

Chapter 6

Genomic Designing of Climate-Smart Coconut



S. V. Ramesh, V. Arunachalam and M. K. Rajesh

Abstract Coconut (*Cocos nucifera* L.), belonging to the family Arecaceae, has earned the epithet ‘*Kalpavriksha*’ (“Tree of Life”) because of its multitude of uses. Changing and future climate scenarios have imposed severe constraints on the production of coconut with simulation studies revealing that productivity will be severely affected. Nevertheless, plant genomics has offered many novel approaches to meet the exigencies of climate change by identifying novel genetic sources for future climatic conditions and developing suitable cultivars to tolerate increased drought, high temperature, pests, and diseases’ complex. The perennial and open-pollinated nature of the crop and its long gestation period has hampered the application of genomics in coconut improvement. Next-generation sequencing (NGS) technologies have helped in the generation of enormous genomic and transcriptomic sequence information at a relatively low cost. Also, breeders’ toolbox has been improved with the availability of various techniques such as molecular marker kits, association mapping, and genomic selection. This chapter describes the impact of climate change in coconut, progresses made in the field of coconut genomics, and various approaches being followed to develop climate-smart coconut.

Keywords *Cocos nucifera* L. · Genomics · Molecular markers · Climate change · Transcriptomics · Palms

6.1 Introduction

Palms supply various products such as food, fiber, fuel, and wood, and they constitute an economically important group of plants for human well-being, next only to cereals and pulses. Botanically, palms are classified under the family Arecaceae, a member of

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order Arecales of Angiosperms in the Viriplantae group. Among the palms, coconut (*Cocos nucifera* L.) is an economically valuable crop of humid tropics that offers food, edible oil, coir (fiber), and mineral-rich refreshing drinks, namely tender nut water and inflorescence sap. It is inextricably linked to the lives of people of South, South-East Asia, and the Pacific Islands. Coconut generally grows between 23° N and 23° S latitudes (Kumar and Aggarwal 2013). Even though the crop thrives at 26° N latitude, temperature is a major limiting factor that hinders the growth of the crop beyond the north of these latitudes (Kumar and Aggarwal 2013). The most favorable weather parameters required for the growth and economic yield of coconut comprise an evenly distributed rainfall of 130–230 cm/annum, copious sunlight in the range of 250–350 Wm⁻² along with minimum sunshine period of 120 h/month. Also, a mean annual temperature of 27 °C and humidity of above 60% favor optimal growth and yield of the crop (Child 1974; Murray 1977). The extent of genetic variability in coconut is very high; hence, it possesses high morphological, physiological, and biochemical variations. Undoubtedly, the numerous applications of various parts of coconut trees have earned the epithet “Tree of Life”. Further, the antimicrobial property of coconut husk and rich nutrient contents of coconut water has also been recognized. Despite the importance of coconut in tropical ecosystems, the potential of the crop has not been realized. There are a number of barriers such as non-availability of quality planting materials and true to type progeny seed nuts, biotic and abiotic factors, and fluctuating prices hinder the realization of the production potential of the crop (Buschena and Perloff 1991).

Coconut accessions are a separate set of inter-breeding gene pool as their wild relatives are unknown yet. Further, molecular investigations have revealed that coconut was brought into cultivation in two different geographical locations namely the Indian Ocean and the Pacific Ocean basins (Gunn et al. 2011). In general, enrichment of gene pool by a collection of germplasm (both indigenous and exotic) and classical breeding techniques such as selection, hybridization, etc., are being utilized in the productivity enhancement of coconut (Arunachalam and Rajesh 2008, 2017). Being a perennial crop with a long gestation period, coconut requires enormous land and other resources for experimentation. Nonetheless, breeding approaches have yielded improved cultivars of coconut for specific traits and productivity levels (Nair et al. 2016). Some of the instances of successful breeding efforts are the development of coconut hybrids involving dwarfs and tall forms that have yielded intermediate forms, which are early bearing, disease resistant, and give high economic yields. Introgression of lethal yellowing disease resistance in the coconut palms grown in Latin America and Caribbean islands by crossing the Malayan dwarf forms of coconuts from Malaysia with the indigenous tall forms is worth mentioning (Been 1981). Spontaneous mutants of coconut (*‘Makapuno’*), which results in the development of a jelly-like endosperm (Zuñiga 1953), are governed by a single recessive gene and such nuts possess high commercial value. Coconut is characterized by chromosome number of $2n = 32$ with an estimated genome size of 2950 million base pairs (Mbp) (Gunn et al. 2015).

6.2 Coconut Genome

The availability of genome sequence information of a crop provides a great impetus to the genetic improvement programs as it aids in the development of molecular markers linked to important traits, in addition to the discovery of novel genes, rare alleles, and other regulatory elements. Non-model and non-cereal crops like coconut could not reap the fruits of the first wave of genome sequencing projects which were based on Sanger sequencing technique. However, the relatively cheap next-generation sequencing (NGS) technologies resulted in the discovery of genetic elements unique to palm species such as coconut (Unamba et al. 2015), oil palm, and date palm. Among the palms, the genomes of oil palm, date palm, and coconut are available in the public domain (Al-Dous et al. 2016; Al-Mssallem et al. 2013; Dussert et al. 2013; Singh et al. 2013; Xiao et al. 2017). The chloroplast and mitochondrial genomes of coconut have been sequenced (Huang et al. 2013; Aljohi et al. 2016). The haploid genome size of coconut (C-value) corresponds to the quantum of DNA in its gametic nucleus (pollen or sperm) and is represented in picograms (pg) or in base pairs (bp) (Greilhuber et al. 2005). The preliminary analysis of genome size and ploidy levels of cultivated coconuts are imperative for embarking upon coconut genome sequencing efforts as it helps to decide the optimal depth of reads required for optimal assembly and annotation of the coconut genome (Gunn et al. 2015). Flow cytometry analysis of 23 coconut cultivars, including dwarfs, tall, and hybrids, has estimated that the average genome size of coconut is 5.966 ± 0.111 pg (Gunn et al. 2015). Further, it was deduced that intraspecific variation observed was associated with the process of domestication and tall cultivars showed wide genetic variation compared to the dwarf cultivars.

