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## Review

# Breeding of coconut palm (*Cocos nucifera* L.)

**V. Arunachalam*† and M. K. Rajesh**

**Address:** Division of Crop Improvement, Central Plantation Crops Research Institute, Kasaragod 671124, Kerala, India.

***Correspondence:** V. Arunachalam. Email: vadivelarunachalam@yahoo.com

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## Abstract

This review provides a detailed outline of the developments in the field of coconut breeding. Emphasis is laid on research on both classical and molecular genetic tools for improving the coconut palm. The review begins with a short description of origin of coconut, with mention of fossil data. Cytological studies of the palm, with emphasis on karyomorphology and polyploidy, is provided. Methods of genetic improvement, selection, hybridization and use of spontaneous mutations as applied to coconut are highlighted. This review also tries to explore the aspects of breeding in coconut for tolerance to biotic and abiotic stress with emphasis on mites, phytoplasma and drought. The need to develop cultivars suitable for product diversification for changing markets is emphasized. A compilation of the genetic architecture of the traits known so far is also made. Important morphometric traits with potential to understand diversity are listed. A sketch of recent efforts in utilizing molecular markers for understanding diversity, developing linkage maps and marker-assisted selection is also made.

**Keywords:** Arecaceae, Improvement, Diversity, Molecular, Resistance

**Review Methodology:** We searched the CAB Abstracts, Agricola and used the keywords coconut, breeding, resistance and diversity to narrow down the search and to retrieve the required information. Additional information was collected from the coconut time line website and also from proceedings of symposia held on coconut.

## Introduction

Coconut palm (*Cocos nucifera* L.) is one of the most important multi-purpose tree crops of the humid tropics. It is placed under the monotypic genus *Cocos*, sub-tribe Butiinae, tribe Cocoeae, sub-family Arecoideae and family Arecaceae. Coconut yields many commercial products [1] such as lauric oil [2], biofuel [3], fibre [4] and a refreshing health drink [5]. It is a large, single-stemmed tree, which grows as tall as 10–12 m. It supports the lives of millions of people in coastal and island ecosystems in tropics.

Genetic improvement of a perennial crop such as coconut is very difficult and protracted. The extended juvenile phase, the long interval between generations, the palm's heterozygous nature, the sizeable area required for planting experiments and the extensive period of experimentation required for obtaining results are the major reasons for the slow progress of crop improvement programmes for coconut. Despite these constraints, much progress has been made in coconut breeding [6–10].

## Origin and Cytology

The origin of coconut remains debatable and fossil evidence [11] has been reported from South Asia [12] and Australia [13], but the diversity remains highest in the Melanesian region [14]. It is a diploid species with a large genome size of 2150 Mb [15] distributed on 16 pairs of chromosomes [16].

Karyomorphological studies have revealed a larger chromatin content in Chowghat Green Dwarf than West Coast Tall of India [17]. Endosperm tissues are generally

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†Genetic Transformation Laboratory, International Crops Research Institute for Semi-Arid Tropics, Patancheru 502324, AP, India.

seen with normal triploid cells, but a few cells show a high degree of polyploidy ($\geq 6\times = 96$) [18]. However, in makapuno mutant coconut fruits, the buttery endosperm is characteristically polyploid (48×) [19]. Haploidy is rare and has been reported in a less vigorous twin palm [20]. Research on coconut cytology, karyomorphology, polyploidy in endosperm and meiotic abnormalities in mutants and dwarves has been extensively reviewed [21].

## Morphometric Analysis of Diversity

Numerous phenotypic characters have been employed for discriminating botanical forms of coconut [22, 23]. Palms belonging to tall varieties, also known as typica, are slow-growing plants with long internodes, large leaves and inflorescences. They are mainly cross-pollinated forms with large fruits and usually large kernel per fruit. Dwarf varieties are fragile, generally self-pollinated (except Niu Leka) and quick-growing forms of coconut. They are classified as nana and javanica based on their stem and fruit morphology. They produce shorter leaves, with fewer leaflets and smaller fruits on shorter inflorescences compared with tall varieties. Fruits of this variety have generally smaller kernel, but are suitable as tender coconut in most cases. Niu Leka is a rare dwarf which is allogamous and has large fruits. The International Coconut Genetic Resources Network has prescribed a set of descriptors and protocols (STANTECH) for characterizing the coconut germplasm [24]. Foliar traits, especially fibre thickness of leaf sheath, were good indicators for analysing coconut diversity [25]. Phenotypic plasticity of foliar traits has been studied in detail in Mexican populations of coconut [26]. The number of leaves was a highly plastic trait, since the coconut palm adjusts to the environment by altering its growth rate. Floral traits and their phenology have also been used for categorizing the coconut accessions based on their pollination systems [27, 28]. Fruit components, especially the weight of the fruit and husk proportion, were found suitable for classifying the coconut populations [29] and for understanding the clinal variation [30]. In general, populations from Pacific Ocean [31] and Indian Ocean [25, 32] have shown high levels of diversity. A comprehensive review on coconut genetic resources is available [33].

