

Chapter 3

Botany, Origin and Genetic Resources of Coconut



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Abstract The coconut palm, *Cocos nucifera* L., native of the humid tropics, is a versatile, multipurpose palm with slender unbranched stem crowned with a cluster of long green pinnate leaves producing fruit bunches borne on the leaf axils. The stem lacks bark, cambium, and with no secondary growth features, volume once formed remains unaltered. Similarly, the fibrous roots never expand in thickness after formation. The palm neither produces branches nor forms vegetative buds on the stem, the only vegetative buds being those at the apex of the stem and if this bud gets killed, the palm dies. The palm is non-tillering and monoecious, the spadix bears distinct male and female flowers and the fruits take about 10–12 months to mature. *C. nucifera*, though a monotypic species with no known wild/domesticated relatives, still presents considerable intraspecific diversity and heterozygosity. Systematic classification of the genetic diversity in the crop, using the distinct morphological features of the palm, has been attempted by many. The genetic resources in this crop are conserved mainly in field gene banks, in the coconut-growing countries. Various aspects covering botany, morphology, phylogeny, development, varieties, their classification, the variability reported and the genetic resources in the crop are discussed.

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3.1 Introduction

Coconut, *Cocos nucifera* L., a monoecious perennial palm, belongs to the lower group of flowering plants called monocotyledons. It is a monotypic species under the genus *Cocos* (Dransfield et al. 2008) and is placed in the family Arecaceae (formerly Palmaceae) and the subfamily Arecoideae (one of five subfamilies) which includes a total of 27 genera and 600 species. Formerly, the genus *Cocos* included over 30 species, distributed mainly in Central and South America. Later, Beccari (1916) distinguished *Cocos* as a monotypic genus with *Cocos nucifera* as the sole species and categorised the rest of the species into nine other genera. This systematic classification of *Cocos* was justified by Tomlinson (1961) based on detailed anatomical examination of these genera. The taxonomic information of the coconut palm is listed below.

Kingdom: Plantae
 Subkingdom: Tracheobionta
 Super division: Spermatophyta
 Division: Magnoliophyta
 Class: Liliopsida
 Subclass: Arecidae
 Order: Arecales
 Family: Arecaceae
 Genus: *Cocos*
 Species: *C. nucifera* L

3.2 Origin and Distribution

The name *Cocos*, for *coconut* and its relatives in other European languages, goes back to Spanish word *coco* meaning ‘spectre or goblin’, with reference to the three marks on the nuts which make it look like an eerie face. The botanical species’ name *nucifera* is a neo-Latin formation meaning ‘bearing nuts’ (*nux* = nut and *ferre* = bring/carry/bear).

In India, coconut is referred to as *narikela* in Sanskrit, and almost all names of coconut in the Indic languages are based on this, e.g. Hindi *nariyal*, Urdu *nariyal*, Marathi *nara*, Parsi *nargil* and in Telugu *Kobbarikaya/nalikeram*. Further, the first element in the Indic languages resembles the several Austronesian names of coconut, e.g. Tagalog *niyog*, Malaysian *nyiur* and Hawaiian *niu*. The Polynesian and Melanesian term *niu* and the Philippine and Guamanian term *niyog* are said to be based on the Malay word *nyiur*. Some of the other vernacular names for coconut include the following: tengu and kobbari in Kannada; nalikeram and thenga in Malayalam; tengai in Tamil; kokosneut in Afrikaans; coco in Catalan, Spanish; kokoyashi in Japanese; kelapa and nyiur in Indonesian/Malay; kelapa in Portuguese; pol in Sinhalese; cot dua in Vietnamese; niu in Hawaiian; maprao in Thai; and so on.

Coconut is considered to be an ancient species with a long history of domestication and cultivation. It is presumed that early humans, while domesticating habitats

in coastal areas, started domesticating the coconut palms, resulting in the absence of wild forms in the present-day coconut population. The origins of the coconut palm are a subject of controversy, with two divergent points of thought: most authorities claiming South Asian origin, while others claim its origin in West Coast of Central America and in the adjacent islands of the Pacific. The various arguments and evidences presented in support of the origin of coconut are given hereunder.

Martius (1850) considered the West Coast of Central America as the centre of origin of coconut. This was supported by Cook (1901). On the other hand, De Candolle (1886), in the second edition of *Origin of Cultivated Plants*, opined the origin of coconut in the Indian archipelago. Asiatic origin of coconut has been advocated by Beccari (1917), Mayuranathan (1938) and Nayar (1978). Child (1974) reviewed the literature and postulated the likely origin of coconut in the Old World and that it would not be possible to assign a precise habitat in the Pacific Ocean as the centre of origin of the coconut. Purseglove (1968, 1985) also supported a Pacific origin of coconut. Harries (1978) opined that speculation on the origin, without extra evidence, is futile, considering the widespread distribution of the palm and the divergent opinions implicating a large area from Africa to South America. He postulated that the evolution of the cultivated coconut (niu vai) occurred from the primordial *Cocos*, which he designated as niu kafa. He speculated that the large fruited coconut might have originated from a smaller fruited progenitor and further suggested that the coconut can be compared to the small fruited *Nypa* palm, *Nypa fruticans* Wurmb, and contrasted it with the large fruited coco de mer (double coconut), *Lodoicea maldivica* (Gimel.) Pers.

