Chapter 10
Enhancing Genetic Gain in Coconut: Conventional, Molecular, and Genomics-Based Breeding Approaches

S. V. Ramesh, R. Sudha, V. Niral, and M. K. Rajesh

Abstract Coconut (*Cocos nucifera* L.) is a monotypic genus and an important plantation crop with an enormous application value as a food, fuel, and fiber. The crop has also been recently attaining great importance in the field of nutraceuticals worldwide. Development of high yielding cultivars, genotypes having high copra content, genetic sources with characteristic features such as disease resistance [root (wilt) disease and lethal yellowing] and pest resistance (rhinoceros beetle, red palm weevil, mites, and rugose spiraling whitefly), and speciality cultivars (such as makupuno, sweet kernel, and aromatic nut water) are the main objectives of coconut breeders. Various breeding approaches such as conventional breeding techniques of selection and hybridization, molecular breeding approaches namely marker-assisted selection, QTL identification, marker-trait linkage analysis, instances of association analysis, etc. have been resorted to achieve the above-cited breeding objectives. Advances in high-throughput techniques such as genomics, proteomics, transcriptomics, and metabolomics have resulted in the generation of voluminous data and buildup of genomic resources that have a greater role to play in the future molecular and omics-based breeding approaches in coconut. However, it is pertinent to recognize that applying high-throughput techniques in coconut is largely hampered due to its perennial nature, long juvenile phase, outcrossing behavior, and consequently high heterozygous nature. This chapter comprehensively summarizes the advancements made in the field of coconut breeding, including the varietal development programs in India and elsewhere in the world, followed by advancements in molecular breeding techniques. It also provides glimpses of achievements in multi-omics approaches in coconut and discusses the prospects and applications of various high-throughput techniques in the improvement of coconut.

Keywords Coconut varieties · QTL mapping · Molecular breeding in coconut · Palms · Omics

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10.1 Introduction

Coconut (*Cocos nucifera* L.), a member of the palm family Arecaceae in the subfamily Cocoideae, is an economically important, multipurpose palm widely grown in the humid tropics. It is the only species under the genus *Cocos*, and it is a diploid with 32 chromosomes ($2n = 2x = 32$). Coconut offers nutritious food, reviving drink, oil for edible and non-edible purposes, fiber of commercial value, shells for industrial and fuel uses, timber, and a range of miscellaneous products for both household and industrial uses. In the past few years, coconut is increasingly being considered as a health food, with tender coconut water, virgin coconut oil, and coconut inflorescence sap being encouraged for consumption. The palm is grown in more than 90 countries, comprising primarily of coastal areas and island ecosystems. Currently, the coconut production in the world is estimated at 68833 million nuts from 12.08 million ha and productivity of 5777 nuts ha^{-1} (ICC 2019). Mainly the world production is concentrated in tropical Asia, with Indonesia, the Philippines, and India jointly accounting for more than 70% of the total area and production.

Worldwide, coconut populations have been classified into two main groups: the Pacific group with five subgroups (Southeast Asia, Micronesia, Polynesia, Melanesia, and the Pacific coastline of South and Central America) and the Indo-Atlantic group (Perera et al. 2009). The genetic resources in coconut, a crucial component of coconut breeding programs, have been widely exploited through breeding methods such as selection and hybridization for several desirable traits, which have resulted in the development of numerous coconut varieties. Breeding approaches are mostly confined to conventional breeding methods such as mass selection and hybridization, besides using individual palm selection for novel traits. The perennial nature of the palm, heterozygosity, extended juvenile phase, and lack of mass propagation technologies for palms having desirable traits are the major challenges in coconut breeding efforts.

The advent of DNA-based molecular markers has offered novel opportunities such as marker-assisted selection (MAS) to identify target traits of economic and agronomic importance irrespective of the crop's phenological stage and prevailing environmental conditions. These advancements have greatly aided the plant breeders to achieve the crop improvement goals in a relatively easy and effective manner. The accelerated developments and improvements in the field of next-generation sequencing (NGS) techniques have generated voluminous data at the DNA, RNA, protein, and metabolite levels leading to an era of "big data"-enabled molecular breeding. Nevertheless, consolidation of large-scale information and integrating it with particular plant phenotype would not only help in comprehending the molecular and genetic basis of a trait expression but also would aid in their introgression into a desired genotype by adopting multi-omics-based crop breeding. This integration of multi-omics approaches in molecular breeding has greatly assisted the improvement of many crop plants which could not be emulated in coconut. The main reasons for lag in application of multi-omics technologies in coconut are its inherent heterozygosity, stemming from its breeding behavior and lack of genomic resources. This chapter discusses the achievements made in the conventional breeding of coconut leading to robust varietal development programs, followed by the use of molecular markers for genetic diversity assessment and mapping of quantitative trait loci (QTLs). Further, the glimpses of the recent advancements in the field of genomics, proteomics, transcriptomics, and metabolomics in coconut are enumerated discussing the future prospects to enhance the breeding efforts in this economically important palm crop.

10.2 Coconut Genetic Resources

The varietal development programs and the current status and future strategies for coconut breeding worldwide are discussed herein. Despite being a monotypic genus, *Cocos nucifera* L. has substantial genetic diversity in its populations (Arunachalam and Rajesh 2017; Niral and Jerard 2018). The varieties of coconut could be distinguished based on their qualitative traits such as size, shape, nut color, and pest/disease resistance. In contrast, quantitative traits such as precocity of flowering, bunch, nut numbers, and inflorescence/fruit characteristic features are also used to investigate the diversity. Nevertheless, the genetic basis of these phenotypic variations is poorly understood. A global network of coconut growing countries called the International Coconut Genetic Resources Network (COGENT) was set up by the International Plant Genetic Resources Institute (IPGRI) in 1992 (Batugal et al. 2005). The COGENT coordinates the collection of important coconut varieties and their conservation at respective national gene banks and appropriate duplicates at multisite International Coconut Genebank (ICG). The regional-level ICG gene banks are hosted at Indonesia for Southeast and East Asia, India for South Asia and the Middle East, Côte d'Ivoire for Africa and the Indian Ocean, Papua New Guinea for the South Pacific, and Brazil for Latin America and the Caribbean (Ramanatha Rao and Batugal 1998). Though COGENT's International Coconut Genetic Resources Database (CGRD) reveals that over 1416 coconut accessions are being conserved, national breeding programs utilize less than 5% of that germplasm (Batugal 2004, 2005a). However, development of catalogs of conserved germplasm (Ratnambal et al. 1995; Ratnambal et al. 2000; Bourdeix and Batugal 2005; Bourdeix et al. 2010), compiling of descriptors of salient traits of coconut accessions via CGRD (Hamelin et al. 2005), and the improved accessibility of coconut germplasm in ICG and national genebanks have greatly ensured more accessions are being integrated into the crop improvement programs worldwide.

10.3 Coconut Breeding: Current Status

In coconut, inadequate adaptability to wide environmental conditions, lack of high and stable yielding genotypes, and consequent low farm-level productivity are the major limitations (Batugal 1999). Presently, 1837 accessions are conserved in the

24 gene banks and are potential sources for development of high yielding varieties taking into consideration the national requirements and the needs of the local coconut communities (Nampoothiri and Parthasarathy 2018). Hence, the development of coconut varieties possessing disease resistance is of utmost importance in South American and African countries because of the prevalence of the lethal yellowing disease in these regions. In contrast, Vanuatu focuses on varieties that are resistant to coconut foliar decay. Since coconut is largely grown in marginal, rainfed areas in Sri Lanka, India, and Tanzania, the main breeding objective is to develop drought-tolerant genotypes in these countries. While China is involved in developing cold-tolerant lines, the Pacific and Caribbean countries are breeding for cyclone-tolerant varieties.

10.4 Breeding Programs

The first International Coconut Breeders Meet was held in Côte d'Ivoire to standardize the research on coconut breeding techniques during 1996 (Batugal and Ramanatha Rao 1998). Various national breeding programs, in general, aim to evaluate local cultivars against the introduced varieties obtained from the more advanced breeding centers. A follow-up survey conducted by COGENT during 2001–2003 (Batugal 2004) indicated that locally produced hybrids were predominant in national varietal performance trials. Along with the progeny test, most of the coconut growing countries have conducted phenotypic and genotypic characterization of coconut genotypes, evaluation of collected coconut genotypes for general and specific combining abilities, mother palm selection, pollination, and hybrid seed nut production.

10.4.1 Coconut Breeding Program in India

10.4.1.1 Selection

India has been one of the earliest countries to initiate work on coconut breeding, with focus on collection and conservation of germplasm, following the establishment of the Central Coconut Research Station (presently, ICAR-Central Plantation Crops Research Institute) at Kasaragod in the year 1916. The indigenous germplasm collection was strengthened with the introduction of coconut cultivars from the major coconut growing countries, viz., the Philippines, Malaysia, Indonesia, Sri Lanka, Vietnam, and Fiji, way back in 1924. ICAR-CPCRI hosts the National Active Germplasm Site (NAGS) for coconut and maintains the largest collection of 455 accessions, representing coconut germplasm from around 28 countries, encompassing South and Southeast Asia, Caribbean Islands, Indian Ocean Islands, Pacific Ocean Islands, and African countries. In addition, India also hosts the International Coconut Genebank for South Asia (now referred to as International Coconut

Genebank for South Asia and Middle East) with 91 accessions, comprising designated Indian germplasm, germplasm from regional member countries, viz., Sri Lanka and Bangladesh, and accessions collected through prospection from the Indian Ocean Islands of Madagascar, Mauritius, Seychelles, Maldives, Comoros, and Reunion (Niral et al. 2019). India was also the first country to develop a catalog of coconut germplasm, following standardized coconut descriptors (IPGRI 1995), describing 48 conserved germplasm of diverse origin with photographs of the different plant parts and textual information, for the benefit of coconut researchers (Ratnambal et al. 1995). Subsequently, a second volume of the descriptors, describing another 26 accessions, was compiled and distributed in CD-ROM (Ratnambal et al. 2000). Comprehensive characterization of genetic resources has resulted in identification of trait-specific germplasm and registration of seven trait-specific germplasm with the ICAR-National Bureau of Plant Genetic Resources (ICAR-NBPGR). In India, evaluation and selection of promising coconut accessions maintained at the ICAR-CPCRI (Indian Council of Agricultural Research-Central Plantation Crops Research Institute, Kasaragod, Kerala) as well as the several coordinating research centers under the All India Coordinated Research Project on Palms (AICRP on Palms) and State Agricultural Universities (SAUs) have led to the development and release of 30 improved coconut varieties. In the initial years, the focus was on evaluation for higher nut/copra/oil yield (Niral et al. 2009). Subsequently development of varieties for tender nut purpose and inflorescence (neera) sap production was also given greater emphasis (Samsudeen et al. 2013; Niral et al. 2014; Sudha et al. 2019). In tune with changing user needs, Chowghat Orange Dwarf (COD) was the first to be released as an exclusive tender nut variety (Fig. 10.1), and more recently, Kalpa Ratna was released as a multipurpose variety suitable for copra, tender nut, and inflorescence sap production (Fig. 10.2). Screening

Fig. 10.1 COD, a popular dwarf tender coconut variety

Fig. 10.2 Kalpa Ratna, a high yielding multipurpose coconut variety

of germplasm for biotic/abiotic tolerance, with special emphasis on root (wilt) disease tolerance, drought tolerance, and high/low temperature tolerance/climate resilience, is also in progress, and stress-tolerant accessions have been identified (Rajagopal et al. 1990; Nair et al. 2004; Kasturi Bai et al. 2006; Hebbar et al. 2013; Hebbar et al. 2018).