## Classical Breeding

Classical breeding of coconut palm is mainly based on selection of phenotypic traits, hybridization of varietal crosses involving tall and dwarf forms and to some extent, harnessing spontaneous mutations. The main objectives of the breeding programmes are to improve yield in general and to develop varieties tolerant to biotic and abiotic stress and suitable for product diversification in particular.

## Genetic Architecture and Selection

There are two important forms of coconut: tall and dwarf. Seeds of dwarf forms germinate faster and earliness is dominant over delayed germination. Speed of germination is an important trait in taxonomic classification [34]. Germination pattern of varieties differing in resistance to lethal yellowing (LY) disease suggests early germination to correlate with disease resistance [35]. Such correlation needs further investigation, as the dwarf varieties are generally resistant to diseases as well early in germination.

Vivipary is seen in some populations such as Thai Tall [36]. Mangrove plants usually display vivipary as a mechanism for seeds to tolerate salinity and flooding. This trait in coconut needs further investigation for identifying any functional correlation. In many areas, coconut palms are grown in submerged areas, hence the trait of viviparity is an adaptive requirement in those locations. However, this trait if present in a cultivated variety exclusively used as mature nut can become a constraint to farmers. This is because the nuts germinating inside the fruit have poor shelf life. Petiole colour is another useful trait for discriminating hybrid seedlings in nursery, if the parents differ in petiole colour. Two genes, R and G, have been reported to control the petiole colour [37].

There are many theories on origin and genetics of dwarfism such as mutation of single or few gene(s) (either dominant or recessive), inbreeding depression [38] etc.

Most of the tall populations are allogamous and most dwarf populations are autogamous. Polygenic recessive genes control self-pollination in coconut [39]. In a cross between cultivars differing in duration of the female phase, 10 out of 25 $F_2$ progenies had a shorter female phase, which indicated the dominance of short female phase [27]. Long female phase favours self-pollination.

Genetic analysis of yield in coconut [42–44] revealed that high yielders are proportionately low and hence rare in any unselected population. Yield stability and superiority of high-yielding groups has been found even in a poor environment. Hence, selection of mother palms with high yields is a good strategy for their use either as a parent in hybrid programme or for generating open-pollinated progeny. There are a few reports of coconut palms known as pre-potent or elite, which have a blend of many desirable traits of major yield attributes and progeny of these palms inherit most of these traits, possibly as a result of tight linkage. Such elite palms had been identified in different parts of the state of Kerala in India [45]. Farmers' varieties of coconut, raised by farmers for specific trait, yield and adaptation [46, 47], need to be augmented. Komadan is one such elite variety prevalent in Kerala [48].

Mother palm selection promises to improve the first-generation performance by 25–35% [49]. Selection criteria include palms with a large number of leaves at the crown, bearing many bunches of female flowers, high fruit-setting percentage, number of nuts (80–120 nuts per palm per year) [50] and high amount of copra/nut (150 g/nut). Palms producing inflorescences with more spikes and each spike with a single female flower are stable yielders [51]. Vigorous seedlings with large collar girth and a large number of leaves are selected in the nursery [52] to get high-yielding adult palms. Collar girth and number of leaves are highly heritable and correlate positively with yield [53–55]. Vigorous seedlings with brown petiole had higher chlorophyll content and nitrate reductase activity than vigorous plants with orange petiole and dwarf plants. They also had a larger leaf area and shoot dry weight [55]. Although selection of seedlings is based on genetic [54] and biochemical mechanisms [56], the selection need not be stringent as the yield differences between vigorous and intermediate seedlings are not always significant [57].

