shell-less and usually sterile, homozygous recessive genotype (shsh).

The recessive allele (sh) reduces shell thickness, leading to a 30-50 % increase in oil yield in the tenera type (47). Recessive alleles influence fatty acid composition, affecting the nutritional and industrial value of palm oil. High oleic acid mutants through recessive mutations modify fatty acid desaturase (FAD2) genes, leading to high oleic acid content in palm oil, making it healthier and more stable (48).

Disease resistance

Recessive alleles contribute to resistance against lethal diseases affecting oil palm plantations. Fusarium wilt, caused by *Fusarium oxysporum*, affects oil palm yield. Recessive genes linked to pathogen recognition and immune response provide partial resistance (49). Basal Stem Rot (BSR), caused by *Ganoderma boninense*. Recessive alleles provide natural resistance to this disease. BSR-Resistant Varieties recessive genes linked to lignin biosynthesis, which strengthen cell walls and prevent fungal invasion (50).

Drought and stress tolerance

Recessive alleles help oil palm adapt to drought and heat stress, crucial for climate resilience. Water-use efficiency in certain mutations in stomatal regulation genes improve drought tolerance by reducing water loss. Recessive mutations in heat shock protein genes (HSPs) enable oil palm trees to withstand high temperatures without reduced oil quality (51).

Compact growth and high-density planting

Recessive alleles contribute to dwarf and slow-growing oil palm varieties, improving harvesting efficiency. Short-Statured oil palm contains recessive mutations in growth-regulating genes reduce tree height while maintaining high yield. Dwarf oil palm (dp gene), the dp recessive allele leads to shorter palm trees, making harvesting more efficient and reducing labor costs (52). Recessive mutations in GA biosynthesis genes reduce tree height, leading to shorter and more manageable palms (53).

Coconut

Pigmentation

Studies on guam tall coconut revealed no morphological differences between pink-husked and normal husked types, but biochemical analysis showed that pink-husked coconuts have significantly higher total phenol content in their tender nut water. The anthocyanin content in the exocarp of pink-husked coconuts was notably elevated at 25.97 mg per 100 g fresh weight, whereas it was negligible in normal husked types, explaining their distinctive pink coloration. Furthermore, tender nut water from pink-husked coconuts exhibited antioxidant activity, indicating potential health benefits (54). Higher polyphenol levels in certain coconut varieties also contribute to increased pigmentation through oxidation processes (55). Pink pigmentation of coconut is represented in Fig. 2.

Fruit traits and oil quality

Recessive alleles influence fruit size, kernel thickness, oil content and copra yield, which are crucial for the commercial value of coconuts, for example, dwarf vs. tall coconut varieties. The dwarf trait in coconuts is controlled by a recessive allele (*dw*), leading to shorter, early-maturing palms

Fig. 2. Pink husk coconut.

(56). Dwarf varieties are self-pollinating, have smaller nuts and produce high oil content, making them suitable for hybrid breeding programs. For example, a high lauric acid content the recessive alleles influence fatty acid biosynthesis, increasing lauric acid content, which is highly valuable in the food and cosmetics industries (57).

Disease resistance

Recessive alleles contribute to natural resistance against lethal diseases affecting coconut plantations. Lethal yellowing (LY), caused by phytoplasma, leads to massive coconut tree losses. Recessive alleles regulate lignin biosynthesis, which strengthens cell walls and enhances LY resistance (58). Root wilt disease (RWD) resistance the recessive alleles modulate stress-response genes, providing natural resistance to RWD caused by phytoplasma infections (59).

Drought and salt tolerance

Coconuts are often grown in coastal and drought-prone regions, requiring stress-tolerant varieties for sustainable cultivation. Drought-resistant coconuts-recessive alleles regulate stomatal closure and deep root system development, improving water-use efficiency, which enhances drought tolerance (60). Salt tolerance in coastal coconuts the recessive mutations in osmoprotectant-related genes allow coconut trees to withstand high salinity levels, making them adaptable to coastal regions (59).