The varieties released so far for cultivation in the country are highlighted in Table 10.1.

10.4.1.2 Exploitation of Hybrid Vigor

The first hybridization attempt in India was made in 1930, involving tall and dwarf types [West Coast Tall (WCT) × Chowghat Green Dwarf (COD)] (Patel 1937). Since then, many hybrids have been tested involving many tall × dwarf (T × D), dwarf × tall (D × T), and tall × tall (T × T) crosses. Also, the advantages of hybrids compared to the local tall cultivars were well recognized. Even though hybrids from both the cross combinations are high yielding, hybrids derived from D × T cross have a discrete advantage over hybrids from T × D cross as large-scale production of these hybrids is possible by emasculating dwarf mother palms and allowing natural pollination with the pollen of tall palms in the vicinity. Hence, in the recent past, the production of D × T hybrids has been promoted rather because of their relative ease in production (Nair et al. 2016). Also, hybrid coconuts are characterized with early bearing and high yielding traits (nut, oil, and copra yield palm^{-1}).

Further, offsprings of the crossing of tall and dwarf coconut accessions were evaluated at ICAR-CPCRI and other AICRP on palm (AICRPP) centers resulting in development of many hybrid varieties. Consequently, the crossing of unrelated

Table 10.1 Improved coconut varieties developed for cultivation in India through selection

Variety	Salient features	Institution responsible for the release
Chandra Kalpa	Drought-tolerant, high oil (72%)	ICAR-CPCRI
Kera Chandra	High yield, dual purpose for tender nut and copra	ICAR-CPCRI
Kalpa Pratibha	High yield, dual purpose for tender nut and copra	ICAR-CPCRI
Kalpa Mitra	High nut and oil yield, drought-tolerant	ICAR-CPCRI
Kalpa Dhenu	High nut and oil yield, drought-tolerant	ICAR-CPCRI
Kalpatharu	Drought-tolerant, high yield, ball copra	AICRP on Palms (AICRPP), ICAR-CPCRI. Kasaragod
Pratap	High yield	Dr. BalasahebSawant Konkan Krishi Vidyapeeth (Dr. BSKKV), Maharashtra
Kamarupa	High yield	Assam Agricultural University (AAU), Assam
Aliyarnagar Tall 1-ALR (CN) 1	High yield	Tamil Nadu Agricultural University (TNAU), Tamil Nadu
KeraBastar	High yield	AICRPP, ICAR-CPCRI
KeraKeralam	High yield	AICRPP, ICAR-CPCRI
Aliyarnagar Tall 2-ALR (CN) 2	High yield	TNAU, Tamil Nadu
VPM-3	High yield, drought-tolerant	TNAU, Tamil Nadu
Kera Sagara	High yield	Kerala Agricultural University (KAU), Kerala
Double century	High yield	Acharya N. G. Ranga Agricultural University (ANGRAU), Andhra Pradesh
Kalpa Haritha	Green color fruits, less eriophyid mite damage, dual purpose for tender nut and copra	ICAR-CPCRI
Kalyani Coconut	High yield	Bidhan Chandra KrishiViswavidyalaya (BCKV), West Bengal
Kalpa Shatabdi	Large fruit, dual purpose for copra and tender nut	ICAR-CPCRI
Kalpa Ratna	Multipurpose for tender nut, copra/oil, inflorescence sap (neera) production, tolerant to moisture stress	ICAR-CPCRI
Kalparaksha	Semi-tall, green color fruits, high nut/copra yield in root (wilt) disease (RWD) prevalent areas, tender nut purpose	ICAR-CPCRI
Kera Madhura	Semi-tall, dual purpose for tender nut and copra	KAU, Kerala

(continued)

Table 10.1 (continued)

Variety	Salient features	Institution responsible for the release
Gautami Ganga	Dwarf, green fruits	Dr. YSR Horticultural University (Dr. YSRHU), Andhra Pradesh
CARI-C1 (Annapurna)	High copra content and tender nut purpose, dwarf, green color fruit	ICAR-Central Island Agricultural Research Institute (ICAR-CIARI), Port Blair, Andaman and Nicobar Islands
Chowghat Orange Dwarf (COD)	Dwarf, orange color fruit, tender nut purpose	ICAR-CPCRI
Kalpa Jyothi	Dwarf, yellow color fruit, tender nut purpose	ICAR-CPCRI
Kalpa Surya	Dwarf, orange color fruit, tender nut purpose	ICAR-CPCRI
Kalpasree	Dwarf, green fruits, superior oil, high yield in RWD areas	ICAR-CPCRI
CARI-C2 (Surya)	Ornamental purpose, orange color fruit	ICAR-CIARI, Andaman and Nicobar Islands
CARI-C3 (Omkar)	Ornamental purpose, yellow color fruit	ICAR-CIARI, Andaman and Nicobar Islands
CARI-C4 (Chandan)	Ornamental purpose, orange color fruit	ICAR-CIARI, Andaman and Nicobar Islands

genotypes of T × T was also performed to produce varieties with high yield and superior-quality copra possessing a certain degree of stress tolerance. Production of T × T hybrids was carried out exploiting palms with high breeding value. Diallel analysis of 16 diverse coconut parental genotypes showed that Gangabondam Green Dwarf (GBGD) is a good general combiner. The combination LCT × GBGD is most suited for an appreciable increase in nut and copra yield based on specific combining ability analysis (Nampoothiri et al. 1999). The crosses WCT × COD, COD × WCT, LCT × COD, MYD (Malayan Yellow Dwarf) × TPT (Tiptur Tall), MYD × WCT, ECT (East Coast Tall) × MOD (Malayan Orange Dwarf), ECT × MGD (Malayan Green Dwarf), GBGD × ECT, ECT × MYD, and CGD × WCT are instances of successful coconut hybrids in India (Fig. 10.3). In order to exploit the possibility of developing high yielding dwarf hybrids combining desirable traits of early flowering and higher rate of bunch observed in dwarfs, work on development of D × D hybrids was initiated at ICAR-CPCRI during 1999, and 21 dwarf × dwarf hybrid combinations were planted for evaluation during 2003 (ICAR-CPCRI 2004). The D × D hybrids recorded positive heterosis for growth as well as yield traits and were also observed to show earliness in flowering. Earliest flowering, 15 months after planting, with regular bunch production was recorded in MYD × CGD. The MYD × NLAD (Niu Leka Dwarf) hybrid (Fig. 10.4) recorded compact crown, large inflorescence with more number of medium-sized fruits, and high tender nut water content and sturdy trunk, while COD × GBGD showed early flowering with high nut yield, highlighting the prospects of D × D hybrids for commercial exploitation (ICAR-CPCRI 2014).

Fig. 10.3 Chandra Sankara, a popular Dwarf × Tall coconut hybrid

In India, 21 coconut hybrids (11 T × D; 8 D × T; and 2 T × T) have been developed by ICAR-CPCRI and SAUs under the AICRPP for commercial cultivation in different regions of the country (Niral et al. 2019). The hybrid MYD × WCT (released as Kalpa Samrudhi) also recorded higher fruit, copra, and oil yield as compared to the MAWA (MYD × WAT) hybrid (Jerard et al. 2015). Table 10.2 lists the coconut hybrids released for commercial cultivation in different regions of India.

10.4.2 Coconut Breeding Program in Sri Lanka

The coconut breeding program has been in vogue in Sri Lanka since the setting up of the Coconut Research Institute (CRI) of Sri Lanka in 1928. The requirements of the local coconut industry has led to the identification and selection of coconut accessions with high nut yield and copra content (Peries 1994; Liyanage et al. 1988).

Fig. 10.4 MYD × NLGD, a promising Dwarf × Dwarf coconut hybrid

In Sri Lanka, coconut production depends on the annual rainfall pattern since it is widely grown under rainfed conditions, and tall coconut cultivars are predominantly grown in Sri Lanka. In the early 1940s, coconut improvement programs had commenced with crossing selected Sri Lanka Tall cultivars to develop the improved T × T hybrids (CRIC 60). During 1965, breeding for D × T hybrid (CRIC 61) was also initiated. In 1955, the first isolated seed garden was established for the mass production of improved cultivar CRIC 60. In the early 1970s, the coconut biotechnology program was initiated at CRI.

A coconut germplasm conservation program initiated in Sri Lanka during 1984 has led to the preservation of over 90 distinct accessions and diverse ecotypes in CRI field genebanks (Samarajeewal et al. 2005). In Sri Lanka, coconut germplasm conservation has primarily focused on ex situ conservation of phenotypically diverse coconut collections and randomly identified collections from different parts of Sri Lanka. Later, in situ conservation of farmers' collections was given due importance for sustainable production. In 1992, a new and uncommon dwarf form, Sri Lankan

Table 10.2 Coconut hybrids released for commercial cultivation in India

Hybrid	Parents	Important traits	Institution responsible for release
Chandra Sankara	COD × WCT	High yield	ICAR-CPCRI
Kera Sankara	WCT × COD	High yield, drought-tolerant	ICAR-CPCRI
Chandra Laksha	LCT × COD	High yield, drought-tolerant	ICAR-CPCRI
Kalpa Samrudhi	MYD × WCT	Dual-purpose variety, drought-tolerant, good nutrient use efficiency	ICAR-CPCRI
Kalpa Sankara	CGD × WCT	Tolerant to root (wilt) disease, high yield	ICAR-CPCRI
Kalpa Sreshta	MYD × TPT	Dual-purpose variety, high yield	ICAR-CPCRI
Laksha Ganga	LCT × GBGD	High yield	KAU, Kerala
Ananda Ganga	ADOT × GBGD	High yield	KAU, Kerala
Kera Ganga	WCT × GBGD	High yield	KAU, Kerala
Kera Sree	WCT × MYD	High yield	KAU, Kerala
Kera Sowbhagya	WCT × SSAT	High yield	KAU, Kerala
VHC-1	ECT × MGD	High yield	TNAU, Tamil Nadu
VHC-2	ECT × MYD	High yield	TNAU, Tamil Nadu
VHC-3	ECT × MOD	High yield	TNAU, Tamil Nadu
Godavari Ganga	ECT × GBGD	High yield	ANGRAU, Andhra Pradesh
Konkan Bhatye Coconut Hybrid 1	GBGD × ECT	High yield	Dr. BSKKV, Maharashtra
Kalpa Ganga	GBGD × FJT	High yield, suitable for ball copra production	UHS, Bagalkot, Karnataka
Vasista Ganga	GBGD × PHOT	High yield	Dr. YSR Horticultural University (Dr. YSRHU), Andhra Pradesh
Abhaya Ganga	GBGD × LCT	High yield	Dr. YSRHU, Andhra Pradesh
VHC-4	LCT × CCNT	High yield	TNAU, Tamil Nadu
Vynateya Ganga	PHOT × GBGD	High yield	Dr. YSRHU, Andhra Pradesh

Brown Dwarf, with a high number of female flowers and yield, was identified and used in hybrid production. Sri Lanka Brown Dwarf was used to produce two new coconut hybrids by crossing it with Sri Lankan Tall (hybrid CRISL2012 or Kapsuwaya) and San Ramon Tall (hybrid CRISL2013 or Kapsetha). CRI has developed and released six improved coconut cultivars for coconut growers, and among them, four were D × T hybrids (Dissanayaka et al. 2012).