An origin for the whole Coccoeae tribe in western Gondwanaland seems most compatible with the present-day distribution. It has been hypothesised that the tribe probably differentiated shortly before the break up of that supercontinent. Members radiated and became very diverse in the Americas; some rafted on the African and Madagascar Plates, where they survive to the present day; others rafted on the Indian plate, where they are now extinct. With its ability to float, the coconut became independent of plate tectonics for its dispersal. The wild type dispersed by floating between the islands and atolls fringing the continental plates. It is further postulated that the coasts and islands of the Tethys Sea could have been the ancestral home of the coconut, from where it dispersed by floating to other islands in the Indian Ocean and from there into the Pacific (but not into the Atlantic) Ocean (Harries 1990, 1992, 1995).

Gunn et al. (2011) based on extensive genetic analysis, reported genetic differentiation between coconut populations of Indian Ocean and Pacific region and absence of substantial genetic admixture between the two major genetic subpopulations, in spite of the absence of any known reproductive isolating barriers and also extensive movement of coconuts by humans between these oceanic basins, concluded independent origins of coconut cultivation in the Pacific and Indian Ocean basins.

Considering the absence of wild types in coconut (Baudouin et al. 2014) and the fact that *Cocos nucifera* L. is a monotypic species, the origin of this palm has been hypothesised on the basis of historical accounts, fossil records and current status of dissemination and distribution of the palm. Coconut fossils have been discovered in India [10 to 13 cm long *Cocos*-like fruits in the Deccan Plateau (Prasad et al. 2013;

Srivastava and Srivastava 2014) and 3 to 16 cm long *Cocos*-like fruits in west central region (Kaul 1951; Shukla et al. 2012), Madagascar [coconut shell fragments (Crowther et al. 2016)], New Zealand [3 to 5 cm long *Cocos*-like fruits (Hayward et al. 1960; Endt and Haywar 1997)], Australia [10 to 13 cm long *Cocos*-like fruits (Rigby 1995)], French Polynesia [whole coconuts (Lepofsky et al. 1992)], Vanuatu [coconut endocarp fragments (Spriggs 1984)] and Columbia, South America [25 cm long *Cocos*-like fruits with only 4 mm thickness (Gomez-Navarro et al. 2009)]. Nayar (2017a) observed that among the fossils of *Cocos*-like fruits recovered so far, some of the fossils from India, Australia and Columbia in South America come within the size and morphological characteristics of present-day coconuts, especially natural stands of coconut observed in Nicobar Islands and Lakshadweep (both in India; Balakrishnan and Nair 1979; Samsudeen et al. 2006; Jerard et al. 2017), eastern Philippines (Greuzo 1990) and New Guinea (Dwyer 1938), while those from New Zealand and some material of India appear to be of some other taxa related to *Cocos*. He also hypothesised that the process of domestication or ennoblement of the coconut could have begun in the islands and coastal regions bordering northern Indian Ocean (Arabian Sea, Bay of Bengal), Malesia and the westernmost region of the Pacific Ocean. Nayar (2017b) has reviewed elaborately on coconut origin and domestication in his book *The Coconut: Phylogeny, Origins, and Spread*. Phylogenetic studies in the last few decades do not support an American origin of coconut, in spite of the fact that members of the subtribe Attaleinae are predominantly distributed in South America (Baudouin et al. 2014; Gunn et al. 2015), except for two genera (*Parajubaea*, *Voanioala*) in Madagascar and one (*Jubaeopsis*) in South Africa (Dransfield et al. 2008). The plausible origin of the coconut palm encompasses a vast region, the Indian archipelago, northern Indian Ocean, the Philippines in Southeast Asia, New Guinea and the Western Pacific, covering Northern Indian Ocean, Malesia, Melanesia and Micronesia. The progenitor of present-day coconut is also not known. Phylogenetic studies have indicated some affinity of *Cocos* with that of *Attaleina*, *Syagrus* and *Parajubaea* (Baker et al. 2009; Meerow et al. 2009, 2015).

However, the results have not been consistent, differing between studies (Gunn 2004; Baker et al. 2009; Meerow et al. 2009, 2015; Baker and Couvreur 2013a, b). It has also been postulated that the nearest relative might even have become extinct, since much of this region had been subject to severe geological and climatic perturbations in the past (Prebble and Dowe 2008). Regardless of its origin, coconut has spread across much of the tropics, probably aided by sea currents and also in many cases by seafaring people. *Cocos nucifera* is, hence, regarded as a semi-domesticated species with evolution of local populations having varying degrees of dependence upon humankind.