Tree architecture and yield improvement

Recessive alleles influence tree height, branching and flowering time, affecting yield potential and ease of harvesting. Early-flowering coconut varieties the recessive alleles regulate hormonal pathways, leading to early flowering and fruiting, which reduces the time to first harvest (61). Molecular markers used in coconut include simple sequence repeats (SSR), random amplified polymorphic DNA (RAPD), amplified fragment length polymorphism (AFLP) and single nucleotide polymorphisms (SNP) (62). SSR markers are particularly favored for their codominance, high polymorphism, reproducibility and relatively low DNA requirement, making them effective for genotyping, hybrid identification and diversity studies. SNP markers have emerged recently due to advances in sequencing technologies, offering finer resolution for genetic diversity and trait mapping (63).

Quantitative trait loci (QTL) analysis in coconut breeding has identified genomic regions that control key traits such as flowering time, yield components and fruit quality, facilitating marker-assisted selection for improved coconut varieties (64). QTLs have been detected for early flowering and yield traits, which are crucial for coconut breeding programs focused on enhancing productivity and reducing the juvenile phase before flowering (65).

Rubber

Latex yield and quality

Regulation of ethylene biosynthesis genes: Certain recessive alleles have been found to regulate ethylene biosynthesis genes, which leads to improved latex flow and enhanced rubber production. Ethylene is known to stimulate latex yield by affecting latex regeneration and flow duration, thus these recessive mutations contribute to higher yields in rubber-producing plants (66).

REF/SRPP gene family mutations: Mutations within the rubber elongation factor (REF) and small rubber particle protein (SRPP) gene family, which encode structural proteins abundant on rubber particles, enhance the efficiency of rubber biosynthesis (67). These mutations can increase latex yield by improving the biosynthetic process of natural rubber. REF/SRPP proteins are fundamental for stabilizing rubber particles and promoting polyisoprene chain elongation, acting as key contributors rather than catalytic enzymes in rubber formation (68). Dry rubber content (DRC) the recessive mutations affect cis-polyisoprene biosynthesis, leading to improved rubber elasticity and quality (69).

Disease resistance

Recessive alleles contribute to resistance against fungal and bacterial infections, which significantly impact rubber plantations. South American Leaf Blight (SALB) caused by *Microcyclus ulei*, devastates rubber plantations. Recessive alleles enhance pathogen recognition and immune response, providing genetic resistance (70). Powdery mildew and Corynespora leaf fall the mutations in stress-related transcription factors help in controlling fungal growth and enhancing leaf disease resistance. Powdery mildew, caused by *Oidium heveae*, reduces latex yield. Recessive mutations in jasmonic acid signaling genes improve plant immunity by enhancing systemic resistance mechanisms (71).

Drought and cold tolerance

Recessive alleles are crucial for enabling rubber trees to adapt to abiotic stresses such as drought, water scarcity, temperature extremes and cold, which are increasingly important as rubber cultivation expands into drier and colder regions (72).

Recessive alleles contribute to enhanced drought tolerance by regulating root system architecture and stomatal control. These genetic factors improve water-use efficiency by promoting deeper root systems for better water uptake and optimizing stomatal density to reduce water loss, thus increasing survival chances in water-limited environments (66). The regulation of stomatal density and root depth by recessive alleles improves the rubber tree's ability to retain water and efficiently absorb soil moisture. This genetic control enhances drought resilience and maintains latex production under water stress (73).

The regulation of stomatal density and root depth by recessive alleles improves the rubber tree's ability to retain water and efficiently absorb soil moisture. This genetic control enhances drought resilience and maintains latex production under water stress (73).

Heat stress tolerance by Heat Shock Protein (HSP) Genes through recessive mutations in HSP genes bolster protein stability under high temperatures, preserving the function and integrity of latex-producing cells. This molecular protection mechanism is vital for rubber trees facing heat stress in expanding cultivation regions with rising temperatures (74).

Cold tolerance via Dehydration-Responsive Genes (DREB family) for recessive mutations in genes of the DREB family enable rubber trees to withstand low-temperature stress, facilitating successful growth in higher altitude or cooler climates. This adaptability supports the geographic expansion of rubber cultivation into traditionally non-suitable regions (75).