10.4.3 Coconut Breeding Program in Indonesia

In Indonesia, the breeding program under the aegis of the Research Institute for Coconut and Palme (RICP) have led to the industrialization of the coconut industry. The aims of the breeding program are the development of coconut hybrids possessing early bearing, high copra yield, suitable for marshy or drought regions, resistant to diseases, requiring low input, and suitable for food industry purposes (Hengky et al. 1998).

Collection of coconut ecotypes from adjoining areas of Java was the initial research activity followed by surveys in 11 provinces of Indonesia (Liyanage 1974) to identify coconuts for seed gardens and select useful genotypes for the coconut improvement program. The best performing populations, viz., Tenga Tall (DTA) (North Sulawesi), Nias Yellow Dwarf (GKN) (North Sumatra), Bali Tall (DBI) (Bali Island), and Palu Tall (DPU) (Central Sulawesi), were planted at the Mapanget Experimental Garden. The research priority was accorded for the production of D × T hybrid seeds by setting up appropriate seed gardens. Later collections were planted at the research farm at Pakuwon, West Java, and coconut accessions from different parts of Indonesia were planted at the Bone-Bone Experimental Garden, South Sulawesi (Novarianto et al. 1998).

Initially, the main objective of systematic coconut breeding in Indonesia was to identify the diverse coconut populations in Moluccas Provinces and East Nusa Tenggara and initiate efforts to characterize the accessions and conserve them at ICG for Southeast and East Asia (ICG-SEEA) at Sikijang, Riau, Indonesia. These exploratory surveys have identified seven ecotypes (six Talls and one Dwarf) (Novarianto et al. 1998). Later the exploration surveys in different provinces of Indonesia collected 107 accessions and are being conserved in experimental gardens of the Indonesian Coconut and Palmae Research Institute (ICOPRI) and the ICG-SEEA. Notable among them is Mamuaya Tall from North Sulawesi, which is currently being used as genetic material for breeding and distribution in seed gardens.

Around 15 coconut ecotypes were used in the national breeding program. The addition of dwarfs and talls sourced from local and exotic lands has further increased the genetic variability. For instance, Igo Daku, Mapanget, Bali, Riau, Sawarna, Tenga, Palu, and other local talls were found to yield high copra.

The hybrid PB 121 was introduced from Port Bouet, Côte d'Ivoire, in 1975 to develop coconut hybrids having resistance to nut fall and bud rot as these two disorders were a serious menace. Exploratory surveys jointly conducted by the Directorate General of Estate Crops and Coconut Division Director of IRHO (Institut de Recherches pour les Huiles of Oléagineux) to identify sources resistant to bud rot disease caused by *Phytophthora* sp. revealed that most of the standing hybrids were susceptible to the disease. However, some genotypes such as RLT, DJP, PYT, and DBI (Bali Tall) were relatively resistant to bud rot, while hybrid PB 121 and WAT were susceptible. Hence, the hybrid of MYD × PYT was found to be highly resistant to the disease. Three D × T hybrids, namely, KHINA-1 (Nias Yellow Dwarf ×

Tenga Tall), KHINA-2 (Nias Yellow Dwarf × Bali Tall), and KHINA-3 (Nias Yellow Dwarf × Palu Tall), which yield 4–5 t copra ha^{-1} year^{-1} and flower within 3 years after planting were released during 1984 by the Ministry of Agriculture. Later four T × T hybrids, developed by hybridization between selected Mapanget Talls (MPT), viz., KB-1, KB-2, KB-3, and KB-4, with potential to yield 4–4.5 t copra ha^{-1} year^{-1} (Balitka 1989), were also released. The other T × T hybrids produced were Tenga Tall (TGT) × Bali Tall (BAT), TGT × TGT, BAT × TGT, TGT × Palu Tall (PUT), BAT × PUT, and BAT × BAT (Novarianto et al. 1998).

Further, to develop new hybrids with high yield, early bearing and requiring medium inputs, the following crosses were made: Raja Brown Dwarf (RBD) × Mapanget Tall (MPT), NYD × Takome Tall (TKT), Bali Yellow Dwarf (BYD) × MPT, and BYD × TKT. To develop coconut hybrids with high yield, early bearing and suited for swampy area conditions, the following crosses were made: NYD × Riau Tall (RUT), TebingTinggi Dwarf (TTD) × RUT, and Salak Dwarf (SKD).

More than 90 coconut germplasm have been selected and collected in the International Coconut Genebank (ICG) at Indonesian Palm Crops Research Institute (IPCRI) and the Assessment Institute for Agricultural Technologies, North Sulawesi. Approximately 40 coconut accessions were officially released as superior national varieties and superior local varieties (Novarianto et al. 1998).

In situ exploration and characterization of coconut germplasm in early 2016 led to the discovery of Bido coconut in Morotai Island, North Maluku Province (Novarianto et al. 2016). The Bido coconut begins flowering at the age of 3 years and produces many fruits of large fruit size with the fresh meat weight of 534 g nut^{-1}, with short stems; the rate of growth in the height of the trunk is slower than the local tall coconut. Bido coconut pollen has been used as a male parent to pollinate the three superior Dwarf coconut varieties (Nias Yellow Dwarf (NYD), Yellow Dwarf Bali (BYD), and Raja Brown Dwarf (RAD)). The offsprings of these crosses were expected to be superior coconut hybrids. Table 10.3 lists the important coconut varieties released in Indonesia.

10.4.4 Coconut Breeding Program in the Philippines

Traditionally, coconut stands in the Philippines are dominated by talls (97%), as MYD × WAT hybrids and Philippine Coconut Authority (PCA) local hybrids (PCA 15-1, PCA 15-2, and PCA 15-3) occupied relatively less area (Magat 1993). The prominent tall populations grown are Baybay (BAY), Bago-Oshiro (BAO), Macapuno (MAC), Laguna (LAG), San Ramon (SNR), Hijo Tall (HJT), and Tagnanan (TAG). The dwarf varieties include Tacunan (TAC), Catigan (CAT), Aromatic (ARO), and Kinabalan (KIN).

The Bureau of Plant Industry (BPI), Tiaong, Quezon; Visayas State College of Agriculture (ViSCA), Baybay, Leyte; and College of Agriculture, University of the Philippines (UPLB), Los Baños, Laguna, were involved in germplasm collection (Santos et al. 1984). The collected germplasm was planted in the PCA Research

Table 10.3 Coconut varieties of Indonesia released by the Ministry of Agriculture

No.	Variety	Important traits	Origin
1.	Mapanget Tall	High yield	North Sulawesi
2.	Tenga Tall	High yield	North Sulawesi
3.	Bali Tall	High yield	Bali
4.	Palu Tall	High yield	Central Sulawesi
5.	Sawarna Tall	High yield	West Java
6.	KimaAtas Tall	High yield	North Sulawesi
7.	Banyuwangi Tall	High yield	East Java
8.	Jepara Tall	High yield	Central Java
9.	LubukPakam Tall	High yield	North Sumatera
10.	Rennel Tall	High yield	Rennell Island, Pacific
11.	Takome Tall	High yield	North Maluku
12.	Sikka Tall	High yield	Nusa Tenggara Timur
13.	BojongBulat Tall	High yield	Jogyakarta
14.	Kramat Tall	High yield	Gorontalo
15.	Molowahu Tall	High yield	Gorontalo
16.	Adonara Tall	High yield	Nusa Tenggara Timur
17.	Panua Tall	High yield	Gorontalo
18.	Mastutin Tall	High yield	Nusa Tenggara Barat
19.	Sri Gemilang Tall	Swampy tolerant	Indragiri Hilir
20.	Kopyor PuanKalianda Tall	Soft endosperm	South Lampung
21.	Buol St-1	Semi-tall	Central Sulawesi
22.	Nias Yellow Dwarf	dwarf	Nias, North Sumatera
23.	Bali Yellow Dwarf	dwarf	Bali
24.	Salak Dwarf	Many nuts per bunch, dwarf	South Kalimantan
25.	Raja Dwarf	dwarf	North Maluku
26.	Kopyor Green Dwarf	Soft endosperm	Pati, Central Java
27.	Kopyor Brown Dwarf	Soft endosperm	Pati, Central Java
28.	Kopyor Yellow Dwarf	Soft endosperm	Pati, Central Java
29.	Kopyor PuanKalianda	Soft endosperm	Lampung
30.	KB-1 (MT #32 × MT # 32)	High yield	IPCRI
31.	KB-2 (MT #32× MT #2)	High yield	IPCRI
32.	KB-3 (MT #32 × MT #83)	High yield	IPCRI
33.	KB-4 (MT #32 × MT #99)	High yield	IPCRI
34.	KHINA-1 Hybrid	High yield	IPCRI
35.	KHINA-2 Hybrid	High yield	IPCRI
36.	KHINA-3 Hybrid	High yield	IPCRI
37.	KHINA-4 Hybrid	High yield	IPCRI
38.	KHINA-5 Hybrid	High yield	IPCRI
39.	Red Cungap	High antioxidant	Banten
40.	Bido Tall	High yield, early bearing Morotay	North Maluku Source

Source: Elsje Tenda (2004), Novarianto et al. (1994), and Tampake et al. (2002)
KB-Kelapabaru = new hybrid; KHINA = Kelapa Indonesia (Indonesian coconut)

Centers at Davao and Zamboanga (both in Mindanao) and Albay (Luzon) (Santos and Rivera 1998). Currently, the Philippines have 224 coconut accessions in the International Coconut Genetic Resources Database (CGRD) of the COGENT. Sixteen coconut varieties were registered with the Philippine National Seed Industry Council (NSIC), whereas the report of the Research, Development, and Extension Branch of the Philippine Coconut Authority (RDEB-PCA) states that 15 coconut hybrids are registered.

The use of nine tall and seven dwarf promising populations has led to the development of 97 hybrids since the early 1970s. Screening of 31 cultivars for cadang-cadang disease (either by artificial inoculation or natural screening) resistance led to the development of 6 hybrids and 3 selfed lines at Albay Research Center.

Three PCA-recommended hybrids, Malayan Red Dwarf or MRD × TAG (PCA 15-2), MRD × BAY (PCA 15-3), and CAT × LAG (PCA 15-1), are being produced by assisted pollination technique. BAY, a local tall cultivar, is also recommended as planting material. Promising varieties like CAT, TAC, MRD, ARO, BAY, and RIT are used for the multiplication and purification of seed nuts for seed gardens. Eleven accessions, viz., Rennel Island Tall (RIT), West African Tall (WAT), Gazelle Peninsula Tall (GPT), Vanuatu Tall (VTT), Markham Valley Tall (MVT), Malayan Red Dwarf (MRD), Malayan Yellow Dwarf (MYD), Sri Lanka Green Dwarf (SGD), Karkar Tall (KKT), Equatorial Guinea Green Dwarf (EGD), and Aromatic Green Dwarf (AROD), are of foreign origin as a part of global coconut breeding program of COGENT. Apart from the 11 introduced accessions, 22 genotypes are hybrid/line collections. The first three locally produced hybrids, namely, PCA 15-1 (CATD × LAGT), PCA 15-2 (MRD × TAGT), and PCA 15-3 (MRD × BAYT), were mass-produced using the assisted pollination breeding technique for the planting/replanting program. Other hybrids that produced PCA 15-4 (CATD × TAGT) and PCA 15-5 (CATD × BAOT), among others, were also registered with the National Seed Industry Council (NSIC).