Heritability of coconut for many morphometric and agronomic traits [44, 58] is medium (0.45) for the number of leaves and high for internodal length (0.63). Heritability of seedling characters, collar girth, number of leaves, plant height and rate of germination ranged from 0.62 to 0.76 [54]. Heritability of yield attributes such as number of bunches and nuts are medium to low in coconut [42, 43]. Heritabilties of number of leaves, number of bunches and number of female flowers, nuts per bunch and annual nut yield varied from 0.42 to 0.58 [54]. Physiological traits such as shoot dry weight, net assimilation rate and chlorophyll content show high (0.64–0.81) heritability [56]. Thus, a breeder can plan a selection criterion by judiciously combining a few highly heritable traits, such as internodal length, seedling traits and physiological parameters, that correlate with the trait of interest (higher yield or resistance to biotic or abiotic stresses).

New techniques such as tissue culture of embryos in highly osmotic medium with 170 mM NaCl [59], petiole inoculation of the pathogen *Thielaviopsis paradoxa* [60], and colour development by acid treatment (8.8 N HCl) [61] had aided screening for tolerance to drought, stem bleeding disease and copra quality, respectively.

## Pollination and Seed Production

Coconut palm is a monoecious palm with protandry; it is predominantly cross-pollinated mainly by insects and wind [62]. Honeybees play a significant role in pollination compared to other insects [63] and agents. Overlapping of intra and interspadix male and female phases allow cross-pollination. Generally, tall varieties are cross-pollinated and dwarf varieties are self-pollinated. Female phase lasts 2–3 days and the male phase lasts 7–10 days and the variation is these phases and the overlapping of phases has been extensively studied in many coconut varieties [27, 28].

For hybridization, the inflorescence of the female parent is split open and after the male flowers are manually removed, the inflorescence bagged to prevent pollination by foreign pollens. These bags are stitched with a transparent plastic slit. Pollen from male parent is collected and stored well in advance. Pollen of coconut can be extracted after oven drying of male flowers at 40 °C. At low temperatures, reliable storage can be done in sealed conditions for 2–3 months after drying pollen with silica gel. Freeze-dried pollen retains viability for four months without reduction in viability [64, 65]. When the female flowers reach receptivity, pollen is dusted preferably during 10 am to 12 pm [10]. Unfertilized female flowers dry and abscise two days after pollination. Isolated seed gardens at least 300 m away from other coconut cultivation areas are essential for preventing contamination by unwanted pollen. Seed gardens should be ideally free from pests and diseases and located away from disease hotspots and with high proportion of heavy bearers. The coconut seed garden at Ambakelle in Sri Lanka is a good example.

The nursery area should ideally have good irrigation facilities, be free from soil-borne pathogens and termites and with ample shading. A system of planting alternate rows of dwarf and tall parents is ideal for raising dwarf×tall hybrids after removing the male flowers of inflorescences of dwarf palms and allowing pollen from tall palms to fertilize. This practice is in use at CPCRI Kidu farm, Karnataka, India.

## Hybrid Vigour

Hybrid vigour was first reported in a varietal cross between Fiji Dwarf and Malayan Dwarf as early as 1928 [66]. Hybrid seedlings of tall and dwarf crosses show vigour for collar girth, number of leaves and height [67]. All four possible combinations of tall and dwarf hybrids had been evaluated and each hybrid has been found to possess its own merits and demerits. Tall×dwarf hybrids are promising in rain-fed areas with low soil-moisture conditions [68], whereas dwarf×tall hybrids are early in bearing and fit the hybrid seed industry because of the ease in emasculating the short female palm. PB 121, a dwarf×tall hybrid also known as Mawa hybrid [69], was tested globally with varying degrees of success. Based on these initial results, many countries have evolved dwarf×tall hybrids including a Malayan dwarf and either a local or imported but adapted tall variety from their region, for example, in Thailand [36] and Jamaica [70]. The strategy combines the advantage of adaptation from the local tall and early bearing from dwarf varieties. Even though these hybrids have the advantage of early bearing, they have poor shelf life of fruits giving a poor price during market gluts [36]. Undesirable traits of early germination and fragility of dwarfs are also passed on to these hybrids. Naturally crossed dwarfs (NCDs) are putative hybrids produced by allowing emasculated dwarf palms for receiving pollen from tall. Tall×tall hybrids have the advantage of producing fruits with high copra content, but have a long pre-bearing phase. Dwarf×dwarf hybrids with extreme precocity [68] and suitability as tender coconut have also been tested.