Tree architecture and growth traits

Recessive alleles to produce tree height, branching patterns and leaf development, affecting plantation management. Dwarf and compact growth traits the recessive genes in gibberellin biosynthesis pathways result in shorter trees with increased branching, making latex harvesting easier (76).

Arecanut

Fruit and nut quality improvement

Recessive alleles influence fruit size, kernel thickness and biochemical composition, which affect the economic value of arecanut. High tannin and alkaloid content the recessive alleles regulate the biosynthesis of tannins and alkaloids (e.g., arecoline), which determine nut flavor and medicinal properties (77). Variants with lower tannin content are preferred for softer chewing nut varieties. Dwarf arecanut varieties the recessive mutations in gibberellin biosynthesis genes lead to shorter tree height, making harvesting easier and increasing yield per unit area (78). High alkaloid content for processing the recessive alleles regulate arecoline biosynthesis, increasing alkaloid concentration, which is desirable for chewing and medicinal uses (79).

Disease resistance

Recessive alleles contribute to natural resistance against fungal and bacterial diseases, which are major constraints in arecanut production. Koleroga (Mahali) Disease caused by *Phytophthora arecae*, leads to heavy nut drop. The recessive alleles enhance lignin biosynthesis and antifungal responses, improving resistance to Phytophthora infections (80). Fruit rot, caused by *Phytophthora arecae*, leads to severe yield loss. The recessive genes regulate lignin and phytoalexin production, enhancing disease resistance (81). Yellow leaf disease (YLD), caused by phytoplasma infection, affects leaf chlorosis and nut production. Certain recessive mutations help regulate chlorophyll retention and stress response genes, reducing disease severity (82).

Drought and salinity tolerance

Arecanut requires consistent moisture, but with climate change, drought-tolerant varieties are essential. Drought-resistant arecanut varieties the recessive alleles in root development genes improve water uptake efficiency, making trees more resilient to drought (83). Salt-tolerant arecanut in coastal areas the recessive mutations enhance the accumulation of osmoprotectants, enabling better adaptation to saline conditions (84).

Tree architecture and yield enhancement

Recessive alleles affect tree height, leaf arrangement and flowering time, influencing yield potential. Early-bearing arecanut cultivars the recessive alleles influence hormonal pathways (GA and ABA balance), leading to early flowering and fruit setting, improving commercial productivity (85).

Palmyrah

Palmyrah palm is crucial for marginal environments due to its exceptional adaptability to arid and semi-arid regions with poor soils and low rainfall, where conventional crops often fail (86). It thrives in sandy, nutrient-poor lands typical of desert and marginal areas, providing ecological benefits such as soil stabilization and drought resilience (87). Its deep root system helps sustain the tree in harsh conditions, making it a sustainable crop for desert agriculture (88). Palmyrah produces a wide range of nutritious foods including sap (neera), fruit, tuber flour and jaggery, which are vital for food security in these water-scarce regions (89). The palm's value-added products offer income-generating opportunities for marginalized farmers, improving livelihoods and nutritional outcomes (90). As a multipurpose tree with nearly 800 uses, it supports diverse agroforestry systems crucial for sustainability in fragile ecosystems (91). Its cultivation aids in diversifying agricultural production, reducing reliance on rain-fed crops and enhancing resilience against climatic variability. Promoting palmyrah in marginal zones strengthens food security by providing a reliable source of calories and micronutrients year-round (87). Research highlights its potential to increase farming income while sustaining desert economies (90).

Pigmentation

In palmyrah controlled breeding experiments in palmyrah showed that the pink flesh trait appears only in individuals that inherit two copies of the recessive allele from their parents. Heterozygous individuals (*Pp*) display the normal yellow or white flesh color, masking the pink trait (92). Anthocyanin biosynthesis pathway genes, such as *Chalcone Synthase (CHS)* and *Dihydroflavonol 4-Reductase (DFR)*, play a crucial role in pigment formation in palmyrah. Mutations or reduced expression of regulatory genes may result in pink pigmentation being expressed only in recessive individuals (93). Similar to other fruit varieties, the color change in palmyrah fruit flesh is triggered by the oxidation of phenolic compounds in the presence of specific enzymes. This process is influenced by the genetic composition of the plant, particularly the activity of the enzymes involved in anthocyanin biosynthesis (94). Pink pigmentation of palmyrah is represented in Fig. 3.