Santos et al. (2000) reported that these hybrids were selected based on their stable yield performance and economic profitability. Registered local Tall and Dwarf varieties are TACD, CATD, TAGT, BAOT, and BAYT. The PCA has introduced the SynVar 001, known as Genetically Multi-Ancestored Farmers Coconut Variety (nicknamed "GMA Coconut Variety"), which is considered the hybrid of hybrids. The F1 hybrids derived from six Tall populations having reasonably a good general combining ability formed the base populations of the GMA. GMA is thus an open or cross-pollinating population of highly heterozygous individual palms. Farmers can use the subsequent seed generation for successive planting and making them more self-reliant. Two Dwarf varieties of the Philippines, Tacunan Green Dwarf (TACD) and Galas Green Dwarf (GALD), which were superior to the famous Thai aromatic varieties Nam Hom (HOM) and Nam Wan (WAN), were developed for young tender coconut.

The introduced hybrid MYD × WAT (MAWA) produced inflorescence earlier than the local talls and consequently produced fruits a couple of years earlier than the local genotypes. MAWA produced small-sized nuts compared to local talls and yielded an average of 229 g of kernel per nut, whereas local tall like BAY yielded 476–534 g of kernel per nut.

The PCA recommended nine hybrids derived from the local cultivars, viz., Tagnanan Tall (TAGT), Catigan Green Dwarf (CAT), Laguna Tall (LAGT), Baybay Tall (BAYT), and Bago-Oshiro Tall (BAOT), and the introduced varieties Malayan Red Dwarf (MRD) and Polynesian Tall (PYT). These hybrids started flowering from the third to fourth year onward. The average number of nuts per palm ranged from 117 to 155, and copra yield per hectare ranged from 4 to 6 tons. The local Tall BAYT was comparatively good, producing 114 nuts per palm with a copra yield of 5 t ha^{-1}. Among the nine hybrids, MRD × TAGT (PCA 15-2) and MRD × BAYT (PCA15-3) were outstanding, giving the highest number of nuts (144–155 palm^{-1}) and copra yield (6 t ha^{-1}).

10.4.5 Coconut Breeding Program in Thailand

Coconut germplasm collection was established in Thailand in 1965 when a few cultivars from local and foreign countries were collected and exploited in the Chumphon Horticulture Research Centre (CHRC). A coconut germplasm genebank (COGENT/ADB project), with 20 local coconut accessions, was later established at Kanthuli, Surat Thani Province, in 1997 (Petchpiroon and Thirakul 1998).

The talls were traditionally preferred. Initially, the coconut palm was confined to the west and east coasts and off-shore islands; however, coconut has expanded to inland areas. Phenotypic differences were observed between the coconut varieties grown on the two coasts of peninsular Thailand. Pak Chok (PCK) and Thalai Roi (TLR) were the two populations grown on West Coast. Owing to their small to medium-sized nuts with more husk and less meat than the predominant talls, these varieties are not grown on a large scale. The commercial coconuts are Maphrao Yai or Thai Tall (THT), which has large, green, or reddish-brown round-shaped fruit. In the country's central region, the Toddy variety is another tall population grown because of its relatively high sugar content in the inflorescence sap. Besides, dwarfs are also being grown for a tender nut purpose (Petchpiroon and Thirakul 1998).

In the national coconut genebank at Kanthuli, Thailand, 34 coconut ecotypes were collected and conserved. Characterization was done for the 20 existing accessions maintained in Chumphon Horticulture Research Centre (CHRC). The tall forms include Hua Ling, Thalai Roi, Pak Chok, Pulak Wan, Klang, Maphraeo, So, Yai, and YaiPhiset. The dwarf form includes Mu Si, Nok Khum, Nam Hom, Mu Si Khieo, Thung Khlet, Mu Si Luang, Nalike, Mu SI Som, Fai, and Pathiu. Besides, a miscellaneous group consists of rare coconut varieties whose affinities are not clearly understood; this includes Phuang, TuenDok, Thale Ba, Nim, Lao Tan, and KonChuk.

Suricha, Thalaeba, and Saiboa were the promising tall coconut varieties for sap and sugar production, yielding about 4–6 L of fresh sap palm^{-1} day^{-1}, whereas Kheekai and Krati varieties produced 3–4 L sap palm^{-1} day^{-1}. Because of their high sap yield per spathe and their strong leaf petiole to support tappers (sap collectors), these tall varieties were preferred by farmers. Sawi Hybrid No. 1 was also identified as a suitable variety for sugar production because of more spathe production and sap yield stability. Aromatic Dwarf and Green Dwarfs were also being grown for sap production. Among the Dwarfs, Green Dwarfs such as aromatic coconut (Nam Hom) and sweet water coconut (Nam Wan) were extensively grown on a commercial scale.

In contrast, other Dwarfs, such as Yellow, Red, and Brown Dwarfs, were found growing in home gardens for tender nuts. These dwarf varieties are considered rare and endangered. A pink mesocarp-type palm from Nam Wan variety was also found to be a rare variety. Recommended hybrids of Thailand include Sawi Hybrid No. 1, Chumphon Hybrid 60 (THT × WAT), and Chumphon Hybrid No 2 (MYD × THT). Studies have shown that the MYD × WAT hybrid was the most precocious with the highest yield, followed by the THT × WAT hybrid, whereas the THT yielded the least. The results of the local hybrid varieties trial had shown the MYD × THT hybrid was also precocious as that of MYD × WAT and had bigger nuts. Higher yields and drought resistance are the objectives of the current coconut improvement program.

10.4.6 Coconut Breeding Program in Vietnam

The Institute for Research on Oils and Oil Plants, also known as the Oil Plants Institute of Vietnam (OPI), established in 1980, undertakes research activities pertaining to coconut. The objectives of the Vietnam coconut breeding program are to produce elite planting materials that can adapt to a wide range of ecological conditions in the country. In the field genebank of Dong Go Experiment Station, 45 coconut accessions (11 exotic and 34 local accessions) have been conserved. These accessions possess traits for oil, copra content and tolerance to the acid sulfate soil of the Mekong Delta and adapted to alluvial soils of the Mekong Delta, sandy soil of Central Vietnam's coastline, for the industrial zones, highlands and mountain areas of Central Vietnam, island area, for tender nut purpose for the Mekong Delta, and rare and precious traits (Long 1998).

Superior performance was observed with some populations, e.g., Sri Lanka Green Dwarf, Catigan, West African Tall, Malayan Yellow Dwarf, Hijo Tall, and San Ramon. The coconut hybrids have been produced locally using the available genetic materials PB121, PB141, JVA1, JVA2, MYD × Ta Tall, Tam Quan × Hijo Tall, MYD × Rennel Tall, and MYD × Palu Tall, and the Rennell Tall and Palu Tall pollens were collected from Indonesia.

Ta is the most extensively grown traditional variety in the country. It has large-sized fruits with 260–280 g of copra nut^{-1}. Dau is the second most promising variety under cultivation, with a high number of medium size nuts per bunch and high copra content of 180–220 g of copra nut^{-1}. Giay is another popular variety in the central region, particularly along with the coastal areas, and it has big-sized nuts and a high number of nuts per bunch. However, Bi or Bung coconut variety has the largest nut size (2.7 kg) but with a low number of nuts bunch^{-1}. Some genotypes with special characters are Ngot (sweet), Sap (Macapuno), Soc (stripe), and Dua (aromatic).

Eo, Xiem, and Tam Quan were the three distinct dwarfs mainly preferred for nut water because of their aroma and high water sugar content (9.8%). Eo variety produces brown color small-sized nuts (20–40 nuts per bunch). Xiem variety has green color nuts with big size (15–20 nuts bunch^{-1}). Tam Quan coconut variety has yellow color nuts with good fruit component parameters. Among the dwarf types, Tam Quan is considered the most promising material.

PB 111, PB 121, PB 132, and PB 141 hybrid seed nuts were introduced into the country in 1984, followed by introducing JVA1, JVA2, and CRIC 65 in 1986. The seedlings of indigenous hybrids, i.e., Tam Quan × Ta, Eo × Ta, and Tam Quan × BAOT, were evaluated in Dong Go Station, and MYD × Palu Tall, MYD × Rennel Tall, and MYD × Ta were being evaluated at Binh Thanh Experimental Station. Trang Bang coconut seed garden is producing the hybrid PB 121, and it is the only coconut seed garden in the country operating under the assistance of IRHO.

10.4.7 Coconut Breeding Program in Papua New Guinea

Nationwide coconut prospection surveys were conducted by the Coconut Breeding Section of Papua New Guinea (PNG) Cocoa and Coconut Research Institute (CCRI), leading to the planting of 42 talls (Rennell Tall and 41 local) and 11 dwarfs (5 among them are exotic). A hybridization program was initiated involving the crossing of selected local talls with three dwarfs, viz., Malayan Red Dwarf (MRD), Malayan Yellow Dwarf (MYD), and PNG Brown Dwarf (PBD). The progenies from these crosses were planned to undergo both general combining ability tests to identify suitable hybrid combinations. The trials include both population and single plant improvement to select the best parents for future hybridization programs. The IPGRI and the Government of PNG signed a Memorandum of Agreement through the Department of Agriculture and Livestock to establish the International Coconut Genebank for the South Pacific (ICG-SP) with PNG-CCRI as host (Faure and Moxon 1998).

The high yield and early bearing of the MAREN hybrid (Malayan Yellow Dwarf × Rennell Tall) than the local cultivars have been demonstrated in PNG at Bubia and Kerevat (Brook 1985). However, MAREN is susceptible to beetle attack. Compared with MRD × RT, the low yield was observed with MAWA (MYD × WAT), which is also susceptible to beetle attack. Rennell Tall outyielded the local tall varieties; however, it is also susceptible to beetle attack. The common insect pests include two beetles, one weevil, and a tree hopper. Most of the exotic accessions and cultivars are susceptible to beetle attack causing palm death. The 78 series of D × T hybrids developed are being field-tested. Besides, four Dwarf and four Tall accessions have been used to develop new progenies for GCA trials.

10.4.8 Coconut Breeding Program in Fiji

In Fiji, the Taveuni Coconut Centre (TCC) has been maintaining four dwarf varieties (MD, MYD, MRD, and NLD) along with three tall varieties (FJT, RLT, and ROT). Progenies of Fiji Tall palms, which were selected from two populations of Taveuni, were maintained and monitored by TCC. It is the source for germplasm selection for breeding programs, mainly on pure Fiji Tall or on hybrids of Fiji Tall. The notable precocity of the hybrids is inherited from Malayan Dwarfs. The Niu Leka Dwarf confirmed its peculiar character of being a late bloomer (only 33% of palms flower after 50 months) (Kauvere 1998).

TCC has established a cooperation scheme involving Fiji, France, and the European Economic Council (EEC). Under bilateral cooperation between Fiji and France, regular breeding activities are carried out. In 1992, hybridization work commenced, and emphasis was given to breeding for total copra content since wide variation exists in copra/nut ratio between accessions. The trait has a high heritability value and makes sure its rapid improvement by selection.

The germplasm maintained at TCC is characterized according to CIRAD (Centre de Coopération Internationale en RechercheAgronomique pour le Développement) standards and is utilized in breeding programs. Susceptibility of the germplasm to the endemic disease, coconut foliar decay (CFD), is evaluated in the field and by artificial inoculation under controlled condition.

The D × T hybrid evaluation is one of the major breeding activities. Four D × T hybrids were developed; these hybrids had Malayan Red Dwarf as their female parent and Fiji Tall, Rennell Island Tall, Rotuman Tall, and Niu Leka as male parents. The performance of the hybrids was then compared with Fiji Tall.