3.3 Varieties of Coconut

The coconut palm, though a monotypic species with no known wild/domesticated relatives, exhibits considerable intraspecific variability, widely differing from each other in morphological characters, particularly with respect to fruit characters and plant habit.

Considerable diversity is observed in the fruit size, fruit shape and fruit colour of coconut palm. The fruit colour varies from yellow, shades of green and brown to orange. Shapes of the coconut fruit are broadly classified as round, oblong or elliptic. Further, based on the equatorial view, the shape of coconut fruits can be classified as angled, round or flat based on the curvature of the fruit and the presence of ridges on the fruit. Variations are recorded in shape of the nut inside the fruit, and these are broadly categorised as round, oval and oblong.

Based on relative plant habit and a group of morphological characteristics, coconut palms are broadly categorised into two groups, viz. the tall and the dwarf (Narayana and John 1949). Tall palms grow to a height of 20–30 m, have a sturdy stem, commence flowering 5–7 years after planting and continue bearing up to the age of 80–100 years. Tall palms are normally cross-pollinated and hence highly heterozygous. The fruits are generally medium to large in size and produce higher quantity and good quality copra with fairly high oil content. Among the indigenous Indian tall cultivars, West Coast Tall, East Coast Tall, Benaulim Tall, Tiptur Tall, Andaman Ordinary Tall and Laccadive Ordinary Tall are predominantly grown in different areas. Some popular exotic tall cultivars elsewhere are Fiji Tall, Rennell Tall, Philippines Ordinary Tall, Sri Lankan Tall, West African Tall, Panama Tall, Malayan Tall, Jamaican Tall and San Ramon Tall.

Dwarf palms have gained commercial importance due to their early bearing, short stature, tender nut qualities and resistance to certain diseases. They are of shorter stature, 8–10 m high when 20 years old, and start bearing about 3–4 years after planting and have a short productive life of about 40–50 years. The dwarf palms are more homozygous than tall, due to a high degree of self-pollination. They produce nuts, which are generally small to medium in size. The dwarfs are presumed to have originated from tall either through mutation or by inbreeding (Swaminathan and Nambiar 1961; Purseglove 1968). The popular dwarf cultivars grown in India are Chowghat Green Dwarf, Chowghat Orange Dwarf, Kenthali Orange Dwarf and Gangabondam Green Dwarf. Among the exotic dwarf cultivars, Malayan Yellow Dwarf, Malayan Orange Dwarf and Malayan Green Dwarf have become popular in most of the coconut-growing countries of the world. Further, selection and hybridization in nature resulted in intermediate types.

The tall and dwarf types have been utilised for development of hybrids, combining the early flowering trait of dwarfs with the hardiness and high-yielding character of tall parents, simultaneously exploiting hybrid vigour.

3.3.1 *Native Varieties and Classification Systems*

The earliest documented reference to the native varieties of coconut was in Rumphius' *Herbarium Amboinense* (1741), which listed 13 varieties from the Netherlands Indies. Subsequently, numerous attempts have been made to document the different forms of coconut. Miquel (1855) listed 18 varieties with Latin names and descriptions, which was used by Dutch workers to refer to the different coconut

populations in Dutch colonies. Different varieties of coconut in the Philippines, along with a few Latin varietal names, have been reported. In the 1950s, FAO initiated a questionnaire-based survey and documented the different coconut types in 18 countries (Mao 1959). In 1970, FAO published a list of descriptors of coconut on the basis of information obtained from 30 independent sources (Harries 1970).

Narayana and John (1949), acknowledging the need for categorisation as essential for proper understanding of the variations and forms of coconut, attempted the first systematic classification of the known coconut varieties (Table 3.1). They categorised coconut varieties into two groups, viz. tall and dwarf. The tall were further differentiated into three varieties and nine forms, while the dwarf were differentiated into two varieties and two forms. These varieties and forms were named mostly after the countries from which they were originally obtained or where they are largely grown or after a particular distinguishing character.

Table 3.1 Varietal classification system proposed by Narayana and John (1949)

Variety	Forms	Important features
Talls		
Spicata	–	Inflorescence unbranched (spikeless), with numerous female flowers and few male flowers
Androgena	–	Male tree, inflorescence contains numerous male flowers, does not produce female flowers and nuts
Typica	Ramona	Large nuts and high copra content
	Kappadam	Robust with high tender nut content
	Gigantea	Robust with majestic appearance, large fruits, high copra content, less nut yield
	Nova-guineana	Robust with stout trunk, massive crown with large number of long leaves and bunches, susceptible to fungal disease/insect pests
	Cochin-chinensis	Robust with stout trunk, large number of leaves and bunches, thin kernel, susceptible to fungal disease/insect pests
	Malayensis	Stout trunk, poor yield, green nuts, less copra/oil content, sweet tender nut water and with peculiar aroma, pink colour at base of buttons
	Siamea	Comparatively short with stout trunk, compact crown, medium-yield, green nuts, tender nut water sweet, high copra oil content
	Laccadive	Regular bearer, high yield, medium-size fruits, good quality and quantity of copra, good toddy yielders
	Pusilla	High female flower production, high setting percentage, small size fruits, good quality copra, very high copra oil content, suitable for ball copra production
Dwarfs		
Nana	Nana	Dwarf, short trunk, high yield, good quality and quantity of copra, suitable for tapping
	Maldiviana	Dwarf, short thin trunk, small crown, short leaves, sweet tender water, poor quality of copra
Javanica	–	Intermediate between tall and dwarf, robust, short trunk, prolific and early bearer