Fruit yield and quality improvement

Recessive alleles influence fruit size, sugar content and pulp consistency, which are crucial for processing and market

Fig. 3. Pink flesh palmyrah.

value. High-sugar palmyrah varieties have recessive mutations regulate sugar biosynthesis genes, leading to higher sucrose accumulation in fruits and sap (89). These varieties are preferred for jaggery and toddy production. Seedless or soft-pulp varieties mutations in seed development genes result in smaller or reduced seed size, increasing the edible portion of the fruit (95).

Drought tolerance

Palmyrah thrives in arid and saline regions, making drought and salt tolerance key breeding targets. For example, deep-rooting and water conservation traits the recessive alleles regulate root architecture genes, promoting deep root growth, which enhances drought tolerance (96).

Disease resistance

Although palmyrah is naturally resistant to many diseases, certain fungal infections and pests affect productivity. Resistance to leaf spot and stem rot recessive alleles in pathogen-defense genes enhance fungal resistance, reducing leaf spot and stem rot infections (97).

Molecular markers

Various molecular markers such as RAPD have been used to study the genetic diversity as well as for sex identification. While most of the economically important produces are obtained from female palm the sap of the male palm is much sweeter and more in quantity (98). Molecular markers like RADP and ISSR is used to study the genetic variability among the palms (99).

Cashew

Pigmentation

The pink color in cashew apples is controlled by recessive genes affecting anthocyanin biosynthesis. Controlled crosses between pink and non-pink cashew varieties confirmed that pink coloration appears only in homozygous recessive offspring (100). The pink coloration is attributed to the upregulation of anthocyanin-related genes, such as *Chalcone Synthase (CHS)* and *Dihydroflavonol 4-Reductase (DFR)*. These genes are involved in the flavonoid biosynthesis pathway and their expression is controlled by recessive genetic factors (101). Anthocyanin accumulation in higher levels of anthocyanin in cashew apples result in a deeper pink to red coloration (102). Pink pigmentation of cashew is represented in Fig. 4.

Fig. 4. Pink cashew.

Yield and nut quality improvement

Recessive alleles influence nut size, shell thickness and kernel weight, improving commercial value. Large-kernel cashew varieties certain recessive alleles regulate seed development genes, producing larger nuts with higher edible kernel yield (103). Thin-shell cashew for easy processing mutations in pericarp development genes result in thinner shells, reducing processing costs and increasing kernel recovery rate. High-Juice cashew apples the recessive genes control sugar accumulation and fruit expansion, leading to juicier and more palatable cashew apples for beverage production (104).

Disease resistance

Cashew is affected by fungal, bacterial and viral infections, leading to significant yield loss. Recessive alleles contribute to disease resistance mechanisms. Powdery mildew (*Oidium anacardii*) is a major threat to cashew plantations. Certain recessive mutations enhance plant immune responses and reduce fungal colonization (102). Cashew blight resistance some recessive alleles provide resistance to bacterial blight (*Xanthomonas axonopodis*), a disease affecting leaves and nuts (105).

Drought and salinity tolerance

Cashew is often grown in semi-arid and coastal regions, making drought and salt tolerance essential traits. Deep-rooting and water conservation traits the recessive alleles influence root system architecture, leading to deep-rooting trees with better drought resilience (106). Salt-tolerant cashew varieties the recessive mutations regulate osmolyte accumulation genes, improving cashew tree survival in saline soils (107).