Inbreeding depression has been studied in India [71], Sri Lanka [72] and Indonesia [73]. The criteria for investigating it were endosperm weight, embryo weight and leaf production [72]. Three generations of selfing of three coconut families revealed that the effect of inbreeding depression varied between families, but all of them showed depression for height of the palm [73]. Recently, a composite variety [74] was developed in the Philippines that combines the desirable traits of many tall varieties and also makes it easy for producing seeds in farmers' gardens.

## Harnessing Mutations

Spontaneous mutations are reported in coconut for many characters, e.g. foliar (plicata), persistent leaf bases [75], floral (spicata) [76], fruit flavour (Aromatic Nam Hom of Thailand) [77] and fruit composition (makapuno) [41] and these have immense potential in breeding programmes and coconut industries. Other mutants [10], such as albino seedlings, fruits' edible husk (Kaithathali) are also known and need to be exploited. Presence of albino seedlings indicates the parent palm's heterozygous state for a deleterious mutation for chlorophyll content. Such palms could be avoided for use as mother palms in future. The spicata mutant of coconut, which has many female flowers on an unbranched inflorescence, is a heterozygous state of a single dominant (Ss) gene [40]. Makapuno, a mutant coconut with jelly-like endosperm, has great potential in confectionery industry and is caused by recessive alleles (mm) of a single gene [41].

Makapuno is a single recessive mutation reported from the Philippines [41, 78] where the endosperm becomes buttery hence makapuno embryos cannot germinate in nature. Palms heterozygous for the makapuno mutation (*Mm*) produce normal (*MM*/*Mm*) and makapuno (*mm*) fruits based on the pollen received. Mutants similar to makapuno type have also been reported from other locations: Coco Gra (Seychelles) [32], Kopyor (Indonesia), *Thairu* or ghee or *nei Thengai* (India), Dikiri Pol (Sri Lanka), Mapharao Khati (Thailand), Sap (Vietnam), Niu Garuk (Papua New Guinea) and Pia (Polynesia).

Deficiency of α-D-glycosidase is seen in the mutant makapuno endosperm [80]. This deficiency in the embryo of makapuno seed (*mm*) and hard jelly state of endosperm renders it incompetent for germination in nature. Hence, seedlings of makapuno (*mm*) type have been retrieved successfully using embryo culture [79]. This technology is now commercialized, being the only way to germinate makapuno seeds, and has immensely benefited farmers of the Philippines.

Genetic load, measured by frequency of deleterious mutations, is higher in dwarf forms than tall and hybrids [81]. This conclusion results from the autogamous nature of dwarf forms. Natural selection tends to eliminate the genetic load progressively in self-pollinating varieties. Branching of inflorescence is highly correlated to sex expression in coconut palm. Spicata mutant palms produce unbranched inflorescence with high degree of female flowers and were reported for the first time from India [76]. The ratio of male and female flowers is 0.25 : 1 in spicata palms compared to 280 : 1 in ordinary talls. Progenies of spicata mother palm segregate into mutant *spicata* and wild type or *typica* (monoecious) in about equal numbers. Androgena mutant palms [82] with high degree of maleness, show increased branching at secondary level, whereas intermediate wild types predominately produce inflorescences with primary order of branching and monoecious sex expression. Two out of the five inbred lines of Markham Valley Tall had mutants showing secondary spikelets, but with a normal pre-bearing period [83]. This indicates that the trait was the result of either recessive alleles or inbreeding depression. Spicata and androgena mutants, being highly heritable, show potential in developing a dioecious coconut variety. Modification of sex expression is important for generating variation in pollen fertility/sterility and/or increased/reduced fruit set. One could also expect to develop new genetic stocks from these mutants for related traits, such as branching of inflorescence.

Coconut palm usually produces a single spathe covering the inflorescence. However, mutants with two to five spathes have been reported to occur in West Coast Tall populations in India such as bispatheate [84], tri-spatheate [85] and penta-spatheate [86]. Multi-spatheate palms have also been reported from Hainan Island of China [87].