This method of classification was quoted by Gangolly et al. (1957) in their review of literature on varieties of coconuts, which also formed the basis of the chapter on varieties by Menon and Pandalai (1960), but being cumbersome was not used for classifying the coconut varieties further. Since the varieties from the Pacific Islands, Africa or America were not included, this classification was not considered comprehensive.

Liyanage (1958) adopted the classification of Narayana and John (1949), primarily based on fruit size and appearance, to classify the varieties of Sri Lanka. He reduced the coconut varieties to three – *typica*, *nana* and *aurantiaca* – by not including *androgena* and *spicata* varieties. The new variety, *aurantiaca*, was considered to be semi-tall, distinct from either the tall or the dwarf groups. The forms corresponded with some of those in the Indian system but had different names. The variety *typica* had eight forms, viz. *typica*, *kamandala*, *bodiri*, *navasi*, *ran thembili*, *gon thembili*, *pora pol* and *dikri pol*; variety *nana* had three forms, viz. *pumila*, *eburnea* and *regia*; and *aurantiaca* had two forms, namely, King Coconut/*rath thembili* and *navasi thembili*. Carlos (1963) identified four botanical varieties, viz. *typica*, *nana*, *javanica* and *spicata* in the Philippines. McPaul (1962) grouped the coconuts of Fiji under two groups, tall and dwarf. Rattanapruk (1970) classified the coconuts in Thailand into three varieties based on the nut characteristics and age at fruiting.

Fremond et al. (1966) put forth another system of classification, on the basis of pollination characteristics. They divided the varieties into two groups, viz. autogamous or self-pollinating as in the case of most of the dwarfs and allogamous or cross-pollinating as in the tall. However, this classification also has limitations as the dwarfs are easily cross-pollinated when surrounded by tall, and tall are also capable of self-pollination (Whitehead 1965a; Rognon 1976). Further, this method of classification requires testing of pollination behaviour of the local forms from different countries under controlled condition, which presents a lot of practical difficulties.

Harries (1978) put forth a method for practical identification of coconut varieties to enable comparison of varieties irrespective of their country of origin and the conditions under which they grow. He advocated the use of fruit component analysis for characterising and classifying varieties. According to Harries, the fruits of a palm being the physiological sinks are not only the most interesting but also the most uniform despite the exposure of palms to variations in the growing conditions. He further reasoned that by considering the relationship between the fruit components rather than absolute values, the effects of fruit size and fruit number are reduced. Based on these assumptions, Harries (1978) recommended a system of classification based on contrasting the proportion of husk in the fruit with the fresh weight of the fruit. He introduced the concept of coconut variety identification based on the *niu kafa-niu vai*-introgression method. According to Harries, the *niu kafa* type represents the coconuts, which have evolved through natural selection in uninhabited islands and coral atolls. These coconuts are named after a variety characterised by long angular, thick-husked fruits. It has the capability of slow germination, which facilitates its survival under natural conditions. The *niu kafa* type being large fruited is suited for copra production and coir processing and has therefore been introduced

into inland areas for commercial cultivation. As a result the identity of its distinctive natural habitat has been lost.

The niu vai type, on the other hand, derives its name from a variety used as a source of sweet uncontaminated water. According to Harries (1979), the coconut palm was first used by humans as a source of water. Therefore, this selection pressure led to an increase in the volume of the liquid endosperm in the immature fruit. This caused a change in the fruit characters, with these being spherical with larger inner cavity and lesser husk. The competition for light and space resulted in these nuts developing the ability to germinate quickly and producing vigorous seedlings. Harries did not include the dwarf varieties under niu vai and niu kafa types as these evolved much later and can survive only under cultivation. The two ancestral types maintain their distinctive characteristics in the Central American isthmus, where these populations are geographically isolated (Richardson et al. 1978). However, in Asia and Pacific, human intervention through migration and cultivation has brought these forms together, and the resulting opportunity for cross-pollination has allowed the development of intermediate forms through introgression. This introgressive hybridization has resulted in the development of many of the cultivated types available today.