Tree architecture and harvest efficiency

Table 2. Major recessive traits across plantation crops

Traits	Crop	Gene/markers	Advantage	References
Low caffeine content	Tea	Specific SNP markers (e.g., associated with TBF trait)	Enhances flavor profiles and marketability for decaffeinated products	(136)
Bean size and quality	coffee	QTLs and SNP markers	Enables early selection of plants with superior quality and bean size, valuable for specialty coffee	(137)
Small bean size	Cocoa	SNP and molecular markers	Useful for flavor profile development and marker-assisted selection	(138)
Dwarf growth habit	Coconut	SSR markers, SCoT markers	Compact plant architecture, self-pollination, early flowering; better yield per unit area	(4)
Nut size and yield	Arecanut	RAPD and ISSR markers	Contribute to yield stability and improved nut size selection	(139)
Nut weight	Cashew	SSR and SNP markers	Larger nut weight improves market value and financial returns	(140)
Kernel type (fruit quality)	Oil palm	sh locus (sh recessive allele)	Determines shell-less pisifera type linked to higher oil yield and improved processing	(141)
Growth traits	Rubber	QTL markers	Enhanced growth characteristics and rubber yield when recessive alleles fixed homozygously	(142)
Tree stature and fruit yield	Palmyrah	SSR markers and QTLs	Key for optimizing plant structure and productivity	(143)

Cashew trees have a large canopy, making nut collection labor-intensive. Mutations affecting growth traits improve plantation efficiency. Dwarf and compact growth forms the recessive genes in gibberellin biosynthesis pathways produce shorter cashew trees, allowing easier nut harvesting and higher planting density (108). Major recessive traits across plantation crops represented in Table 2.

Recessive alleles in perennial crops, although often overlooked in traditional breeding, represent a significant reservoir of hidden genetic potential that can be harnessed to improve traits such as yield, stress tolerance and longevity. These alleles may remain unexpressed under dominant conditions but can be revealed through targeted breeding strategies, including inbreeding and genomic selection, to unlock valuable phenotypes (109). Advances in genetic mapping and molecular breeding now allow the identification and pyramiding of beneficial recessive alleles to enhance crop resilience and sustainability. Harnessing this genetic diversity is crucial for developing perennial crops that can provide multiple harvests from single plantings while preserving ecological resources. Recognizing and exploiting recessive genetic variation is vital for the future development of resilient and productive perennial agriculture (110).

Main issues associated with conventional hybridization in plantation crops

Conventional hybridization has been instrumental in improving yield, quality and resistance in plantation crops such as coconut, oil palm, rubber, coffee, tea and cocoa. However, it faces several challenges due to the perennial nature and complex reproductive systems of these crops (111). Challenges in using recessive alleles for genetic improvement represented in Table 3.

Long gestation period

Most plantation crops take several years to mature, making breeding programs time-consuming. Coconut hybrids take 3-5 years to start fruiting, delaying the evaluation process (112).

Low hybridization success rate

Many plantation crops exhibit self-incompatibility and sterility, reducing successful cross-pollination. In rubber (*Hevea brasiliensis*), genetic barriers often limit the success of controlled pollination (76).

Limited genetic diversity

Continuous hybridization can lead to a narrow genetic base, making crops more vulnerable to pests and diseases. In cocoa (*Theobroma cacao*), repeated use of a few elite clones has raised concerns about genetic erosion (113).

Large space requirements

Hybridization trials in plantation crops require large land areas for field testing over multiple years. In oil palm breeding, progeny trials demand significant resources and labor (53).

Environmental influence on hybrid performance

The success of hybrids depends on environmental factors like climate, soil conditions and management practices. Tea hybrids (*Camellia sinensis*) often show variable performance across different agro-climatic zones (114).

Pest and disease susceptibility

Some hybrids, while high yielding, may become more susceptible to new or evolving diseases. In coffee (*Coffea* spp.), certain Arabica × Robusta hybrids are prone to rust under changing climates (11).

High cost and resource intensity

Conventional hybridization requires long-term investment in research, labor and field maintenance. Oil palm breeding

Table 3. Challenges in using recessive alleles for genetic improvement

Challenge	Impact	Example Crops	Reference
Homozygosity Requirement	Slow breeding, needs multiple generations	Tea, coffee	(11, 125)
Inbreeding Depression	Reduced yield and vigor due to selfing	Rubber, cashew	(144, 145)
Linkage with Undesirable Traits	Poor resistance-related agronomic traits	Coffee, oil palm	(146, 147)
Low Allele Frequency	Difficult to identify/use in breeding	Coconut, arecanut	(148)
Environmental Influence	Unstable trait expression in field	Cocoa, palmyrah	(149, 150)
Long Breeding Cycle	High cost and time for new varieties	Rubber, oil palm	(151)
Large-Scale Commercialization	Difficult propagation and adoption	Cocoa, arecanut, coconut	(131)
Limited Biotechnology Use	Regulatory and technical challenges in gene editing	Cocoa, oil palm	(152, 153)

can take 15-20 years from initial crosses to commercial release (115).