CFD is a severe disease that restricts the exploitation of exotic materials for varietal improvement. Hence, the research priority is given to the less sensitive ecotypes to CFD, like Rennell Island Tall, to improve the local cultivars. Further selected ecotypes will be crossed with the local tolerant ones.

10.4.9 Coconut Breeding Program in Vanuatu

Vanuatu germplasm collection, which comprises local and imported ecotypes, is entirely maintained in a field genebank. Talls, T × T hybrids, and D × T hybrids are the three major coconut types grown in Vanuatu.

The Vanuatu Agricultural Research and Training Centre (VARTC), located at Saraoutou, Santo Island, is engaged in undertaking coconut breeding programs. The main goals of the breeding program are tolerance to CFD, high yield, nut size at least equivalent to that of Vanuatu tall (VTT), germination curve similar to that of the VTT, tolerance to low levels of fertilizer, and ability to adapt under the local cultural management conditions. Hence, tall and of T × T hybrid development activities remain important, although D × T would give a higher yield (Duhamel 1998).

The exploitation of CFD tolerance sources existing in the local ecotypes is important for developing planting materials in Vanuatu. Introgressions of genes from exotic ecotypes were carried out to rectify the productivity limitations of these ecotypes. This recombination enforces the application of selection pressure at each generation for tolerance to CFD.

Presently, the Vanuatu coconut germplasm resources consist of three types of cultivars, namely:

- A tall cultivar (VTT) – CFD tolerance, precocious, small nuts, and average productivity
- A local hybrid [VRD (Vanuatu Red Dwarf) × VTT] – CFD tolerance, very small nuts, and very slow germination
- Hybrids of introduced ecotypes – productive but CFD susceptible

The breeding program of VARTC has several lines of actions, aiming to produce different types of improved cultivars. Hybrids involving the local cultivars VTT and VRD and the introduced Rennell Island Tall (RIT) and Brazilian Green Dwarf (BGD) were developed. The MRD was also crossed with RIT to develop hybrids that performed better than the local VTT in copra yield but are highly susceptible to CFD. The BGD crossed with either VTT or RIT produced the best copra yields of 4.4–5.2 t ha^{-1}; however, the hybrids were highly susceptible to CFD. Relatively low copra yield (3.3–3.7 t ha^{-1}) was observed with VRD × VTT hybrids, but these were found to be more tolerant to CFD. The lowest copra yields of 2.6–2.8 t ha^{-1} were observed with both the traditional and improved VTT types, but the yield is comparable with the hybrid MRD × RIT.

10.4.10 Coconut Breeding Program in Côte d'Ivoire

The Centre National de Recherche Agronomique (CNRA) is the authority for agronomic research nationwide in Côte d'Ivoire. The Marc Delorme Research Station in Abidjan located in the southern part of the Côte d'Ivoire is the headquarters for the Coconut Program of CNRA. From 1967 to 1986, a total of 53 coconut accessions were introduced. Coconut research activities were executed mostly in collaboration with the French Government. Conservation and evaluation of coconut accessions in the field genebank, utilization of the germplasm to detect the best combinations among the ecotypes, and improvement through the production of hybrids identified through progeny tests were the breeding strategies in Côte d'Ivoire (De Lamothe 1970; Gascon and De Lamothe 1976). This method has been restructured into two different axes (D × T and T × T) using the reciprocal recurrent selection (Bourdeix et al. 1990, 1991a, b).

The coconut yield is often limited by phytopathological problems. *Phytophthora katsurae* is the only disease with economic significance causing bud rot and premature nut fall in infected palms. In addition to chemical control methods, few disease-tolerant hybrids are being released by the Marc DELORME Research Station. The

Aceria mite is an important pest that damages fruits, causing a reduction in the copra content. At Marc Delorme Research Station, production performance and physiological characteristics under drought conditions of young and old coconut varieties and hybrids have also been studied (Konan 1997; Repellin et al. 1994a, b), with the objective of identifying drought-tolerant lines. Further, in collaboration with Ghana, 30 varieties and hybrids from CNRA have been tested for resistance to LYD (Konan et al. 2002).

Côte d'Ivoire germplasm collection became the centerpiece of the International Coconut Genebank for Africa and the Indian Ocean (ICG-AIO) from 1996 onward. Generally, an average Ivorian coconut grove consists of 52% West African Tall (WAT) and 48% hybrids. PB121 (Malayan Yellow Dwarf × WAT) is predominant among the hybrids. PB111 (Cameroon Red Dwarf × WAT) and PB141 (Guinean Green Dwarf × WAT) were the other cultivated hybrids. WAT is the only local ecotype that is phenotypically very homogeneous and represents more than 50% of coconut palms. The yield difference between the West African Tall and the hybrids was highly significant. Best F_1 hybrids yielded twice as much as the local WAT at the Marc DELORME Research Station. The copra yield was 3.1 t and 2.1 t for the hybrids and the WAT, respectively (De Taffin et al. 1991). Similarly, the hybrids outyielded the local cultivars in several cultivated areas of Côte d'Ivoire.

In 1953, the Institut de Recherches pour les Huileset Oléagineux (IRHO) introduced 53 ecotypes from different tropical areas at the Marc DELORME Research Station since local cultivars showed limited genetic variability. These ecotypes display broad geographic diversity within a large population size. The different ecotypes have their origin from Latin America, Africa, the Caribbean, the Pacific, the Indian Ocean, and Southeast Asia. This important field genebank consists of 36 talls and 17 dwarfs.

In addition to the 53 ecotypes, 160 selfed families of West African Tall, which are selected genitors, and 25 tall × tall hybrids were used for breeding and germplasm conservation.

A total of 121 inter-ecotype hybrids were tested in Côte d'Ivoire from 1965 to 1993. The first genetic trials compared 35 hybrid combinations from intercrossing 35 parent ecotypes wherein WAT was used as a control. Seven inter-ecotype hybrids were identified, which was significantly superior to the control WAT. None of them performed less than the control, and four of these yielded twice that of the WAT. The other early breeding trials used PB121 as a control (De Lamothe and Benard 1985). These trials resulted in new promising hybrids which were very productive during the adult stage (9–12 years) and highly tolerant to *Phytophthora* than the control PB121. PB213 (WAT × Rennell Tall) and improved PB121 are being used as a control for the breeding trials since 1993 (Bourdeix et al. 1992). Thirty years of continuous breeding research resulted in 121 inter-ecotype hybrids (26% of the possible combinations). In the tall × tall hybrids, the basic trials comprised crossing every new accession with two complementary tall testers with known characters. WAT and Rennell Tall are being used as testers in Côte d'Ivoire. In Dwarf × Tall hybrids, basic trials consisted of crossing every new accession with a single tester. The tall cultivars were tested with the Malayan Yellow Dwarf, while for the dwarfs one tall ecotype was used as a tester (WAT and improved WAT × Rennell Tall hybrid). The complementary trials have more complicated crossing schemes. These trials are intended to provide genetic information on the type of gene action involved in coconut hybrid vigor.

Relative precocity is the main advantage of the Dwarf × Tall hybrids. Nevertheless, this advantage over the T × T hybrids is not sufficient for eliminating the latter. The yield of the WAT × RIT hybrid is equivalent to the widely grown hybrid PB121 in the ninth year. However, this T × T hybrid later out yielded the PB121 control (IDEFOR/DPO 1992).

In 1970, the second phase of the breeding program was initiated (Gascon and De Lamothe 1976) to improve the best detected hybrids individually. In this method, to improve PB122 (MYD × Polynesian Tall), 45 selected TAT (Tahitian Tall) palms were crossed individually with the same Malayan Yellow Dwarf (MYD) population. These half-sib progenies were tested in comparative hybrid trials.

The improvement of an inter-ecotype hybrid involved two complementary crossing designs: palms from each population were crossed individually onto a set of palms in the other population and reciprocally. When unequal levels of variability exists in two populations, then this approach can be simplified. The male parents were tested individually and were later selfed to obtain progenies for conservation and multiplication. Pollen obtained from these self-pollinated progenies will be used for hybrid seed production. The results showed that selecting 7–8% of the best families resulted in 15–30% genetic gain depending on the trials (Bourdeix et al. 1989). Based on the trials, the following guides were formulated for effective breeding strategies:

- Progeny test is important, especially for genitor selection, and it cannot be replaced with a phenotypic selection of parents.
- Genetic progress is mainly due to the improvement in the number of nuts per bunch. In some cases, the percentage of copra in the fruit without water is slightly improved.

Since 1976, the complex hybrids were developed in Côte d'Ivoire. Evaluation of the genetic variability of hybrid progenies and selection of outstanding individuals for multiplication were the objectives of this program. The following combinations of crosses were being tested:

GYD × (WAT × TAT)	(WAT × TAT) × RIT
GYD × (WAT × RIT)	LMT × (WAT × RIT)
(CRD × MYD) × (WAT × RIT)	(CRD × RIT) × (EGD × WAT)
(MYD × WAT) × (EGD × RIT)	(MRD × RIT) × (WAT × TAT)
(MRD × MYD) × (WAT × TAT)	(MRD × WAT) × (TAT × VNT)

Le Saint and de Lamothe (1987) reported that the hybrid between the Malayan Yellow and Red Dwarfs yielded 3.8 t of copra ha^{-1} during the adult phase, at a planting density of 170 palms ha^{-1} in Côte d'Ivoire. The control cultivar MYD produced one t of copra ha^{-1} in the same trial, which was less than the hybrid, and the yield is comparable to the D × T materials (IRHO-CIRAD 1989). However, dwarfs are not broadly adapted, and they are not tolerant to drought (Ziller 1962). These undesirable traits could be transmitted to their hybrid progenies, and there is less genetic variability than talls. Thus, the long-term genetic potential of the dwarfs is limited. However, the precocity and the more number of bunch production are valuable traits of the dwarf ecotypes. For accumulating such desirable genes, D × D hybrids should be created and incorporated in a breeding scheme, although the primary goal may not be to release this type of material (Bourdeix et al. 1991a).

D × T and T × T were the two important breeding schemes. Production of three-way hybrids using D × D, D × T, or T× T female genitors was suggested by Harries (1991). Some accessions with composite characters could be exploited for fruit or hybrid seed nuts production based on the demand. Based on the outcome of the genetic trials (Bourdeix et al. 1990, 1991a, b), new directions of the coconut breeding program were proposed at the Marc DELORME Station. The proposed method was based on the reciprocal recurrent selection (RRS) method (Comstock et al. 1949). Improvement of T × T and D × T hybrids are the two main areas. The conception of the D × T axes was relatively simple. The dwarfs and the talls are two different types with some complementary characters, and the combining ability between these two types is very good. The conception of the T × T was more difficult. The tall ecotypes represented the main component of the genetic variability in coconut. Some combinations expressed high heterosis. Morphological approaches (Harries 1978; N'Cho et al. 1993) provide some idea on the partitioning of the tall population. However, the current knowledge of coconut genetic diversity is not enough for efficient exploitation in breeding programs.