A draft genome of coconut was reported by Alsaihati et al. (2014) based on the seven libraries of paired-end and mate-pair genome sequencing using Illumina's HiSeq platform. In addition, it was also estimated that 50–70% of the genome was repetitive sequences with the size of the genome standing at ~2.6 Gb. Various genome assembly and annotation techniques and tools were utilized (ALLPATHS-LG and SOAPdenovo2), and ultimately a quality draft genome, with a coverage of 94.5%, was assembled using a custom bioinformatics pipeline. This assembly has only a gap of around 10%. Whole genome sequence of coconut cultivar Hainan Tall was obtained by Xiao et al. (2017). This sequencing effort generated a scaffold length of 2.2 Gb, representing over 91% of the estimated genome of coconut. Interestingly, the coconut genome has been predicted to encode 28,039 proteins, whereas the genetically related palms such as *Phoenix dactylifera* (variety PDK30), *Phoenix dactylifera* (variety DPV01), and *Elaeis guineensis* were predicted to encode 28,889, 41,660, and 34,802 proteins, respectively. Also, it was deduced that the major chunk of coconut genome (72.75%) comprises of transposable elements, among which long-terminal repeat elements (LTRs) contribute to over 92% of transposable elements (Xiao et al. 2017). Evolutionary molecular genomic analysis using the Bayesian molecular clock revealed that divergence between coconut and oil palm happened around 46.0 (25.4–83.3) million years ago (Xiao et al. 2017). Comparative genomics divulged that coconut has acquired many ion channel/transporter gene families such

as Na^+/H^+ antiporters, carnitine/acylcarnitine translocases, potassium channels, and potassium-dependent sodium-calcium exchangers. These gene families have greatly helped coconut in its environmental adaptations to salt stress, accumulation of fatty acids, and potassium. To complement these efforts, the genome sequence of dwarf coconut variety, ‘Catigan Green Dwarf’ (CATD), was made available recently. Comparative genomics of tall and dwarf coconut genomes revealed 58,503 variants (Lantican et al. 2019). Genome sequence data of coconut, thus, is an invaluable resource for the development of high-density linkage maps, molecular maps, genome-wide SSRs, identification of quantitative trait loci (QTLs), association mapping, and molecular breeding efforts to develop varieties that are resilient to climate change, pests, and disease outbreak and improved biochemical features.

6.3 Organelle Genomes of Coconut

The genome sequence analysis of a subcellular organelle, chloroplast, of a dwarf form of coconut revealed that its size is 154,731 bp and harbors 130 genes and four pseudogenes (Huang et al. 2013). Even though the genome of coconut was smallest among the palms, genome organization, gene content, and repeat structures display colinearity with other palms (Huang et al. 2013). However, some of the unique features of the chloroplastic genome include *rps19*-like gene pseudogenization and relatively high RNA editing sites. Coconut mitochondrial genome (Oman Local Tall cultivar) was found to be around 679 kbp with an estimated GC content of 45.5%. The mitochondrial genome encodes 72 proteins, nine pseudogenes, 23 tRNAs, and 3 rRNAs (Aljohi et al. 2016). Interestingly, the other mitochondrial genome of family Arecaceae is that of date palm (*Phoenix dactylifera*) (Fang et al. 2012). Comparative analysis showed that chloroplast-derived regions of coconut mitochondria are just 5.07% of the total assembly, whereas 93.5% of the mitochondrial DNA of the date palm is derived from chloroplast (Fang et al. 2012).

6.4 Coconut and Climate Change

According to the United Nations Framework Convention on Climate Change (UNFCCC), climate change is defined as “A change of climate which is attributed directly or indirectly to human activity that alters the composition of the global atmosphere and which is in addition to natural climate variability observed over comparable time periods”. Thus, UNFCCC clearly distinguishes the climate change phenomenon from ‘climate variability’, which is the result of natural causes. Among the climatic factors that influence the growth and development of crops, rainfall, temperature, and CO_2 are predominant factors. On the one hand, higher temperatures directly interfere with the process of photosynthesis, affect the accumulation of photosynthates in the sink (Kumar et al. 2008; Asseng et al. 2015; Hatfield and

Prueger 2015), and shorten the growth period. On the other hand, low-temperature conditions damage the tissues and slow down the metabolic process, thereby affecting the growth and development of crops. The projections of frequent droughts and heavy precipitations suggest that perennial crops such as plantations will be exposed to multiple stresses even during the same growing season (Kumar et al. 2012). The drought situations will be further aggravated by increased light conditions causing photo-oxidative damages to the cell membranes of plants leading to leaf scorching and yield reduction (Kumar and Kasturi Bai 2009). Nevertheless, increased CO₂ concentrations in the atmosphere will benefit the C₃ crops such as coconut to accumulate relatively more biomass (Ainsworth and Long 2005). Under nitrogen-limiting environmental conditions, the accumulation of protein might decline. Hence, it is imperative to supply the required quantum of water and nutrients to reap the benefits of elevated CO₂ [ECO₂] conditions. Analysis has also revealed that projected yield levels (in the 2030s) of crops such as maize, mustard, wheat, rice, and sorghum will witness a decline of 2.5–12%. Nevertheless, yield levels of coconut in the west coast and northeastern regions of India are projected to increase (Kumar and Aggarwal 2013).