Harries (1981) has studied and classified a few of the present-day coconut populations into niu vai and niu kafa types. According to him, the West African Tall and the coconuts along the Atlantic and Caribbean coast of America, such as Jamaica Tall, belong to the niu kafa type, while the Malayan Tall belongs to the niu vai type. He considered the Tahiti Tall to be a variable population, as a result of greater introgression between niu vai and niu kafa types. The coconut populations in most islands in the Pacific Ocean are introgressed forms similar to the Tahiti Tall but sufficiently different to warrant distinct names. Within these introgressed types, he observed that niu vai and niu kafa types occur as minor variants. Harries (1981) concluded that the techniques such as the electrophoresis of polymorphic enzymes would show the relationship between varieties and anticipated that these studies would support the niu kafa-niu vai-introgression theory.

Satyabalan (1997) utilised the then available information on known varieties/cultivars of coconut to comprehensively classify them under different groups. On the basis of the ratio of fruit component traits, tall coconut varieties were categorised into five groups, while dwarf varieties were categorised into three groups under each of the colour groups, viz. green, yellow and red/orange: Group I corresponding to small nuts with less copra content, Group II with medium to large fruits with medium copra content and Group III with medium to large fruits and more copra content (Table 3.2). This classification did not consider the brown dwarfs and the Niu Leka Dwarf which has a much larger fruit with higher copra and shell content showing similarity to palms of the tall variety and unlike the normal green, yellow and orange/red dwarfs.

Therefore, the widely used method of classifying coconut varieties is on the basis of their morphology and growth habit. The coconut varieties are generally classified as tall and dwarf, prefixed by the name of the country of origin.

Table 3.2 Varietal classification by Satyabalan (1997)

Variety	Groups	Important features	Regional distribution/example of varieties
Talls			
Talls	Group 1	Very large fruits, spherical or ovoid shape, thin husk; husked fruit large, spherical, with thin meat, more water and thin shell; copra content >300 g, <30% of husked fruit weight	Southeast Asia, Oceania and America, Thailand Tall, Bali Tall, San Ramon Tall, Malayan Tall, Rennell Tall, Rotuma Tall, Tahiti Tall, Panama Tall, Ecuadorian Tall
	Group 2	Large fruits, spherical or ovoid shape, thin husk; husked fruit large, spherical, with thin meat, more water and thick shell; copra content 200–300 g, <30% of husked fruit weight	Southeast Asia, Oceania and America, Africa; Thailand Klarng, Borneo Tall, Tenga Tall, Philippines Laguna Tall, Philippines Lono, Solomon Tall, Fiji Tall, Natava Tall, Rangiroa Tall, Surinam Tall, Nigerian Tall
	Group 3	Large fruits, spherical or ovoid shape, thin husk; husked fruit large, spherical, with thick meat, less water, thick shell; copra content 200–300 g, >30% of husked fruit weight	All coconut-growing regions Park Choke Tall, Guam Tall, Polynesian Tall, Jamaican Tall, St. Vincent Tall, Atlantic Tall, West African Tall, Zanzibar Tall, Ceylon Tall
	Group 4	Medium-sized fruits, spherical or ovoid shape, thick husk; husked fruit medium, spherical, with thick meat, less water, thick shell; copra content <200 g, >30% of husked fruit weight	All coconut-growing regions Standard Kudat Tall, Philippines Dalig Tall, Solomon Tall, New Hebrides Tall, Blanchisseuse Tall, West African Tall, Mozambique Tall, Kenya Tall, Gon thembili, Laccadive Ordinary Tall, Laccadive Micro Tall, Benaulim Tall
	Group 5	Medium-sized fruits, spherical or ovoid shape, thick husk; husked fruit medium, spherical, with thin meat, more water, thick shell; copra content <200 g, <30% of husked fruit weight	All coconut-growing regions Park Choke Tall, Kong Thein Yong, Klapawangi, Fiji Tall, Niu Ui, Solomon Tall, Kiriwana Tall, Kavieng Tall, Surinam Tall, Seychelles Tall, Indian East Coast Tall, Indian West Coast Tall
Dwarfs			
Green Dwarfs	Group I	Small fruits; husked fruits with high percentage of shell (26–39) and copra (32–43)	Chowghat Green Dwarf, Ayiramkachi, Pumilla
	Group II	Medium-sized fruits; husked fruits with lesser percentage of copra (23) and slightly lesser shell (23–27)	Nam Hom (aromatic coconut), Nok Koom
	Group III	Medium-sized fruits, husked fruits with slightly higher percentage of copra (25–35) and lesser shell (20–25)	Equatorial Green Dwarf, Guinea Green Dwarf, Mu-se-keo, Thailand Green Dwarf, Thungkhled, Pathiu Green Dwarf; Malayan Green Dwarf, Gangabondam Green Dwarf

(continued)

Table 3.2 (continued)