There is a lack of accurate technique for assessing genetic distances between and among ecotypes in the T × T hybrid improvement. Two artificial populations were created and improved in respect of each other by half-sib RRS based on two founder ecotypes. The choice of the founder ecotypes should take into account the different constraints of the specific breeding program. The availability of the material and phytopathological status have to be considered. One of the ecotypes should be a local variety. The analysis of genetic trials guided the choice of the WAT (Côte d'Ivoire and Benin) and the RIT (Pacific) as founders in Côte d'Ivoire. These two ecotypes showed good combining ability between themselves as well as with other dwarf and tall ecotypes. Some genitors with excellent general combining ability were identified from these two ecotypes (Bourdeix et al. 1989, 1992), and using these genitors as testers has several advantages.

Further, multilocation trials to identify suitable coconut hybrids and varieties for Africa, Latin America, and the Caribbean were also undertaken. Côte d'Ivoire, along with six other countries, viz., Tanzania, Benin, and Mozambique in Africa; Brazil and Mexico in Latin America; and Jamaica in the Caribbean, was involved in the implementation of the Common Fund for Commodities (CFC)-funded project, a collaborative activity between IPGRI-COGENT, CFC, and the Portuguese governments, which included testing six hybrids from Côte d'Ivoire and ten hybrids from the participating countries (Konan 2002).

CNRA experiments identified two varieties, Vanuatu Tall and Sri Lankan Green Dwarf, as highly tolerant of LYD in Ghana. Using these varieties as parents, the CNRA is now producing hybrids to check the spread and destruction of the disease. Initially, the CNRA MarcDelorme Coconut Station identified six outstanding hybrids, viz., PB111 (CRD or Cameroon Red Dwarf ×WAT), PB121 (MYD × WAT), PB123 (MYD × RIT), PB 132 (MRD × TAT or Tahitian Tall), PB 213 (WAT × RIT), and PB 214 (WAT × VTT). These hybrids were precocious (40–57 months after field planting) under Côte d'Ivoire conditions. The nut yield is 100–132 nuts palm^{-1} year^{-1} which is 34–138% higher than the control, WAT. Besides, their copra yields ranged from 3.15 to 4.8 t ha^{-1} or from 86 to 135% more compared with WAT.

10.4.11 Coconut Breeding Program in Ghana

The germplasm collection maintained in Ghana was brought from other countries, particularly Côte d'Ivoire. Eight accessions, viz., Tacunan Green Dwarf, Catigan Green Dwarf, Panama Tall, Tagnanan Tall, Laccadive Ordinary Tall, Andaman Ordinary Tall, Vanuatu Tall (VTT) and West African Tall (Benin), and three hybrids, viz., Sri Lanka Green Dwarf (SLGD) × VTTV, VTT × Panama Tall, and MYD × VTT, were collected from the Marc Delorme Station in Côte d'Ivoire to expand the lethal yellowing (LY) trials for resistant varieties in Ghana. All the cultivars in the country are considered to be at risk of Cape St. Paul Wilt Disease (CSPWD), a lethal yellowing-type disease because of the nature of CSPWD. Hence, the most pressing problem of the coconut industry in Ghana is the CSPWD. In Ghana, this lethal yellowing disease is causing widespread death of palms. Similar diseases are also noticed in Florida, the Caribbean, South America, Togo, Cameroon, and Nigeria (Romney 1972). Efforts are being made to devise suitable disease control measures. Some coconut hybrids, particularly MYD × Panama Tall, are considered resistant to the Caribbean strain of lethal yellows; they are, however, reported to be susceptible to the disease in East Africa. The occurrence of different strains of lethal yellowing phytoplasma in different parts of the world might be the reason for this. Researchers at Rothamsted Research Station in the UK proved that the East and West African strain of LY MLO is different (Tymon et al. 1998).

VTT, SLGD, MYD × VTT showed some degree of tolerance against LY disease. In Jamaica, crosses of MYD with Panama Tall exhibited high tolerance against LY disease. MRD, CRD, and MRD × Polynesian Tall (PYT) were the other cultivars or hybrids which have shown a lesser degree of tolerance. Dery and Philippe (1995) reported that VTT is relatively tolerant to LYD (also locally known as Cape St. Paul Wilt Disease or CSPWD). Bourdeix (2000) reported that the VTT cultivars in Ghana were introduced from Côte d'Ivoire, which is quite variable. Harries (1995) also confirmed the general variability of VTT. The coconut breeding program in Ghana is currently geared toward developing hybrids resistant or highly tolerant to CSPWD.

10.4.12 Coconut Breeding Programs in Other Countries

10.4.12.1 Bangladesh

The Agricultural Research Institute (BARI) has developed two high-yielding coconut hybrids: BARI Narikel-1 and BARI Narikel-2. These hybrids are broadly adapted and capable of producing 65–70 nuts palm^{-1} and suitable for cultivation throughout Bangladesh. In addition, Sri Lankan Tall and Malayan Yellow Dwarf are the two introduced varieties recommended by BARI to the country's coconut growing communities (Batugal 2005b).

10.4.12.2 China

Hybrid derived from Malayan Yellow Dwarf (MYD) and the local Hainan Tall (HAT) was recommended by Wenchang Coconut Research Institute. This hybrid (WY78F1) is early flowering (3–4 years) and has three- to fourfold increase in terms of nut yield (80 nuts palm^{-1} year^{-1}) and copra yield (4 t ha^{-1} year^{-1}) (Batugal 2005b).

10.4.12.3 Tanzania

Evaluation of six hybrids, with the local East African Tall (EAT) as the pollinator, was undertaken at the Mikocheni Agricultural Research Institute (MARI). The mother palms involved Malayan Green Dwarf (MGD), CRD, Pemba Red Dwarf (PRD), MYD, and MRD and improved EAT populations. Apart from the yield performance, the hybrids are also being tested for their resistance to lethal disease and tolerance to drought stress (Batugal 2005b).

10.4.12.4 Mexico

The development of hybrids resistant to lethal yellowing disease is the main objective of coconut research at the Instituto Nacional de Investigacion Agropecuaria Y Forestal. Hybrids were mostly derived from crosses between improved Pacific Tall populations and MYD. Intrapopulation crosses of selected Pacific Tall were also done, and these are being tested (Batugal 2005b).

10.5 Application of Molecular Markers in Coconut Improvement Programs

Molecular markers have been widely employed in investigating the evolutionary lineage, in the reconstruction of phylogenetic relationships, in the investigation of heterosis, in hybrid authenticity, in the assessment of genetic diversity of the germplasm holdings, in genetic mapping and QTL mapping studies, in marker-assisted breeding, including marker-assisted backcross breeding, and in association mapping studies, etc. (Nadeem et al. 2018). Among these, marker-assisted selection (MAS) is a concerted strategy of utilizing traditional breeding approaches in conjunction with DNA, RNA, or protein markers linked to agronomic or economic traits of importance. In the context of coconut, the development of an array of molecular markers and relatively dense genetic linkage maps has greatly aided in the crop improvement programs. DNA-based molecular markers such as inverse sequence-tagged repeat (ISTR) (Rohde et al. 1995), randomly amplified polymorphic DNA (RAPD) (Ashburner et al. 1997), restriction fragment length polymorphism (RFLP) (Lebrun et al. 1998), and amplified fragment length polymorphism (AFLP) (Perera et al. 1998) were effectively developed and employed generally for germplasm diversity analysis. Later the developments in the field of genome sequencing and high-throughput sequencing platforms have enabled the generation of simple sequence repeat (SSR) markers (Perera et al. 1998; Perera et al. 2000; Rivera et al. 1999; Teulat et al. 2000; Meerow et al. 2003; Rajesh et al. 2008; Ribeiro et al. 2010). The use of molecular markers in coconut has greatly facilitated the identification of genetic distinctness of a genotype and assessment of genetic diversity, markers linked to eriophyid mite resistance, lethal yellowing disease resistance, hybrid authenticity, etc. (Shalini et al. 2007; Rajesh et al. 2015; Jerard et al. 2017; Preethi et al. 2020). As stated above, great quantum of research work on molecular markers in coconut has been dedicated to germplasm diversity analysis; however, investigations pertaining to marker-trait analysis, association mapping studies, and use of novel genomics tools are not uncommon (Cardena et al. 2003; Shalini et al. 2007; Rajesh et al. 2013, 2014; Boonkaew et al. 2018; Saensuk et al. 2016). Application of molecular markers in coconut improvement programs is enlisted in Table 10.4.

Market-trait association analysis in coconut using bulked segregant analysis of DNA of contrasting coconut accessions (West African Tall, Malayan Yellow Dwarf, Atlantic Tall) identified 12 RAPD molecular markers putatively linked with the lethal yellowing disease resistance (Cardena et al. 2003). Similarly, five molecular markers linked to coconut mite resistance were identified by Shalini et al. (2007) based on SSR and RAPD analysis. Besides biotic resistance, marker-trait association studies have been performed for agronomic traits such as palm habit, which profoundly influence plant protection and harvest operations. Rajesh et al. (2013) identified RAPD markers, later developed into sequence-characterized amplified region (SCAR) markers, to differentiate tall and dwarf genotypes of coconut. Genotypic differentiation of "pandan-like" aromatic and non-aromatic coconut

Table 10.4 Applications of molecular markers in coconut improvement

Sl. no.	Applications	Molecular markers employed	References
1.	Genetic differentiation of coconut genotypes	Restriction fragment length polymorphism (RFLP)	Lebrun et al. (1998)
2.	Genetic diversity and evolutionary lineage analysis	Randomly amplified polymorphic DNA (RAPD)	Ashburner et al. (1997)
3.	Genetic diversity of talls and dwarfs	Amplified fragment length polymorphism (AFLP)	Perera et al. (1998)
4.	Genetic diversity	Inverse sequence-tagged repeat (ISTR)	Rohde et al. (1992)
5.	Genetic diversity of accessions from various geographic regions	Inter simple sequence repeats (ISSR)	Manimekalai and Nagarajan (2006)
6.	Genetic polymorphism	Simple sequence repeats (SSRs)	Rivera et al. (1999)
7.	Genetic distinctness analysis	SSRs	Meerow et al. (2003)
8.	Genetic markers linked with mite resistance	SSRs	Shalini et al. (2007)
9.	Genetic markers linked with LYD resistance	SSRs	Konan et al. (2007)
10.	Genetic diversity	SSRs	Rajesh et al. (2014)
11.	Genetic diversity and the population structure analysis	SSRs	Jerard et al. (2017)
12.	Genic SSRs for genetic diversity analysis	EST-SSRs	Preethi et al. (2020)
13.	DNA polymorphism studies	Start codon targeted polymorphism (SCoT) markers	Rajesh et al. (2015)
14.	Distinction of aromatic and nonaromatic coconuts	Gene-specific markers	Vongvanrungruang et al. (2016)
15.	Detection of biallelic SNPs linked to aroma trait	Gene-specific markers from transcriptome sequences	Saensuk et al. (2016)
16.	Differentiating tall and dwarf genotypes	RAPD converted to SCAR marker	Rajesh et al. (2013)
17.	Hybrid detection	RAPD	Rajesh et al. (2014)

accessions was performed by developing a type-specific DNA marker (Vongvanrungruang et al. 2016) and a functional marker that could distinguish SNP variations between these two genotypes (Saensuk et al. 2016).

Nevertheless, large-scale utilization of molecular markers in backcross breeding to incorporate a gene of agronomic or economic importance or association mapping analysis is severely lacking in coconut. The untapped potential of molecular breeding in coconut could be attributed to serious impediments such as a relatively long breeding cycle, difficulties in identifying and following appropriate selection protocols for yield and yield attributing traits, pest and disease resistance conferring genes, etc., specific to perennial crops. In this context, it is imperative to identify molecular markers tightly linked to the trait of interest, and genetic linkage maps are very useful resources.