Anatomical, morphological, and biochemical features such as stomatal density, root system density, and stored sugars play a role in drought tolerance of coconut palm (Gomes and Prado 2007). Coconut seedlings displayed increased levels of heat-stable protein fractions in response to stress by high temperature, flooding, and high irradiance (Kumar et al. 2007). Epicuticular wax content of leaves increased in coconut during drought (Kurup et al. 1993) in Tall, T x D, and D x T hybrids. Deposition of wax aids in adaptation to drought stress in plants. QTL mapping of wax composition in coconut leaves was attempted (Riedel et al. 2009), where several simple sequence repeat and amplified fragment length polymorphism (AFLP) markers associated with the wax compositional trait were identified.

6.5 Projected Effects of Climate Change on Coconut

Over 90 countries spread across tropical regions of Asia, America, East Africa grow coconut. Among them, Indonesia and the Philippines together contribute around 56% of the global coconut production which is followed by India and Brazil (Burton 2019). Major coconut growing states of India are Kerala, Karnataka, Tamil Nadu, Andhra Pradesh, Telangana, Maharashtra, West Bengal, and Assam. Coconut plantations generally provide sustenance to the millions of farming communities in these regions.

Interestingly, over 70% of coconut production in India is confined only to the 20 districts of Kerala, Tamil Nadu, and Karnataka making it more susceptible for changes in climatic factors. Thus, coconut plantations are predominantly grown in ecologically sensitive zones such as coastal regions and in island ecosystems. Also, coconut being a perennial crop faces the effects of climate change even during a single generation or in the standing population. In all likelihood, coconut will encounter increased CO₂, elevated temperatures, frequent droughts and flood situations, and

biotic stresses during its 60 years of economic yielding period. Coconut, being a perennial crop, is vulnerable for drought or high-temperature stress for a relatively long period. Therefore, elevated temperature and drought stresses during the critical period of inflorescence development affect not only the nut yield of current year but also three more ensuing years (Kumar et al. 2002; Rajagopal and Kasturi Bai 2002). Also, the physiological and biochemical effects of water-deficit stress and the productivity of coconut have been studied in detail (Gomes et al. 2008). Nevertheless, coconut has many adaptive strategies to withstand the stress conditions (Kasturi Bai et al. 2009). Leaf anatomical and morphological features have been linked to drought tolerance in coconut. Epicuticular wax on the upper epidermis of the leaves and scalariform thickenings in the tracheids are the major traits that define drought tolerance in coconut (Kumar et al. 2000). Also, dwarf cultivars consume more water owing to high stomatal frequency (number of stomata/unit leaf area), low epicuticular wax, and poor stomatal regulation (Rajagopal et al. 1990). Contrarily, tall varieties are found to have conservative water utilization pattern (Voleti et al. 1993).

6.6 Approaches to Study the Impact of Climate Change in Coconut

A multi-pronged approach has been developed to study the impact of climate change on coconut plantations. These strategies include (a) analyzing the response of coconut seedlings to elevated CO₂ (550 ppm and 700 ppm) and elevated temperature (2 °C), (b) phenotyping for water use efficiency and drought tolerance, (c) surveys, and (d) simulation analysis using InfoCrop-COCONUT model.

6.6.1 *Effect of Elevated CO₂ [ECO₂]*

Exposure of coconut seedlings to elevated CO₂ (550 and 700 ppm) conditions has shown that it benefited growth and development of seedlings owing to increased assimilation of CO₂ and greater photosynthetic rates, thereby resulting in increased shoot and root biomass. Biochemical analysis of coconut leaves exposed to elevated CO₂ showed increase in photosynthates such as soluble sugars, free amino acids, reducing sugars, and starch. Nonetheless, elevated CO₂ has reduced the total phenols, activity of polyphenol oxidase enzyme, root and shoot C: N ratio suggesting that climate change phenomenon might make coconut susceptible to pests and diseases due to reduced leaf polyphenol content (Sunoj et al. 2013). Open-top chamber (OTC) experiments have revealed that biomass of coconut seedlings grown at 550 and 700 ppm CO₂ increases up to 8% and 25%, respectively, compared to 380 ppm CO₂ under ambient atmospheric conditions (Hebbbar et al. 2013a).