Variety	Groups	Important features	Regional distribution/example of varieties
Yellow Dwarfs	Group I	Medium small fruits; husked fruits with high percentage of shell (20–29) and copra (24–35)	Malayan Yellow Dwarf
	Group II	Medium-sized fruits; husked fruits with lesser percentage of copra (21–30) and lesser shell (16–19)	Ghana Yellow Dwarf, Malayan Yellow Dwarf
	Group III	Medium-sized fruits; husked fruits with slightly higher percentage of copra (24–31) and slightly lesser shell (21–27)	Malayan Yellow Dwarf, Nari-kay
Red/Orange Dwarfs	Group I	Medium small fruits; husked fruits with high percentage of shell (20–29) and copra (24–35)	Malayan Red Dwarf, King Coconut, Mapro fire, Thalai Roi
	Group II	Medium-sized fruits; husked fruits with lesser percentage of copra (21–30) and lesser shell (16–19)	Malayan Red Dwarf
	Group III	Medium-sized fruits; husked fruits with slightly higher percentage of copra (24–31) and slightly lesser shell (21–27)	Cameroon Red Dwarf, Malayan Red Dwarf, Chowghat Orange Dwarf

In spite of the absence of wild relatives, the present-day population of the coconut palm presents a wide range of variability broadly grouped into two groups – tall and dwarfs – on the basis of a few important characters like stature, growth characteristics of the palm, precocious nature in flowering and nut and copra characters (Table 3.3). This is the widely accepted classification used for distinguishing coconut cultivars. The tall are the most commonly cultivated ones for commercial production in all coconut-growing regions, while the dwarfs are increasingly being grown for their aesthetic value, as parents for production of high-yielding hybrids as well as for tender nuts.

To conclude, plant habit, fruit colour and other fruit characteristics are presently the most convenient for grouping of the varieties. In most cases, these traits are genetically determined and not solely the effect of environment. However, further refinements are possible for a more fool-proof classification system. Based on molecular marker studies, the present-day coconut populations have been classified into two major groups: the Pacific group with five subgroups (Southeast Asia, Melanesia, Micronesia, Polynesia and the Pacific coast of Central and South America) and the Indo-Atlantic group. The Pacific group includes the domesticated coconut, while the Indo-Atlantic group includes niu kafa coconut types. However, human intervention through migration and cultivation has brought the different forms together and the resulting opportunity for cross-pollination has allowed the development of intermediate forms through introgression. Presently, there is no

Table 3.3 General characteristics of tall and dwarf coconuts

Trait	Tall	Dwarf
Stem height	Relatively more at a given age	Relatively less at a given age
Stem circumference	Sturdy, with bole at base	Thin, without bole at base
Leaf	Longer, wider leaf base, strong attachment to the stem	Shorter, narrow leaf base, weak attachment to the stem
Leaflets	Longer and broader	Shorter with relatively lesser width
Initiation of flowering	Late (5–7 years)	Early (3–4 years)
Mode of pollination	Predominantly cross-pollinated	Predominantly self-pollinated
Colour of fruits and petioles	Generally mixtures of greens and browns in the population	Green, yellow, red-yellow (orange) or brown in the population
Arrangement of leaf scars on the trunk	Widely spaced	Closely spaced
Fruit size	Very small to very big	Small to medium
Copra	High quantity and better quality	Lesser quantity and poor quality
Tender nut water	Low to medium	Medium to high, sweet water
Phenotypic variation	High	Low
Within cultivar	High	High
Between cultivars		
Leaf and bunch attachment	Very strong	Fragile
Root distribution	Generally more dense and plentiful	Less dense and few
Productive life span	About 60 years	About 40 years

single method of classification that can account for all the variability observed in the global coconut populations.

In addition, to the variation described above, variation in coconut endosperm texture and quality, varieties with aromatic water, thick-shelled nuts, thin-husked fruits, pink-husked fruits, persistent inflorescence and leaves have been reported in different natural coconut populations which are dealt under Sect. 3.6. Besides these, a number of abnormalities in stem, vegetative parts, inflorescence and fruit shape have been reported from different coconut-growing regions. These abnormalities, elucidated under Sect. 3.6, are freaks of nature and not distinct varieties, from the botanical point of view.

3.4 Botany and Morphology

The coconut palm is a monocot. The single stem of the palm lacks bark, cambium and secondary growth features, characteristic of gymnosperms and dicotyledons, and hence the stem once formed never alters in thickness, except for a slight shrinkage when the stem gets old. Similarly, the root lacks a taproot, and the roots once formed never grow in thickness. The palm is unbranched and does not form vegetative buds on the stem. The features of the different parts of the palm are described below.