Role of recessive alleles in overcoming hybridization issues

Many plantation crops like cocoa and coffee exhibit self-incompatibility (SI) genes, which prevent self-fertilization and restrict hybridization. Recessive alleles of SI genes can be utilized to break self-incompatibility barriers, allowing controlled hybridization. In *Coffea canephora*, recessive mutations in the S-locus allow self-pollination (116). Sterility in hybrids is often caused by dominant sterility alleles. Identifying and selecting recessive fertility-restoring genes can help restore fertility in hybrids. In oil palm (*Elaeis guineensis*), recessive genes controlling pollen fertility have been identified to improve hybrid viability (53).

Recessive mutations improve seed viability and germination in plantation crops by influencing embryo development and seed storage proteins. In rubber (*Hevea brasiliensis*), recessive alleles associated with seed dormancy-breaking mechanisms have been used to improve germination rates (117). Hybrid vigor is often lost in subsequent generations due to dominant alleles segregating unpredictably. Fixing desirable traits through recessive homozygosity in hybrid breeding programs helps maintain yield stability across generations. In cocoa (*Theobroma cacao*), recessive alleles for pod shape and bean quality traits help maintain heterosis in hybrid populations (118). Many stress-related traits, such as drought tolerance and disease resistance, are governed by recessive alleles. Selecting hybrids with these alleles improves adaptability to varying environments. In tea (*Camellia sinensis*), recessive alleles for low caffeine content have been used to develop improved varieties (119). Applications of recessive mutations in plantation crops represented in Table 4.

Biotechnological approaches for utilizing recessive alleles

Marker-assisted selection (MAS) identifies and selects recessive alleles early in breeding cycles (120). Marker-assisted breeding in coconut utilizes molecular markers like SSR and RAPD to identify and select desirable traits such as early flowering and high fruit yield (121). Genome editing (CRISPR-Cas9) can introduce targeted recessive mutations to improve hybridization efficiency (122). For example, in cocoa (*Theobroma cacao*), CRISPR/Cas9 technology has been applied to develop trees with enhanced resistance and improved traits by exploiting recessive gene functions, thereby accelerating breeding efforts beyond what is possible with conventional methods (123). Rubber tree improvement utilizes CRISPR for targeted gene mutations to enhance latex yield (124). Inbreeding and backcrossing helps fix recessive alleles in elite hybrid lines (53). Biotechnological approaches such as marker-assisted selection and CRISPR genome editing provide effective strategies for exploiting recessive alleles, overcoming limitations of traditional breeding. These tools accelerate crop improvement by enabling precise identification and manipulation of desirable recessive traits (125). Applications of genome editing in plantation crops represented in Table 5.

Future prospects

The future of plantation crop improvement lies in leveraging recessive alleles through integrated biotechnological approaches. Advanced genomic tools like CRISPR-Cas9 offer unprecedented precision in introducing beneficial recessive mutations without lengthy breeding cycles. This could revolutionize breeding programs for perennial crops like coffee, cocoa and oil palm that traditionally require decades of development.

Table 4. Applications of recessive mutations in plantation crops

Crop	Induced Mutation	Recessive Trait Improved	Reference
Rubber (*Hevea brasiliensis*)	Gamma irradiation	Disease resistance & latex yield	(154)
Tea (*Camellia sinensis*)	EMS mutagenesis	Low caffeine content	(155)
Coffee (*Coffea arabica*)	EMS mutagenesis	Disease resistance	(156)
Oil palm (*Elaeis guineensis*)	Transposon mutagenesis	Fruit color genetics	(157)
Cocoa (*Theobroma cacao*)	TILLING	Bean quality & pod color	(158)
Coconut (Cocos nucifera L.)	GA mutation	Dwarf varieties	(159)
Coconut (*Cocos nucifera* L.)	Na+ transporter mutation	Salt tolerance	(160)
Arecanut (*Areca catechu* L.)	ABA-related gene mutation	Drought tolerance	(161)
Palmyrah (*Borassus flabellifer*)	Sugar accumulation genes	High-sugar sap yield	(162)
Cashew (*Anacardium occidentale* L.)	Testa thickness mutation	High kernel recovery	(163)