## Tolerance to Biotic and Abiotic Stresses

An area of concern for coconut production is the sensitivity of the coconut palm to biotic and abiotic stress conditions. Coconut palm suffers serious economic injuries from mites attacking the fruit just below the tepals (most commonly, but erroneously, referred to as bracts). Eriophyid mites were originally a serious pest of coconut palms in Latin American and Caribbean regions and later spread to African countries. It is presently a serious pest of coconut in many Asian countries. Biophysical traits of microhabitat of the pest in the plant provide an indirect means for selecting tolerance to mite. Round and dark-green fruits show better tolerance against mite attack than elongated fruits or nuts of other colours [88]. Tightness of tepals also provides tolerance to mite [89], as the gap between the fruit and tepals decides the entry of mite and their predators [90]. This gap is measured by the ratio of length of fruit to radius of perianth (tepal) [91]. A large gap could allow the predatory mites and hence is not congenial for herbivorous mite. Differences for the gap in uninfested fruits are significantly different

[90] among the three varieties Sri Lanka Green Dwarf, Sri Lanka Tall and their hybrid. Sri Lanka Green dwarf has become susceptible to mites as the fruits of this variety are small with an elongated shape. Hence, the gap in the fruits of this variety before infestation is large enough for the eriophyid mite to enter, but too small for the predatory mite. However, this perianth fruit rim gap in infested fruits does not differ significantly and hence accessible to predatory mites. Access of predatory mites long after the eriophyid mites reach a sufficient population is insufficient to keep the pest populations below normal levels. Hence, the measurement of the gap in uninfected fruits is important and needs breeders' attention. A good ideotype for tolerance to mite needs to consider the size, shape and perianth–fruit rim gap of 2-month-old nuts before the mite could infest. Aestivations of inner tepals in coconut is of two types: contortion (with regular twisting or overlapping of tepals at one end); and imbricate (with irregular twisting or non-overlapping of inner tepals or one tepal overlapping at both ends). Aestivation also decides the tightness of the tepals [89] and consequently, the population of different herbivorous and predatory mites [92]. Tall varieties possess a higher percentage of contorting tepals than dwarf varieties, whereas dwarf×tall hybrids are intermediate [93]. Drought is a pre-disposing factor which makes coconut palms susceptible to mite attack, since the growth rate of fruits is slow because of the lack of available soil moisture [94]. The spicata mutant has shown a fair level of tolerance to eriophyid mite [95, 96].

When Chowghat Orange Dwarf cultivar was used as a pollen parent, the hybrids were susceptible to rhinoceros beetle [97]. Java Tall, Klapawangi, Kenthali and Andaman Giant varieties have shown fair level of tolerance to burrowing nematodes [98].

Coconut palm suffers serious yield losses because of fungal and phytoplasma pathogens. A well-coordinated resistance breeding effort was developed against LY disease, caused by a phytoplasma, in Jamaica and Mexico [99, 100]. However, a breakdown of resistance was reported in Jamaica recently [101]. Genetic contamination contributed marginally to increasing losses to LY [102, 103] and cautions the need for a stringent seed production plan and not allowing mixing of pollen from undesirable plant/varieties. Nevertheless, this factor is insufficient to account for the high mortality rate experienced. Root (wilt) disease is a serious concern in Southern India, where the disease-free Chowghat Green Dwarf and West Coast Tall palms in disease hot spot areas are used in breeding programmes for evolving field-tolerant high-yielding hybrid seedlings for diseased areas [104, 105].

Drought, cold and heavy wind are three major constraints to coconut cultivation. Drought tolerance of coconut cultivar depends on many phenotypic and physiological traits. A cultivar with many roots and fine root density is less affected by drought [106]. Physiological traits of leaf such as stomatal frequency and index, chlorophyll fluorescence, epicuticular wax content [107, 109] and lipase and protease activity [109] are important physiological and biochemical parameters found useful for discriminating a drought tolerant cultivar from a susceptible one.

Coconut is highly susceptible to low temperatures and nut formation is affected below 13 °C. Spear leaf damage and drying of leaves and uneven and wrinkled meat in the nut are the symptoms of cold damage [110]. Hainan Tall of China [87] and Kamrup Tall of India [111] are the two cultivars that possess tolerance to cold. WY78 hybrid (Malayan Dwarf×Hainan Tall) possesses tolerance to cold and wind [87].

Heavy winds also damage coconut palms in cyclone-prone areas. Dwarf plants are more susceptible to wind compared to talls and hybrids because of their fragile stem and smaller canopy. Palms with large collar region, well-anchored root system and strong stem offer an ideotype for these areas [112]. During cyclone, mortality of a coconut palm depends on height of the palm and girth of bole [113]. Malayan Dwarf×Thai Tall [113] and Pilipog or Tacunan Green Dwarf×Laguna Tall [114] hybrids have been reported to record low mortality in cyclone-prone areas. Palms producing thin-husked fruits showed tolerance to wind than those with thick-husked fruits [29].