6.6.2 *Effect of Elevated Temperature [eT]*

Exposure of coconut seedlings to elevated temperature conditions of 3 °C above 31 °C has adverse effects on their growth and development due to reduced photosynthesis, reduced leaf area growth, and reduction in chlorophyll content. Greater reduction in photosynthates (sugars, reducing sugars, and starch) and polyphenols were observed. However, elevated temperature conditions have induced greater deposition of epicuticular wax on the surface of coconut leaves (Hebbar et al. 2013b). Effect of elevated temperature (ET) on the quality of the copra, oil composition, and nut yield of coconut grown in various agroclimatic conditions has also been studied in detail (Kumar 2005). Atmospheric temperature exerted greater influence on the ratio of saturated to unsaturated fatty acids. This ratio showed upward trend with the increase in minimum temperature, whereas it showed a slight decline decrease with the increase in maximum temperature (Kumar 2005). Increase in maximum temperature caused reduction in copra yield and or nut yield; however, oil percentage showed an incremental trend. Genotypic variations in the cardinal temperatures (T_{\min} , T_{opt} , and T_{\max}) for pollen germination and growth of pollen tube were observed in coconut. *In vitro* pollen germination studies revealed that tall genotypes such as West Coast Tall (WCT), Laccadive Ordinary Tall (LCT), Federated Malayan Straits Tall (FMST), dwarf cultivar Chowghat Orange Dwarf (COD) and hybrids (COD X WCT and MYD X WCT) exhibited adaptability to high temperature while the dwarf genotype Malayan Yellow Dwarf (MYD) was found to be least adaptable (Hebbar et al. 2018). Biochemical changes associated with high temperature divulge that a reduction of 20% of soluble protein and inverse relationship between superoxide dismutase (SOD) enzyme activity and pollen germination. Thus, genotypic variations for *in vitro* pollen germination and pollen tube growth allowed categorization of coconut genotypes: Category 1 varieties: relatively high T_{opt} and low T_{\min} and high T_{\max} and thus have wider adaptability and these genotypes also had high germination (e.g., WCT, LCT, COD, and hybrids), Category 2: though sensitive to T_{\min} but exhibited relative tolerance to T_{\max} hence are moderately adaptable for high-temperature conditions [e.g., Philippines Ordinary Tall (PHOT), Cochin China Tall (CCNT), Gangabondam Green Dwarf (GBGD), Chowghat Green Dwarf (CGD), and CRD (Cameroon Red Dwarf)], Category 3: these genotypes showed high T_{\min} and low T_{\max} , coupled with poor germination, and are thus least adaptable to temperature variations (e.g., MYD) (Hebbar et al. 2018). Predicted climate change effects in the selected sites of Sri Lanka showed that an increase in maximum temperature would be an important yield-limiting factor for coconut (Pathiraja et al. 2017). Coconut hybrids have been classified into different heat-tolerant groups based on their pollen germination percentage and tolerance to high temperature. Thus, SLGD × Sri Lanka Tall and Sri Lanka Brown Dwarf × The SLGD Tall were identified as tolerant to ET (Ranasinghe).

6.6.3 Statistical Analysis

A comprehensive study by Peiris (2006), using statistical simulation models, has shown that changes in monsoon rainfall pattern and maximum atmospheric temperature are the two major determinants of coconut production in the changed climatic conditions. Further, it was also deduced that coconut production in the 2040s with the changed climatic parameters, provided all the other external factors remain constant, is projected to remain insufficient to meet the consumption demands (Peiris 2006). Economic analysis of the cultivation of coconut in Sri Lanka deduced that 60% of the variations in the yield could be attributed to the changes in the climatic parameters (Fernando et al. 2007).

6.6.4 Simulation Models

InfoCrop-COCONUT model is a comprehensive tool that helps to analyze the future climate scenarios along with the management practices so as to analyze the regional impacts of climate change, vulnerability and to devise adaptation measures. In addition, the combination of crop simulation models and remote sensing and geographic information system (RS-GIS) offers an opportunity for better land use planning, yield, and calamity forecasting and effective monitoring. Simulation analysis predicted that an increase in productivity of up to 4% (in 2020), and 20% (in 2080) over current yields. In the west coast regions of India, a yield increase of up to 39% is predicted (in 2080), whereas, in east coast regions, a decline in yield of 31% (in 2080) over the yield levels of 2009 was projected (Kumar and Aggarwal 2009). Also, analysis of the potential gains due to adaptation strategies has found an increase in coconut productivity by 4.3–6.8% for the years 2030 and 2080, respectively, over the 2000–2005 productivity levels provided the current management practices are followed (Kumar and Aggarwal 2013). Coconut production forecasting estimates in Sri Lanka revealed that the annual rainfall pattern during the months of January to March determines the yield levels. Among the other weather parameters, ambient temperature and relative humidity significantly contribute to the nut production (Peiris et al. 2004). The process-based models such as InfoCrop-COCONUT could not be applied effectively in the context of Sri Lanka because of the paucity of data. However, analytic hierarchy process (AHP)-based expert system modeling approach has been utilized in climate change prediction and adaptation studies as a decision support tool (Pathiraja et al. 2017).

6.7 Strategies for Developing Climate-Smart Coconut

6.7.1 Genetic Resources

The vast resource of germplasm accessions available in coconut can be screened for tolerance toward various biotic and abiotic stress factors. Tolerant traits such as heat tolerance, viability of pollen at high temperatures, nut retention at elevated temperatures are some of the important selection criteria to obtain climate-resilient varieties (Hebbar et al. 2016). Incorporation of genotypes characterized with improved in situ drought tolerance in crop improvement programs is an important and viable approach to design resilient coconut genotypes for changing climatic conditions. For instance, such an approach in coconut population improvement programs has yielded many drought-tolerant varieties, namely Chandra Kalpa, Kalpatharu, Kera Keralam, Kalpa Mitra, Kalpa Dhenu, Kera Sankara, and Chandra Laksha (Kasturi Bai et al. 2009).