Table 5. Applications of genome editing in plantation crops

Crop	Edited Trait	Genome Editing Method	Reference
Cocoa (*Theobroma cacao*)	Disease resistance (TcNPR3)	CRISPR-Cas9	(123)
Oil palm (*Elaeis guineensis*)	Fatty acid composition	TALENs	(164)
Rubber (*Hevea brasiliensis*)	Latex yield	ZFNs	(165)
Tea (*Camellia sinensis*)	Caffeine-free trait	CRISPR-Cas9	(166)
Coffee (*Coffea arabica*)	Decaffeination genes	CRISPR-Cas9	(167)
Coconut (*Cocos nucifera*)	Drought tolerance	CRISPR-Cas9	(168)
Cashew (*Anacardium occidentale* L.)	Disease resistance (fungal)	CRISPR-Cas9	(169)
	Drought tolerance (ABA genes)	CRISPR-Cas9	(170)
Arecanut (*Areca catechu* L.)	Pest and pathogen resistance	CRISPR-Cas9	(171)
Palmyrah (*Borassus flabellifer*)	Sugar content and yield	CRISPR-Cas9	(93)
	Salt tolerance and drought resistance	CRISPR-Cas9	

Marker-assisted selection will continue evolving to identify valuable recessive alleles controlling disease resistance, climate resilience and quality traits. These technologies will be crucial as climate change intensifies, allowing breeders to develop varieties with enhanced drought tolerance, heat resistance and pathogen defense mechanisms. The emerging field of epigenetics may reveal how recessive alleles are regulated under environmental stress, potentially unlocking new adaptation strategies. High-throughput phenotyping combined with genomic selection will accelerate the incorporation of beneficial recessive traits into elite breeding lines.

Particularly promising is the development of climate-resilient varieties through targeted manipulation of recessive alleles controlling water-use efficiency and temperature stress tolerance. As plantation crops face increasing biotic and abiotic challenges, focus will shift toward pyramiding multiple recessive resistance genes to create durable, multi-stress tolerant varieties. The integration of artificial intelligence with genomic data will enable more efficient prediction of recessive allele effects and optimal breeding strategies, significantly reducing the time and resources required for crop improvement while maximizing genetic gains for sustainable plantation agriculture.

Conclusion

Recessive alleles play a pivotal role in crop improvement by contributing to disease resistance, stress tolerance, yield enhancement and quality improvement in plantation crops such as coconut, cashew, palmyrah, oil palm, rubber, tea and coffee. These alleles are crucial in breeding programs aimed at developing drought-resistant, pest-tolerant and high-yielding varieties. Additionally, recessive mutations influence nutritional composition, such as low-caffeine coffee, high-carotenoid oil palm and antioxidant-rich pink-husk coconut.

Despite challenges such as homozygosity requirements, long generation times and potential linkage with undesirable traits, the integration of advanced biotechnological tools has begun to unlock their breeding potential. Marker-assisted selection enables early and precise identification of desirable recessive alleles, while CRISPR/Cas9-mediated gene editing offers the ability to generate targeted mutations with unprecedented efficiency. Coupled with inbreeding strategies and genomic selection, these tools are transforming how breeders' harness recessive inheritance in perennial systems.

Future research should focus on molecular characterization, hybrid breeding strategies and biotechnology integration to optimize the use of recessive alleles for sustainable agriculture. By leveraging genomic tools and precision breeding, scientists can unlock the full potential of recessive alleles to ensure climate resilience, enhanced productivity and improved nutritional value in plantation crops.

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Authors' contributions

RNK wrote original manuscript, RAK conceptualized the manuscript and reviewed the manuscript, MA and RS reviewed the manuscript and MVP reviewed and edited the manuscript.

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