3.4.1 *Root Growth and Development*

The palm being a monocot has an adventitious root system. Roots emerge from the base of the stem (bole) and continue to be produced throughout the life of the palm. The number of roots varies with age of the palm, girth of the bole, soil fertility and management. It ranges from 1500 to 7000 (Sampson 1923; Copeland 1931; Patel 1938) and in rare instances as many as 11,360 roots have been recorded (Menon and Pandalai 1960). The main roots form a number of secondary roots which branch profusely forming a large absorptive surface through which the palm takes in nutrients from the soil. However, these rootlets are short-lived and are frequently replaced. The roots do not have root hairs. From the main roots and rootlets, numerous pneumatophores develop and serve as breathing organs, facilitating gaseous exchange between the roots and the atmosphere. The tender growing tip of the roots is protected from injury by a root cap.

The main roots of the palm are uniform in size and long-lived. They generally measure around 5–10 metres in length and 8 mm in diameter. However, occasionally, longer roots, up to 25 m in length, have also been reported (Menon and Pandalai 1960). The growing root is initially yellowish-white in colour and gradually turns light red and subsequently becomes reddish-brown with age. Thus in a fairly old and growing root, gradations in colour are generally visible. Coconut roots cannot indefinitely grow into water or withstand continuous water stagnation and submerged portions of the root get decayed. However, when the water table recedes, these roots produce new branch roots and/or rootlets (Sampson 1923; Menon and Pandalai 1960; Ohler 1984). The roots of the coconut palm, in general, can live for many years. However, the rootlets have a very short life span, as influenced by the ecological conditions in the root zone.

The coconut root, both the main roots and rootlets, has three regions, distinct in their internal structure, viz. the root cap, the growing root tip and the absorbing region, a little distance away from the root tip. However, the tissues in rootlets are much smaller and less defined and carry less conducting tissues, especially xylem vessels.

The tip of the root contains the root cap (8–26 layers of dead tissue), covering the tender growing portion of the root and the meristem called calyptragen, which is responsible for the formation of the root cap. The growing root tip, immediately behind the root cap, is undifferentiated and includes the epidermis and uniform meristematic cells which later on differentiate into various tissues. The cells in the absorbing region of the root are differentiated, with three distinct layers, viz., the outer single-layered epidermis, the inner central stele and the thick cortical region in between the epidermis and the stele. The epidermis is the main absorbing tissue, and the cells are much larger, multinucleate (two to four nuclei), thin-walled and short-lived and wither away as soon as the hypodermis attains an impervious sclerenchymatous condition.

The central stele accounts for about one-fifth the diameter of the root and comprises of conducting tissues bordered by a single layer of living cells, the pericycle.

The rootlets and pneumatophores emerge from the pericycle. Immediately beneath the pericycle are 30–55 radially arranged groups of small dividing cells called the procambial strands, which differentiate into the xylem and phloem. The xylem vessels (are large) alternate with the phloem vessels (are inconspicuous). Often, two xylem vessels coalesce to form a bigger vessel, and a mature root may contain about 25 large metaxylem vessels. The companion cells of the vascular bundles, which are initially thin walled, later develop into thick-walled sclerenchymatous bundle sheath and contribute to the tensile strength of the stele. In the centre of the stele is the narrow pith, comprising of living cells, which subsequently disintegrates as the root becomes old. In between two rows of phloem and xylem, there is a narrow ray of cells, which connects the inner ground tissue bordering the central hollow with the pericycle (Patel 1938).

The cortical region accounts for the major portion of the root and comprises of the hypodermis/exodermis, endodermis and mesodermis. The hypodermis lies immediately below the epidermis and comprises of several layers of small and thin-walled cells, which subsequently becomes thick walled, and the epidermis loses its absorbing capacity. The hypodermis protects the central stele by its thick and pliable covering. The central mesodermis consists of large-sized and loose parenchyma enclosing many air spaces and includes tannin cells as well as some empty cells of unknown function. The endodermis has a single row of small cells, whose distinct identity is maintained even in older roots. The inner wall of the endodermal cells is thick as compared to the lateral walls, while the outer wall is thin. A few thin-walled passage cells exist in this layer (Menon and Pandalai 1960).

3.4.2 Stem

The coconut palm has a single, straight stem, greyish in colour, topped by a crown of leaves. It has a single terminal bud, also called the ‘cabbage’, the death of which results in the death of the palm. The stem is marked by leaf scars. The thickness of the stem is determined by its vigour and soil conditions, in addition to varietal differences. In certain varieties, the base of the stem referred to as the bole is swollen. The stem of the coconut palm becomes visible once the bole reaches the full stage of its development. Under favourable conditions, the trunk in a young palm is formed within 3–4 years. In the initial years, the stem gradually becomes thick, and once the maximum size is reached, there is not much change in the stem girth with age. In the tall variety, the base of the trunk (bole) is up to 0.8 m in diameter, tapering quickly to about 0.4 m (Child 1974). However, the stem becomes thinner as the palm grows old as well as under unfavourable growth conditions.