Drought and heat or excessive temperature are the two important factors that affect yield especially during critical stages of plant growth including pollination, flowering, and fruit development. Water use efficiency (WUE) has been shown to vary among varieties/genotypes and considered as one of the important traits to identify and select drought-tolerant genotypes. WUE in coconut is found to be regulated by both efficient water uptakes by root systems as well as controlled water loss through better regulation of stomatal movement (Hebbar et al. 2016). Tall genotypes Kalpadhenu, FMST, Kalpatharu, etc., exhibited high WUE due to a better root system (Hebbar et al. 2016; Ramesh et al. 2019). Nevertheless, dwarf forms of coconut showed high WUE during water-deficit stress by effective stomatal regulation. Stress-tolerant plants in addition to possessing higher photosynthesis accumulated more epicuticular waxes on the leaves for better conservation of moisture.

Pollination, being one of the most sensitive phenological stages to heat stress, in vitro pollen germination characteristics of the coconut genotypes has been studied in detail to ascertain their tolerance/susceptibility for high temperature. Tall coconut cultivars such as WCT, LCT, FMST, and the dwarf cultivar COD and hybrids showed relatively good adaptability to high-temperature stress, whereas the dwarf cultivar MYD was the least adaptable (Hebbar et al. 2018). This technique identified temperature tolerant genotypes suitable for climate-vulnerable regions.

6.7.2 Genome-Wide Approaches

It is pertinent to utilize molecular markers for genomics-assisted breeding in coconut; hence, marker-trait association and QTL mapping form an important objective for the development of climate-smart coconut. Random amplified polymorphic DNA (RAPD) and simple sequence repeat (SSR) markers linked to eriophyid mite resistance (Shalini et al. 2007), lethal yellowing disease resistance (Cardena et al. 2003) and plant habit (Martinez et al. 2010; Rajesh et al. 2013a, b) have been identified.

Similarly, the use of molecular markers in QTL mapping for economically important coconut traits such as earliness in flowering (Herran et al. 2000), nut yield (Lebrun et al. 2001), fruit characteristics features (Baudouin et al. 2006), and epicuticular wax composition (Riedel et al. 2009) has been successful. It is also important to saturate the linkage map of coconut with an additional set of molecular markers so that breeding efficiency is improved in a perennial crop like coconut (Rivera et al. 1999). A global strategy for conservation and utilization of coconut genetic resources have unveiled that effective phenotyping should consider the inclusion of phenology and assessment of biomass assessment so as to ascertain the metabolic efficiency at plant scale. Also, a saturated and robust linkage map is being developed by utilizing the core set of single-nucleotide polymorphism (SNP) and SSR markers. Genotyping by sequencing (GBS) approach is being followed for characterizing the mapping population developed from Côte d'Ivoire and the Philippines to saturate the linkage map and for further QTL mapping studies, respectively. Recently, genomic loci governing domestication traits have been identified by Perez et al. (2019) utilizing GBS approach. Population genomics of Northern South American coconut genotypes reaffirmed the genetic differentiation corresponding to the Pacific and Indo-Atlantic oceanic basins (Table 6.1).

Table 6.1 Putative QTLs for various traits in coconut

Trait(s)	Cross	No. of QTLs identified	Reference
Early germination, early flowering, and yield	Malayan Yellow Dwarf x Laguna Tall	6	Herran et al. (2000)
Number of bunches and number of nuts	Cameroon Red Dwarf x Rennell Island Tall	9	Lebrun et al. (2001)
Fruit and yield components (fruit weight, husk weight, nut weight, shell weight, meat weight, water weight, nut/fruit ratio, shell/nut ratio, meat/nut ratio, water/nut ratio, endosperm humidity)	Cameroon Red Dwarf x Rennell Island Tall	62	Baudouin et al. (2006)
Cuticular wax composition	East African Tall x Rennell Island Tall	46	Riedel et al. (2009)

6.7.3 *Transcriptomic Approaches for Climate-Smart Coconut*

Transcriptome analysis, using RNA-seq and assembly, is a potent technology being widely employed to study the global gene expression pattern. Furthermore, transcriptome analysis has provided greater insights about hitherto unknown metabolic pathways such as sub-components of secondary metabolism, acquired resistance, and molecular features like epigenetic modifications. It has also facilitated in developing a very valuable genomic resource in crops like coconut that were abandoned when the applications of the first generation of sequencing technologies were reaped in crops like rice, tomato, wheat, and soybean (Unamba et al. 2015).

In crops that are devoid of genome sequence information, transcriptome sequencing using RNA-seq approach helps in quantifying the level of transcripts. RNA sequencing (RNA-seq) technologies have helped in the generation of whole transcriptomic sequences of a crop by utilizing bioinformatics tools to assemble short-read sequences (Xia et al. 2011) with improved sensitivity and broad dynamic range. In addition, transcriptome sequencing approaches have yielded fundamental insights into co-expressed genes and their precise role in metabolic processes (Wickramasuriya and Dunwell 2015). The first genome-wide study of transcriptional responses in coconut was conducted by Fan et al. (2013) to study fatty acid biosynthesis and metabolism which identified 347 unigenes associated in this process. Also, it was proposed that the accumulation of medium-chain fatty acids (lauric acid) in coconut could be ascribed to the expression of fatty acyl-ACP thioesterase. One of the most important utility of transcriptomic approaches is to unearth novel candidate genes associated with tolerance/resistance to different abiotic and biotic stresses and genes associated with agronomic traits.