## Product Diversification

Coconut industries are facing several challenges in the changing global scenario and the status of coconut as an oilseed crop is under severe threat. The only commercially exploited genetic variation in coconut is the makapuno mutant in ice cream industry. Tender fruits of coconut offer an eco-friendly health drink, which is marketed in many countries. Variation in tender nut quality in germplasm, especially the suitability and related desirable traits found in King coconut (aurantica), Niu Vai (Water coconut) [30] and nana types such as Chowghat Orange Dwarf, need to be harnessed. Chowghat Orange Dwarf also transmits the trait to their hybrids with tall parents [5], indicating its heritable nature. Coconut germplasm, especially Niu Kafa types (with large fruits and higher husk proportion) [29], specifically Niu Afa of Western Samoa of South Pacific (Sennit Coconut with high fibre (>1600 g) recovery) [30], deserve screening for suitability in the coir industry. Urgent research efforts are essential for identifying contributing traits and suitable germplasm lines with potential for use as desiccated coconut and other emerging products to fit to the recent market trends [115]. A variety for tender coconut needs to possess high total soluble solids, low acidity, and high total and reducing sugars, low sodium and high potassium content and tasty water in nut [5]. A coconut variety suitable for coir should have a high husk proportion in fruit and long fibres.

## Diversity Assessment Using Molecular Markers

An array of molecular markers has been used for addressing different aspects associated with genetic diversity of coconut palms.

Coconut populations from Papua New Guinea, Solomon Islands, Sri Lanka, Mexico and other geographical regions were investigated using leaf proteins and isoenzymatic systems [116–124]. Even though a clear distinction between ecotypes was revealed, only low polymorphism was exhibited.

Foliar polyphenol analysis revealed polymorphism and provided a picture of variability that corresponded to geographical origins [125, 126]. But the application of polyphenol banding patterns in diversity studies was restricted because of its sensitivity to ecological conditions.

With the serious limitations experienced with the biochemical markers, the potential of using DNA-based markers was realized.

A novel PCR-based approach, inverse sequence-tagged repeat (ISTR) analysis, was developed for detection of DNA polymorphisms [127]. Primers complementary to repetitive, copia-like sequences in the coconut genome [128] were used for amplifying a large number of genetic loci with an abundance of polymorphisms occurring among a set of selected coconut genotypes from various geographical regions. This technique was successfully used for analysing 48 East African tall coconut genotypes [129].

The restriction fragment length polymorphism (RFLP) technique was used for the first time in coconut in 1998 for studying the genetic diversity in 10 tall and seven dwarf coconut populations [130]. The study revealed two main genetic groups. The first group, which exhibited maximum polymorphism, included populations from the Far East and from the South Pacific regions considered to be the putative centres of origin of coconut. The second group comprised the populations from India, Sri Lanka and Western Africa. The West African ecotypes were related to the Indian and Sri Lankan ecotypes, suggesting recent extension of the species along the Atlantic Coasts of Africa through nuts originating from the Indian Ocean.

A study of 17 distinct South Pacific coconut populations using Randomly Amplified Polymorphic DNA (RAPD) technique revealed the occurrence of over 60% of the observed variability within populations [131]. Genetic drift and a possible bottleneck in the past of the species were suggested as reasons for the high intra-population diversity. RAPD technique was later used for studying coconut accessions from different geographical regions [132, 133]. The data indicated that tall accessions were more heterozygous than dwarf accessions.

Amplified fragment length polymorphism (AFLP) analysis of 42 Sri Lankan coconut genotypes was conducted using eight primer pairs [134]. More variation was detected in tall forms (typica) than in intermediate (aurantica) and dwarf (nana) forms.

AFLP and SSR markers were used in combination to analyze genetic diversity of 31 genotypes comprising 14 coconut populations from different geographical regions [135]. Populations from South Pacific and South East Asia possessed high diversity. AFLP markers were also used for discriminating root (wilt) disease-tolerant and -susceptible coconut palms from Southern India [136].

Eight microsatellites (simple sequence repeats, SSR) were isolated using a pre-cloning enrichment procedure and were used for studying the levels and patterns of genetic diversity of Sri Lankan coconut populations [137]. The results showed that the Sri Lankan tall coconuts exhibited higher levels of diversity than the dwarfs and intermediates, and the intermediate coconuts were more similar to dwarfs than talls. The results were in agreement with those obtained earlier using AFLPs in the same set of genotypes [134].