10.6 Genetic Linkage Maps in Coconut: QTL Mapping

A genetic linkage map refers to describing the relative positions of the molecular markers and distances among them along a chromosome or linkage group. Availability of a good-quality genetic linkage map plays a significant role in genetic analysis of a trait, accelerates molecular breeding programs, and aids in identifying genetic loci that govern agronomic traits of importance or loci that are linked to biotic or abiotic stress tolerance. Thus, a linkage map is an integral component of any marker-assisted breeding scheme. Even though the physical maps could provide the order of molecular markers, genetic maps are required for validating them and would greatly assist in improving de novo genome assemblies. Also, the characterization of genetic regions linked to quantitative traits and mapping them in linkage maps refer to QTL mapping. It would help analyze the segregation pattern of QTLs and assist the genomics-based breeding in coconut. In coconut, both the strategies of genetic mapping, a) linkage mapping and b) association mapping or linkage disequilibrium (LD) mapping, are followed though the latter is minimally explored (Table 10.5).

Generally, the biparental population is developed from F_2 backcrosses, recombinant inbred lines (RILs), double haploids (DHs), and near-isogenic lines (NILs) (Xu et al. 2017). Owing to its perennial nature, the development of these experimental populations, along with their pedigree information for QTL mapping in coconut, consumes a huge time. Despite the inherent limitations such as limited recombination between the parents causing less mapping resolution (QTLs getting localized to 10–20 cM intervals) and limited phenotypic diversity between the parents, biparental population-based linkage mapping is widely employed in perennials such as coconut. Furthermore, instead of following a conventional strategy of genotyping all the individuals of a population, bulked sample analysis is found to be very effective and cost-efficient for studying the major gene effect or QTLs with a large effect. Rajesh et al. (2013) have effectively utilized this strategy to investigate the palm habit in coconut and identified DNA marker linked to the trait. The strategies of multiparent mapping populations such as nested association mapping (NAM) and multiparent advanced generation intercrosses (MAGIC) in field crops to overcome the limitations of biparental mapping populations remain a challenging task in coconut. Hence, the concept of natural population-based genetic mapping is an invaluable tool to perform linkage mapping studies in crops like coconut due to its high resolution, allelic richness, do away with the tedious development of a mapping population. Thus, linkage disequilibrium or genome-wide association studies (GWAS) utilize the principle of linkage disequilibrium in a set of crop accessions to identify QTLs. This strategy thereby utilizes the phenomenon of historical recombination since the population diversion.

Table 10.5 Salient achievements of trait mapping in coconut through linkage mapping and association or linkage disequilibrium (LD) mapping strategies

Sl. no.	Mapping population	Map length features	QTLs	Molecular markers	References
A. Biparental populations					
1.	Malayan Yellow Dwarf (MYD) and Laguna Tall (LAG)	–	–	ISTR	Rohde et al. (1999)
2.	Laguna Tall × Malayan Yellow Dwarf	Laguna Tall: 2226 cM; MYD 1266 cM	Six QTLs governing precocious germination and yield	AFLP, ISSR, ISTR, and RAPD	Herran et al. (2000)
3.	Cameroon Red Dwarf (CRD) × Rennell Island Tall (RIT)	1971 cM	Nine QTLs linked to yield and yield attributing traits	AFLP and SSR	Lebrun et al. (2001)
4.	Cameroon Red Dwarf (CRD) × Rennell Island Tall (RIT)	1849.8 cM	48 QTLs linked to fruit traits	AFLP and SSR	Baudouin et al. (2006)
5.	African Tall (EAT) × Rennell Island Tall (RIT)	2739 cM	46 QTLs linked to epicuticular wax and other component traits	AFLP and SSR	Riedel et al. (2009)
6.	West African Tall (WAT)-Malayan Yellow Dwarf (MYD)-Atlantic Tall (AT)	–	Markers linked with lethal yellowing disease resistance	RAPD	Cardena et al. (2003)
B. Natural population-based mapping					
1.	79 genotypes across the world	–	SSR locus CnCir73 is linked to fruit component traits	SSRs	Geethanjali et al. (2018)
2.	80 accessions (6 populations, vis., Red Dwarf, Yellow Dwarf, Hainan Red, Hainan Tall, MAWA, and Aromatic Green Dwarf)	–	11 SSR loci linked to the fatty acid content Allele CnFAtB3-359 with a major positive effect	SSRs	Zhou et al. (2020)

In coconut, GWAS-based analysis is very rare. However, Geethanjali et al. (2018) and Zhou et al. (2020) employed this strategy to study the population architecture and the trait fatty acid content. Analysis of genetic diversity of 79 coconut accessions revealed 2–7 alleles and 2 major clades differentiating talls of Indo-Atlantic and South Asia from Indo-Pacific and SE Asia region accessions. Also, SSR locus CnCir73 has been linked to fruit component traits (Geethanjali et al. 2018). Recently, Zhou et al. (2020) performed linkage analysis in 80 accessions for fatty acid content resulting in a grouping of germplasm into subgroups comprising higher-fatty acid and a lower-fatty acid group. Further, Zhou et al. (2020) identified

SSR markers linked to fatty acid content in chromosome 11 and donor genotype (Aromatic Green Dwarf) carrying an allele CnFAtB3-359 with a major positive effect for use in coconut oil breeding. However, applying high-throughput sequencing technologies and the development of suitable bioinformatics and statistical tools are expected to open up the genotyping strategies for rapid genetic mapping of crop plants. Instances of such tools are genotyping-by-sequencing (GBS) (Elshire et al. 2011) and restriction site-associated DNA sequencing (RAD-seq) (Peterson et al. 2012), which have significantly supported the genome-wide rapid discovery of molecular markers, which in turn aids in QTL mapping of traits of importance (Torkamaneh et al. 2017). From a coconut perspective, it is anticipated that integration of GBS and the use of biparental mapping population could be a powerful tool to dissect complex traits. In this context, the availability of whole-genome sequence assemblies of coconut (Xiao et al. 2017; Lantican et al. 2018; Rajesh et al. 2020) has been further utilized to perform GBS to generate a high-density linkage map (Yang et al. 2021). Combining the utility of backcross-mapping population [MYD × (MYD × WAT)] and the high-throughput nature of GBS, the coconut genome sequence has been arranged on to 16 pseudomolecules ensuring over three-fourth of coconut genes in the 16 linkage groups (Yang et al. 2021). This chromosome-scale assembly of the coconut genome is an important step toward establishing a robust genomics-assisted breeding schema in coconut.

10.7 Whole-Genome Assemblies

The inherent complexities of plant genomes could be attributed to their polyploid nature and the presence of repetitive DNA elements interspersed throughout the genome. Among the repetitive sequences, transposable elements (TEs) comprise a major component. They pose a serious impediment to genome sequencing efforts in crops, especially in gene mapping and genome assembly construction (Jackson et al. 2011). However, developments in the field of sequencing technologies and rapid downfall in the cost of sequencing and resequencing have created a massive wealth of genome information of crops, including perennials like coconut. It has created a paradigm shift in crop improvement strategies, especially in marker-trait linkage analysis, QTL mapping, deciphering the expression profile of critical genes, etc. (Jackson et al. 2011). In coconut, the whole-genome sequencing efforts have been undertaken by three independent research groups belonging to China, the Philippines, and India resulting in the genome assemblies of cultivars Hainan Tall, Catigan Green Dwarf, and Chowghat Green Dwarf, respectively (Xiao et al. 2017; Lantican et al. 2019; Rajesh et al. 2020).

10.7.1 Genome Assembly of the Chinese Hainan Tall Cultivar

The Chinese Academy of Tropical Agricultural Sciences sequenced the tall cultivar Hainan Tall, and the draft genome sequence of which was published (Xiao et al. 2017). The cultivar was chosen since it occupies a major area under the crop cultivation in the province of Hainan. The cultivar is also known to exhibit abiotic stress (salinity and drought) tolerance. Genomic analysis revealed the expansion of gene families such as Na^+/H^+ antiporters and ion channels, suggesting their role in imparting abiotic stress tolerance. Further molecular evolutionary analysis of coconut with its relative oil palm suggested that coconut diverged from its relative around 46 mya (Xiao et al. 2017).

10.7.2 The Genome of the Philippine Cultivar Catigan Green Dwarf

A combination of multiple sequencing platforms, namely, Pacific Biosciences (PacBio), Illumina MiSeq, and Dovetail Chicago, and various computational pipelines were utilized to assemble and annotate the genome of dwarf cultivar Catigan Green Dwarf (CATD) (Lantican et al. 2019). The hybrid genome assembly was created using the long sequence reads of PacBio followed by correction using the short Illumina reads. The draft genome assembly was further analyzed with Dovetail Chicago, resulting in 97.6% of genome coverage. Comparative genomic analysis of the dwarf CATD and tall HAT genomes identified 58,503 SNPs for use in coconut molecular breeding. Further, over 7000 genomic and functional SSRs having an immense role in conferring biotic, drought tolerance and involved in oil biosynthetic pathways were also mined. Evolutionary analysis of palm genomes further suggested that palms could have undergone at least three rounds of whole genomic duplications (WGD) during the course of evolution (Lantican et al. 2019).

10.7.3 Genome of Disease-Resistant Cultivar Chowghat Green Dwarf

Rajesh et al. (2020) uncovered the whole nuclear and organellar genome sequences of indigenous cultivar Chowghat Green Dwarf (CGD), which possess root (wilt) disease-resistant trait. Furthermore, the predicted coding sequences in the genome assembly were validated using the multiple transcriptome sequence data available in the public domain. A diverse group of nucleotide-binding site and leucine-rich repeat (NBS-LRR) class resistance-conferring genes was identified from the genome. Though the number of NBS-LRR genes identified was comparable to that of other palms, it was way too less compared to other cereal crops. The candidate

R-genes identified in this investigation warrants a functional validation and further molecular characterization to utilize this genetic repertoire for breeding disease resistance in coconut (Rajesh et al. 2020).

A comparison of genome assemblies of three coconut cultivars is given in Table 10.6.

10.8 Multiple Omics Approaches in Coconut

Application of multiple omics technologies such as transcriptomics, small RNA sequencing, proteomics, and metabolomics has been on the rise in plant breeding to characterize the role of functional elements, RNA, proteins, and metabolites in the

Table 10.6 A comparison of genome assemblies of three coconut cultivars

Parameters	Hainan Tall (Xiao et al. 2017)	Catigan Green Dwarf (Lantican et al. 2019)	Chowghat Green Dwarf (Rajesh et al. 2020)
Sequencing platform(s)	Illumina HiSeq 2000	Pacific Biosciences (PacBio) SMRT, Illumina MiSeq, and Dovetail Chicago	Illumina HiSeq 4000, Pacific Biosciences (PacBio) RSII
Predicted protein coding genes	28,039	34,958	13,707
Repeat elements (% in genome)	72.75%	78.33%	77.29%
BUSCO assessment	74.1%	85.3%	84.6%
Total sequences	111,366	7998	26,885
Total bases	2,202,455,121	2,102,417,611	1,930,087,115
Average sequence length	19776.73	262867.92	71790.48
Median sequence length	1139	120,849	41,589
N50 length	1,217,559	570,487	128,735
Features	First draft genome sequence of coconut	First genome sequence of a dwarf cultivar	Nuclear and organellar genome sequences of a dwarf coconut cultivar
	Role of Na^+/H^+ antiporters in abiotic stress tolerance	Identified SNPs by comparing tall and dwarf cultivar for use in molecular breeding	Mined 112 NBS-LRR genes (40 NBS-LRR loci, 20 CC-NBS-LRR loci, 29 NBS loci, 20 CC-NBS loci, 2 RPW8-NBS-LRR loci, and a single TIR-NBS locus) involved in the disease resistance mechanism

cellular context. Along with genomic technologies, coconut has witnessed the use of other omics approaches in deciphering diverse biological questions ranging from biotic stresses, abiotic stress, fatty acid biosynthesis, and post-harvest management of coconuts (Table 10.7). Notable among them is a study deciphering the molecular basis of root (wilt) disease tolerance in indigenous dwarf cultivar Chowghat Green Dwarf (Rajesh et al. 2018). Besides identifying the differential gene expression pattern of healthy and diseased palms, a molecular model describing the host-pathogen interaction was presented (Rajesh et al. 2018). Earlier, Nejat et al. (2015) investigated the yellow decline disease and provided the molecular basis for coconut-phytoplasma interaction.