Whole transcriptome sequencing (WTS) approaches are a global methodology to study the changes in gene expression using high-throughput sequencing technologies. Hence, until 2012, the whole coconut transcriptome data in the public domain were very scarce as only 774 sequences were available in National Centre for Biotechnology Information database prior to 2012 (Fan et al. 2013). However, on a smaller scale, targeted transcriptomic approaches have yielded valuable results. Expression profiling and cloning of plant resistance (R) genes provide deeper insights into disease progression and even it could identify candidate resistance genes for major diseases. Hence, targeted transcriptomic approaches were employed to gain molecular updates in disease resistance mechanisms in coconut. One of the major components of plant's defense mechanism is R-genes and studies about R-genes has helped in understanding the mechanism of disease prevention, spread, and progress (Hammond-Kosack and Jones 1997). In general, plant-derived R-genes have functional motifs to recognize and bind the pathogen-derived proteins (expressed from avirulence genes of pathogens) (Scofield et al. 1996). This molecular interaction results in a cascade of signal transduction pathways leading to the expression of plant defense-related genes. These defense strategies include hypersensitive response, or apoptosis, production of phytoalexins, physical barriers such as cell wall formation (Dangl et al. 1996). Comparative genomics approach has been followed to delineate the sequence,

structure function, and expression dynamics of *R* genes of coconut using the available genomic sequence of date palm. Thus, resistant gene analogs (RGA) of coconut were studied to gain a molecular understanding of R-gene expression in response to root (wilt) disease. Among the various classes of R-genes, the nucleotide-binding site-leucine-rich repeat (NBS-LRR) class genes are widely characterized (Cannon et al. 2002). The NBS domain possesses several conserved motifs that provide an opportunity to design oligonucleotides and utilize polymerase chain reaction (PCR)-based approaches to search for homologous or similar sequences called RGAs in other related genera or species (Kanazin et al. 1996). Based on this principle, conserved regions of NBS-LRR resistance genes of oil palm and date palm were used to design primers to discover RGAs in the coconut genome (Rajesh et al. 2015).

This study yielded three putative RGAs in coconut [KC465244 (2211 bp), KF002584 (1165 bp), and KM983337 (616 bp)] with sequence similarity to RGAs of date palm, *Oryza*, *Triticum*, *Aegilops*, *Musa*, and *Brachypodium*. Multiple sequence alignment and phylogeny reconstruction showed that coconut RGAs clustered with coiled-coiled-NBS-LRR (CNL)-NBS class sequences. Analysis of amino acid sequences divulged that coconut NBS-LRR-type RGAs have unique TIR or CC motifs in their N-terminus. Further, these putative RGAs showed high expression levels in the leaves of the root (wilt) disease-resistant genotypes. Thus, this study showed that a sequence homology search-based targeted transcriptomics approach could yield potential candidate genes linked to biotic stress tolerance and such candidate genes are a very useful resource in assisting molecular breeding approaches (Rachana et al. 2016).

6.7.3.1 Root (Wilt) Disease

Molecular interactions between host and pathogen provide insights for devising suitable disease control strategies. Of the diseases of coconut palms, root (wilt) disease is a foremost debilitating that seriously hinders productivity. Whole transcriptome sequencing of healthy and diseased Chowghat Green Dwarf (CGD) palms was carried out to study the molecular mechanisms of disease progression and resistance and or susceptibility reactions toward the disease (Rajesh et al. 2013a, b, 2018). RNA-seq analysis yielded over 111 million and 119 million 101 bp clean paired-end reads, respectively, for the healthy and diseased samples (NCBI SRA Accessions are SRX436961 and SRX437650, respectively). Functional annotation using homology-based searches revealed that 37,748 transcripts showing matches to known proteins in UniProt; however, around 36% of transcripts did not show any matches. Further, annotation was carried out using the information obtained from the date palm proteome. This comparative analysis showed that 33,757 (57%) of transcripts could be annotated using date palm proteome. Differential expression analysis between healthy and diseased samples showed a total of 2718 transcripts that were differentially expressed. The gene regulatory network analysis of healthy and diseased

phenotypes showed significant enrichment of metal ion binding, secondary metabolite biosynthesis, and carbon fixation, etc. Notably, proteins like calmodulin-like 41, WRKY DNA-binding proteins involved in plant–pathogen interactions are found to be upregulated.

Based on the leaf transcriptome analysis of diseased and healthy coconut samples, a molecular model has been proposed. This study proposes that the defense response of coconut is triggered by the interaction between membrane receptors and PAMPs or effectors. This interaction initiates the process of signal transduction involving protein kinases and phosphorylations and results in changes in calcium-binding proteins by regulating Ca^{2+} influxes. To this defense response based on signaling cascade, salicylic acid (SA) is also recruited resulting in the orchestration of genome-wide transcriptional reprogramming with the aid of transcription factors (TFs) such as WRKY and NAC domain-containing proteins. This results in the activation of genes involved in defense responses producing phenylpropanoids and causing resistance reactions in healthy palms. Thus, complex defense responses of the healthy coconut palms to one of the devastating diseases which remained elusive long could be resolved by utilizing transcriptome sequencing approaches. Further, analysis of gene expression patterns and identification of genic markers could greatly aid the plant breeders with candidate resistance genes (Rajesh et al. 2013a, b, 2018).