Forty coconut samples from the Philippines were characterized using eight SSR primer pairs [138]. Dwarf plants grouped separately from talls and showed less genetic diversity.

DNA amplification fingerprinting (DAF) and AFLP techniques were compared for studying the relationship among eight coconut accessions [139]. The AFLP approach is more efficient than DAF markers due to the large number of primer combinations. However, the amount of polymorphism detected in both techniques is comparable. The DAF technique standardized was later used for identifying molecular markers, which could differentiate between coconut root (wilt) disease-tolerant and – susceptible palms [140].

Microsatellite analysis of LY disease-tolerant genotypes (Vanuatu Tall and Sri Lankan Green Dwarf) and susceptible genotype (West African Tall) was performed [141]. Genotypes of susceptible West African Tall cultivars are found to be genetically unrelated to the genotypes of the two tolerant cultivars. Fingerprinting based on microsatellites aided in identification of suitable parents to be used in crossing programmes for developing a segregating mapping population for marker-assisted selection of LY resistant genes.

Fifteen SSR microsatellite DNA loci were utilized for analysing genetic variation within coconut germplasm collections at two locations in South Florida, representing eight cultivars [142]. The 15 microsatellite loci were also utilized in a parentage analysis of progenies of the 'Fiji Dwarf' variety at both locations. The Red Malayan Dwarfs were found to be genetically distinct from Green and Yellow ones. Offtype Malayan Dwarf phenotypes could be identified by the SSR loci. Similar results were obtained when the same set of 15 genotypes were subjected to single strand conformation polymorphism (SSCP) analysis using 13 WRKY sequences containing single nucleotide polymorphism (SNP) and one microsatellite [143].

## Marker-Assisted Selection

AFLP, ISSR, ISTR and RAPD markers were used in combination for constructing linkage maps in coconut for the two parents of the cross Malayan Yellow Dwarf × Laguna Tall [144]. Sixteen linkage groups were generated by a total of 382 markers. QTLs for early germination and yield were identified.

AFLP and SSR markers were used to constructing a linkage map in the coconut type Rennel Island Tall [145]. A total of 227 markers were arranged into 16 linkage groups. QTLs were detected for yield characters (number of bunches and number of nuts). QTL analyses were recently performed for fruit component weights and ratios [146] in the same segregating progeny of Rennell Island Tall genotype used in the earlier study, complemented by the linkage map constructed previously [145]. Out of the 52 putative QTLs identified for the 11 traits studied, 34 were grouped in six small clusters. Interestingly, the QTLs for fruit component weight, endosperm humidity and fruit production were found at different locations in the genome, which suggested the need for selection of QTLs for individual traits for efficient marker-assisted selection for yield.

Analysis of mite-resistant and -susceptible accessions using RAPD and SSR techniques resulted in the identification of markers associated with mite resistance in coconut [147]. When stepwise multiple regression analysis of RAPD and SSR data was done, a combination of five markers accounted for 100% of the association with mite resistance.

## Molecular Cloning

Degenerate primers designed on conserved motifs were used for isolating gene sequences sharing homology with resistance gene analogues (RGAs) of coconut [148] and WRKY transcriptional factors [149, 150]. Recently, a partial sequence of a defence-related MAP kinase gene from coconut was published [151], which broadens the scope of analysing host–pathogen interaction. It also provides avenues for genetic engineering of coconut for disease resistance using endogenous genes.

## Conclusion

Conventional tools such as spontaneous mutations, germplasm explorations and hybrid vigour have offered many useful solutions for crop improvement in coconut in the past. Innovations are needed for rapidly screening the available germplasm for tolerance to important biotic and abiotic stress. There is an urgent need to devise and optimize male sterility systems and stringent and cost-effective seed production plans for obtaining sustained results of plant breeding. The germplasm of coconut needs to be screened for traits to get value-added products. Coir, activated charcoal and desiccated coconut are the products to be targeted for suiting the emerging markets. Work on linkage mapping using association mapping strategies need special attention. Molecular marker-assisted selection needs validation and employment for identifying/developing varieties tolerant to major pests and diseases. There is also a need to optimize protocols to harness the latest technologies such as genomics and genetic transformation for evolving durable disease resistance.

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