On the other hand, investigations pertaining to somatic and zygotic embryogenesis were performed utilizing RNA-seq experiments (Bandupriya et al. 2016; Rajesh et al. 2016), which have a great application potential for in vitro multiplication of elite coconut genotypes. The biochemical features and quality profile of coconuts in the transcriptomic studies by Fan et al. (2013) and Saensuk et al. (2016) help identified protein factors responsible for enhanced lauric acid content and genetic basis for the expression of “pandan-like” aroma, respectively. Analyzing the effect of water-deficit stress in coconut seedlings, Ramesh et al. (2020) characterized the differential response of coconut genotypes to drought conditions. Exploration of small RNAs in coconut, though very limited, has provided significant leads in understanding the phenomenon of embryogenesis (Sabana et al. 2020). Similarly, investigations pertaining to coconut proteins have been initially confined to fractionation of various protein components and studying their antioxidant properties (Li et al. 2018; Zheng et al. 2019); however, protein profiling has helped in the identification of functional markers involved in the process of embryogenesis and cold stress acclimatization (Lakshmi Jayaraj 2019; Yang et al. 2020). Application of metabolomics in coconut has been confined to investigating the changes in nut water composition at different maturing stages or during the postharvest period (Zhang et al. 2020; Kumar et al. 2021).

10.9 Conclusions and Recommendations

Precious coconut germplasm is threatened by genetic erosion due to serious biotic and abiotic stresses and anthropological activities which compete for land on which coconuts are grown. These activities hasten the loss of important coconut diversity needed to produce improved varieties. The capacity building in existing national and international genebanks should be continued for sustainable coconut conservation and breeding program. COGENT and its associate institutions like CIRAD, the International Coconut Community [the erstwhile Asian and Pacific Coconut Community (APCC)], and others play an important role in capacity building activities. COGENT is presently working through capacity building and promoting research collaboration among its 38 coconut producing countries and advanced laboratories worldwide. Other than the production of hybrids, emphasis is provided

Table 10.7 Application of multi-omics approaches to enhance the genetic gain in coconut

Sl. no.	Biological phenomena	Genotype(s)	Inference(s)	References
A. Transcriptome sequencing				
1.	RNA-seq analysis of leaf and fruit tissue	Hainan Tall	Expression of genes encoding fatty acyl-ACP thioesterases is involved in the accumulation of medium-chain fatty acids (i.e., lauric acid)	Fan et al. (2013)
2.	Maturing gelatinous endosperm, mature embryo and young leaf	Fragrant dwarf coconut	RNA-directed DNA methylation is an important factor. Small RNA-mediated epigenetic regulation during seed development	Huang et al. (2014)
3.	Coconut yellow decline disease	Diseased and healthy Malayan Red Dwarf	Reprogramming of defense-related gene(s), upregulation of GA-*2ox* (gibberellin-2-oxidase) reduced gibberellins leading to stunted growth, necrosis of inflorescence and premature nut fall. Upregulation of ABC transporter genes was linked to sugar import to maintain the energy source of phytoplasma	Nejat et al. (2015)
4.	Somatic embryogenesis	West Coast Tall	Transcripts involved in somatic embryogenesis [receptor-like kinases (SERK and CLV1), mitogen-activated protein kinase (MAPK), transcription factors (WUS, AP2/ERF, PKL, ANT, and WRKY)], extracellular proteins (AGP, GLP, ECP, and LEA) were studied	Rajesh et al. (2016)
5.	Embryogenesis	Immature embryo, mature embryo, microspore-derived embryo, and mature leaves	Transcripts with putative roles in embryogenesis, viz., chitinase, β-1,3-glucanase, ATP synthase CF0 subunit, thaumatin-like protein, and metallothionein-like protein, were identified	Bandupriya et al. (2016)
6.	"Pandan-like" aroma	Aromatic Green Dwarf coconut of Thailand	Differences in length of transcripts encoding 2AP in aromatic (2371 bp) and nonaromatic (1921 bp) palms	Saensuk et al. (2016)
7.	Host-pathogen interaction during root (wilt) disease	Healthy and diseased CGD palms	A molecular model for coconut-pathogen interaction was put forth	Rajesh et al. (2018)

(continued)

Table 10.7 (continued)

Sl. no.	Biological phenomena	Genotype(s)	Inference(s)	References
8.	Water-deficit stress	Kalpasree (dwarf) and Kalpatharu (tall) having contrasting water use efficiency trait	Genotypic differences in molecular response to water-deficit stress Genic SSRs and the role of long ncRNAs deciphered	Ramesh et al. (2020)
B. Small RNA transcriptomics				
1.	Mature and immature endosperm	–	Mature endosperm-specific miRNA expression pattern identified	Li et al. (2009)
2.	Leaf transcriptome	–	16 miRNAs (of 11 miRNA families) identified	Naganeeswaran et al. (2015)
3.	Embryogenesis		27 novel miRNAs of 15 diverse miRNA families	Sabana et al. (2018)
4.	Cross-kingdom miRNA interaction	Mature and immature nut water	Diverse miRNAs in mature nut water than immature coconut water	Zhao et al. (2018)
5.	Embryogenesis	Embryogenic and non-embryogenic calli	Identified 110 conserved miRNAs and 48 miRNAs specific for embryogenic calli and 21 miRNAs specific for non-embryogenic calli	Sabana et al. (2020)
C. Proteomics				
1.	Nutritional quality using MALDI-TOF/TOF-MS analysis	Mature endosperm	Proteins of classes 7S globulins and glutelin and receptor-like protein kinases were identified Studied the thermal stability of the proteins	Huang et al. (2016)
2.	Antioxidant properties of coconut proteins	Coconut cake	Various protein fractions (albumin, globulin, prolamin, glutelin-1, and glutelin-2) of coconut cake obtained All except albumin showed radical scavenging activity and chelating ability Peptides with antioxidant activity characterized	Li et al. (2018)
3.	ACE-inhibitory and antioxidant peptides of coconut	Coconut cake	Sequential digestion of coconut cake albumin protein fraction yielded bioactive peptides with angiotensin-I converting enzyme (ACE) inhibitory and antioxidant activities	Zheng et al. (2019)

(continued)

Table 10.7 (continued)

Sl. no.	Biological phenomena	Genotype(s)	Inference(s)	References
4.	Embryogenesis investigated using SDS-PAGE and MALDI-TOF/TOF MS	Stages of somatic and zygotic embryogenesis	Seven proteins common to somatic and zygotic embryogenesis identified	Lakshmi Jayaraj (2019)
5.	Cold stress using iTRAQ approach	Hainan Tall, Ben Di (BD) and aromatic coconut, Xiang Shui (XS)	Cold stress upregulated 193 and downregulated 134 proteins in BD. In XS, 140 and 155 proteins were up- and downregulated, respectively	Yang et al. (2020)
D. Metabolomics				
1.	Nut water at four different stages	Chowghat Orange Dwarf (COD) and Malayan Yellow Dwarf (MYD) using GC-MS and UPLC	Amino acid profile during various stages of nut maturity Metabolite profiling differentiated the varieties since COD has biomarkers (caffeic and myristic acids), whereas fumaric and stearic acid was present only in MYD	Kumar et al. (2021)
2.	Metabolomic changes during postharvest and storage period	Hainan-native coconuts using UPLC-MS/MS	Significantly upregulated metabolite biomarkers such as dibutylphthalate, L-leucine, (S)-malate, L-valine, and deethylatrazineetc and downregulated metabolites (gamma-aminobutyric acid zwitterion, acetoacetate, and keto-D-fructose, etc.) are identified	Zhang et al. (2020)

to ensure that the hybrids are evaluated and planted by coconut farmers. Great attention is required for the dispersal of coconut hybrids among farmers, acceptability versus availability of hybrids, economic and anthropological aspect of coconut seed nuts, and cultural coevolution between farmers and their coconut varieties and markets. The adoption of hybrids or varieties produced in breeding programs by the farmers is largely determined by their performance. Hence coconut breeders must put forth efforts to fully understand the basis of varietal preferences of farmers and other end users, and these factors have to be given importance while planning and executing the coconut breeding programs.

COGENT will continue to coordinate coconut breeding program worldwide in collaboration with national programs, partner organizations, farmers, and NGOs. It will be undertaken through prioritized research in coconut breeding involving testing the best hybrids already identified out of the research centers using a farmer's participatory approach, reinforcement of the dispersal of information regarding traditional and hybrids varieties to farmers through publishing catalogs having consistent information, and breeding for characters such as tolerance to biotic and abiotic stresses, adverse growth conditions, and yield attributes and other important traits desired by coconut stakeholders. To establish an efficient and sustainable system for the multiplication and distribution of recommended hybrids, identifying the most suitable ecosystems where the hybrids perform best and technology transfer of suitable cultural management techniques are important to achieve the desired socioeconomic and environmental impact.

It is apparent that conventional breeding strategies of selection and propagation have been effectively utilized in the crop improvement programs of coconut. The application and use of molecular marker technologies in coconut have been largely restricted to examining the genetic diversity of germplasm lines. However, notable contributions such as the development of genetic maps for use in breeding are worth mentioning. It must be emphasized that large-scale implementation of genomics-based advancements in coconut breeding is severely lacking, as is evident from the scarce publications describing novel breeding strategies such as genome-wide association mapping studies, genotyping-by-sequencing, etc. Nevertheless, the initiatives in the genome sequencing front by independent groups in Asia have given an impetus to the generation of very comprehensive information regarding the genes of agronomic and economic importance. Also, efforts in the field of transcriptomics unfolding the molecular intricacies of biotic stress tolerance, embryogenesis, and abiotic stress tolerance are worth mentioning as it adds to the growing body of literature enriching the resources for coconut genomics. A relatively dense genetic linkage map and assembling the genome sequences of coconut into chromosome-like pseudomolecules utilizing the GBS approach is one such instance of moving forward using genomics technologies. It is anticipated that the ever-decreasing cost of genome sequencing would render resequencing of elite germplasm lines a possible strategy to perform large-scale GWAS analysis to develop appropriate genomic selection (GS) models in coconut. Harnessing of multiple omics technologies such as transcriptomics, proteomics, and metabolomics to complement the efforts of genomics would greatly aid in understanding the complex gene regulatory mechanisms underlying important traits such as oil yield, fatty acid composition, and resistance to biotic and abiotic stressors and in vitro recalcitrance. Applying these novel technologies would greatly reduce the long breeding cycle in coconut to develop new and elite varieties and hybrids.

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