6.7.3.2 Coconut–Phytoplasma Interactions

Molecular basis of disease progression and cellular response of coconut to the phytoplasma disease would provide insights regarding the host susceptibility- and resistance-conferring factors. Hence, a study was conducted to generate transcriptome data from the healthy and CYD phytoplasma infected leaves of coconut cultivar, Malayan Red Dwarf using Illumina HiSeq™ 2000 sequencer (Nejat et al. 2015). This study yielded a total of 72,019,264 and 70,935,896 reads from the transcriptome of healthy and infected leaves, respectively. Comparative analysis between the healthy and diseased palms indicates 18,013 transcripts were upregulated and 21,860 transcripts were down-regulated in the infected leaves. Further genes involved in defense responses against pathogen invasion were found to be differentially expressed in coconut infected with CYD phytoplasma. Gene ontology analysis identified the up-regulation of defense responses, signal transduction pathway, protein phosphorylation among others. Genes involved in pathogenesis-related proteins (PRs) were significantly overexpressed in infected tissues. The study thus provided direct evidence that an active defense mechanism is activated in the wake of phytoplasma attack in the MRD coconut. Further, it was also proposed that phytoplasma could not effectively overcome these defense responses of the host and causes rapid death in palm cultivars, viz. Malayan Tall and Jamaica Tall.

6.7.3.3 Fatty Acid Biosynthesis and Metabolism

The first genome-wide transcriptome analysis of coconut was performed by Fan et al. (2013). A total of 347 unigenes corresponding to fatty acid biosynthesis and metabolism were identified, and these unigenes were assigned to the various steps of fatty acid biosynthesis. Most importantly, 20 of these unigenes were predicted to be related to fatty acyl-ACP thioesterase, a crucial enzyme for terminating the elongation of carbon chains. Hence, the observed abundance of medium-chain fatty acids in coconut (lauric acid) could be ascribed to the expression of fatty acyl-ACP thioesterase.

6.7.3.4 Embryogenesis

Somatic embryogenesis (SE), where a single or a group of somatic cells differentiate to form embryonic cells under suitable in vitro conditions, is an ideal system to explore gene expression patterns associated with initial stages of embryo development. The formation of embryos from somatic cells closely resembles the developmental pathway of zygotic embryos (ZEs), and hence, the molecular information generated for the SE pathway could be used to explain the dynamic molecular interactions that take place during early embryogenesis. Rajesh et al. (2016) carried out de novo assembly and characterization of the global transcriptome of coconut embryogenic calli using Illumina paired-end sequencing. Here, transcriptome analysis of coconut embryogenic calli derived from plumular explants of West Coast Tall cultivar was undertaken on Illumina HiSeq 2000 platform. The assembled reads were subjected to annotation, classification, and ontology analysis using BLASTX, Blast2GO, and KEGG programs. Genes known to be involved in somatic embryogenesis, namely protein kinases like receptor-like kinases [somatic embryogenesis receptor kinase (*SERK*) and *CLAVATA 1 (CLV1)*], mitogen-activated protein kinase (*MAPK*), transcription factors [*WUSCHEL (WUS)*, *APETALA2/Ethylene-responsive factor (AP2/ERF)*, *PICKLE (PKL)*, *AINTEGUMENTA (ANT)*, and *WRKY*], extracellular proteins [arabinogalactan protein (*AGP*), Germin-like protein (*GLP*), embryogenic cell protein (*ECP*), and late embryogenesis-abundant protein (*LEA*)] and glutathione S-transferase (*GST*) were identified. Gene ontology (GO) term enrichment analysis identified 8300 transcripts that are associated with biological processes (majority having transcription and regulatory function), 13,193 transcripts with molecular functions (involved in ATP, Zinc ion and metal ion binding processes) and 6076 transcripts associated with cellular components, and the highly expressed one were components integral to membrane followed by the nucleus. Expression analysis indicated that *CLV* was upregulated in the initial stage of callogenesis. Transcripts of *GLP*, *GST*, *PKL*, *WUS*, and *WRKY* were expressed more in the somatic embryo stage. The expression of *SERK*, *MAPK*, *AP2*, *SAUR*, *ECP*, *AGP*, *LEA*, and *ANT* was higher in embryogenic callus stage compared to initial culture and somatic embryo stages. This study was an effort to aid in the development of an efficient in vitro production protocol for coconut which is otherwise recalcitrant to in vitro culture.

6.7.3.5 RNA-Directed DNA Methylation

Huang et al. (2014) performed whole transcriptome analysis to study molecular factors in the seeds and leaves of dwarf coconut palm with a special emphasis on the identification of genetic elements involved in RNA-directed DNA methylation. It was found that small RNA-mediated gene silencing pathways are very active in coconut seeds, including the maturing endosperm. It is a valuable transcriptomic resource and forms the basis for further molecular and functional analysis to assist in molecular breeding and genetic modification. It also has provided a list of highly expressed genes, and hence, suitable tissue-specific promoters could be explored further for use in coconut improvement.

6.7.4 Database and Genomic Resources

Data repository and genomic resources of palms are relatively scarce. However, there are online genomic resources especially for coconut and other genetically related palms and plant genomics in general that help in analyzing the voluminous data generated through various genomic approaches (Table 6.2).

6.8 Perspectives and Concluding Remarks

The basic understanding of key biological processes and gaining molecular insights are important to help breeders in achieving crop improvement goals. Enormous plant breeding population, high-throughput sequencing technology-based datasets, robust computational tools, followed by basic molecular breeding and gene modification tools are the pillars of modern biotechnology-based climate-smart agriculture. Further, tools such as genome-wide association studies (GWAS), genomic selection (GS), association mapping (AM), and exploration of QTLomics are lacking in coconut owing to limited genomic resources. Also, the development of mapping population and genetic resources such as the multi-parent advanced generation intercross (MAGIC) population and the nested association mapping (NAM) population would help in developing high-resolution QTL mapping in coconut (Fig. 6.1).

Transcriptomics studies using RNA-seq could provide an immense wealth of information for genetic manipulation of crop plants so as to make the crops productive and tolerant to biotic and abiotic stresses. Transcriptomics is a relatively cheap and potential technique for harnessing the benefits of biotechnology and to develop better crop phenotypes. The available transcriptome sequences of coconut for various traits would definitely complement the genome sequencing efforts of coconut. Even though many successful instances of the utilization of transcriptomics in coconut and other plantation crops have been conducted, the information obtained

Table 6.2 Genomic resources and organizations for coconut genomic studies

Sl. No.	Organization	Resources	URL
1.	The International Coconut Genetic Resources Network	To promote, collaborate and use coconut genetic resources among the coconut growing nations. Currently, the organization has 39 members	http://www.inibap.org/cogent/
2.	International Coconut Community	International coconut community formed under the aegis of UN-ESCAP with a vision to improve the socio-economic welfare of farmers and other industry stakeholders	http://www.apccsec.org/
3.	Palms of the World Online (Palmweb)	Online palm encyclopedia which includes morphological descriptors, distribution maps' images of palms among others	http://www.palmweb.org/
4.	The European Palm Society	It is a non-profit organization that envisages sharing information about palms across Europe. It also houses European Palm Society Database which provides publicly accessible information about palm species	http://www.palmsociety.org.uk/
5.	TropGeneDB	A database that manages information on genetics, genomics, and phenotypic data of tropical crops (Hamelin et al. 2013)	http://tropgenedb.cirad.fr/
6.	Center for International Cooperation in Agricultural Research for Development (CIRAD) Montpellier France	CIRAD actively participates in scientific collaboration with more than 100 countries including the genomics of palms	http://www.cirad.fr
7.	Coconut Research Institute Sri Lanka	A public-funded research organization in Sri Lanka	http://www.cri.lk
8.	ICAR-Central Plantation Crops Research Institute India	A constituent unit of Indian Council of Agricultural Research that undertakes basic, strategic, and applied research in coconut among other crops	http://www.cpcri.gov.in

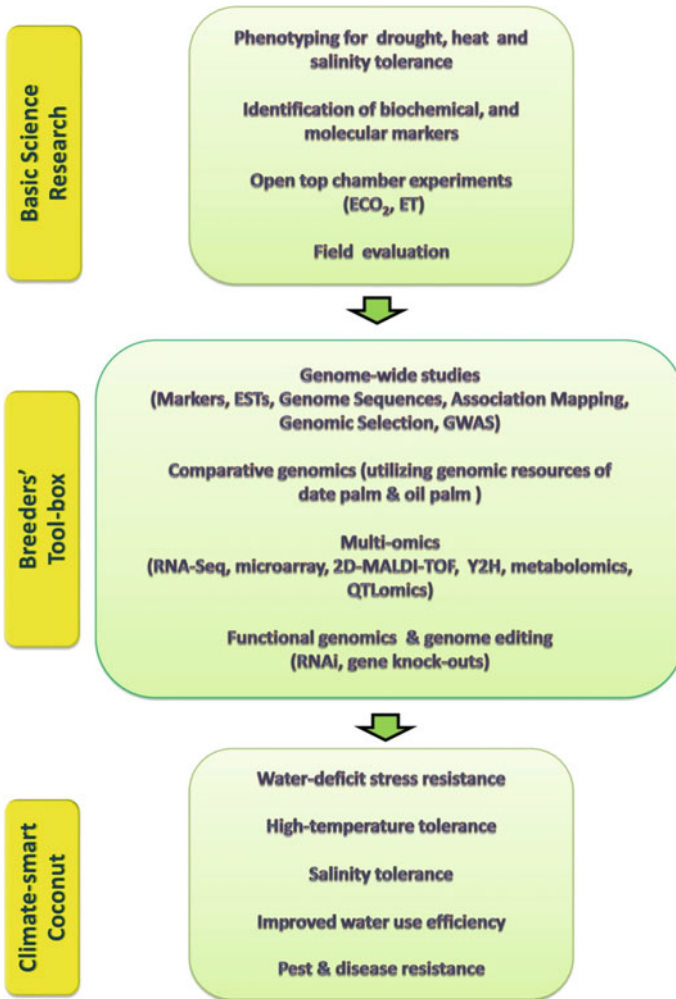


Fig. 6.1 Genomics-assisted breeding of climate-smart coconut. The process involves basic science studies, and the information generated thereof will be utilized by molecular breeders using various genomics tools to develop a climate-smart coconut

from host–pathogen interactions is required to be processed further to identify candidate resistance genes. In this regard, the core commonalities emerging from these studies indicate that secondary metabolite synthesis, particularly phenylpropanoid biosynthesis, activation of jasmonate-based defense pathway, NBS-LRR kinases, etc., are potent candidates for searching resistance-conferring genes. Hence, identification of resistance genes would accelerate the biotechnology enabled “fast-forward breeding” approaches to meet climate change-induced exigencies.

Genome editing technology is a novel approach that accelerates the efforts of plant breeding. It helps in precise and rapid modification of genetic elements for desirable characters such as disease and pest resistance, tolerance to abiotic stressors and in boosting the yield levels. Hence, improved genomic resources of coconut by whole genome sequencing of cultivars targeted resequencing for identification of desired alleles, etc., would add valuable resources for genome editing approaches.

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