The length of the stem is determined by the age of the palm, variety and ecological conditions. Dwarf varieties have shorter trunks than tall varieties. Palms under unfavourable management practices, including under planting with excessive shade and very close planting, exhibit rapid stem elongation. Stem growth is fastest at early stages, with annual height increment of as much as 1.5 m year⁻¹. The incre-

mental growth reduces and the stem tapers down over the years and levels off as the palms grow old, with annual stem elongation of about 10–15 cm from the 40th year. In rare instances, palms with branching, due to damage to the terminal bud, are observed, and up to five branches have been reported (Davis 1969). The stem, being predominantly fibrous, combines stiffness with adequate suppleness and is tough enough to withstand considerable lateral strain, particularly when exposed to severe winds/gales, due to the presence of the numerous vascular bundles (as much as 18,000 in a mature palm).

The stem is derived from the terminal bud, which is approximately 0.5 mm × 0.5 mm in size, visible as a small protuberance at the apex of the trunk and well protected by the leaves in various stages of development. The growing point comprises of a mass of minute cells with dense cytoplasm and large multinucleolate (four to ten nucleolate) nuclei. This region is three to four layered and has meristematic activity. Immediately below this region, in the tender stem, the cells are large and contain numerous procambial strands along with large starch granules and sugar reserves. These procambial strands later differentiate into xylem and phloem bundles. The bundles derived from the procambial strands are closed ones and are scattered throughout the stem. The first formed bundles are comparatively short-lived but bigger than those formed subsequently from the ground meristem. The first formed protoxylem vessels are smaller than the subsequently formed metaxylem. In a young stem, three to nine xylem vessels are observed, and these form a V-shaped tissue, with the base towards the centre of the stem. Small groups of xylem vessels are seen outside or above the xylem, and both are enclosed within a layer of thin-walled cells that subsequently thicken with age and form the fibrous sheath. However, a few cells in certain patches of the fibrous sheath as well as the parenchyma close to the xylem and phloem are not thickened even in old stems. This is mainly confined to the apex of the bundle as a broad round tissue, and the base of the bundle is practically without the fibres. The xylem tissue, V-shaped when young, changes shape with age. The xylem may be found in two or three groups. However, big bundles with many xylem vessels are rare. The most common type of bundle in the old stem is the one with only one big xylem vessel, a small phloem tissue above and a broad fibrous tissue lying at the outermost of the bundle. The vascular bundles towards the centre are more widely spaced than towards the periphery. The number of vascular bundles in the periphery is also few or negligible, instead large numbers of small groups of fibres derived from the ground meristem are observed. Between the central part of the stem and the periphery, the vascular bundles are closely packed with few layers of intervening cells. Occasionally, the separating parenchyma is absent, and therefore, two bundles coalesce into a double bundle. The size of the vascular bundles increases considerably with the age of the palm. The xylem and phloem are enclosed by cells that are initially thin walled but subsequently thicken and form the fibrous sheath.

The cortex comprises of several layers of thin-walled parenchyma and a single layer of epidermis with thicker outer wall. In the parenchyma, tannin cells and air passages occur, mostly towards the periphery. Both the stem and the root lack the

periderm or corky tissue seen in most of the plants. However, the periphery of the stem contains a peculiar storied type of cork cells, called rhytidome.

There is no secondary thickening of stem in coconut palms as they lack bark and cambium (the living and growing tissue between the bark and wood). However, the stem of a seedling is thin, while that of an adult palm is stout. The thicker stem as the seedling grows older is the result of increased meristematic activity of the growing point resulting in the formation of more and more cells and vascular bundles, thereby forming the bole, which appears as an inverted cone. Once the bole is formed, the stem of almost uniform girth begins to appear.

3.4.3 Leaf

The first few leaves of a growing coconut seedling have the pinnae fused together and appear as entire leaves. After about six to eight leaves have been formed, the subsequent ones tend to split into leaflets. By about 3–4 years, the trunk becomes visible with a single terminal growing point, from where new leaves develop.

The adult coconut palm bears a crown of leaves at the apex, comprising of the opened leaves and those surrounding the bud in various stages of development. The number of leaves in the crown varies with the variety and ecological and cultural conditions. Generally, the crown of an adult palm carries, in addition to the opened leaves, a similar number of leaf primordia, in different stages of differentiation. These leaves belong to four distinct sets. The first set comprises of the oldest 10–12 leaves, from the axils of which fruit bunches have been harvested. The next set comprises of the next older 10–14 leaves, supporting fruit bunches in different stages of development. The third set includes the younger 10–12 opened leaves, with spadices in various stages of development in their axils. The last set comprises of leaves in the cabbage with the outermost ones in different stages of unfurling and the remaining which have not yet emerged.

The leaves are long and vary from 3 to 6 m in length depending on the variety, age of the palm, soil fertility and vigour of the palm. The individual leaf consists of a strong petiole, extending to form a rachis with numerous leaflets (150–250) inserted on it. The leaflets on either side of the rachis are not exactly paired, with one-half having about two to ten leaflets more than the other side. The leaflets are also long (60–150 cm), narrow, linear, tapering and lanceolate. The leaves when young retain the stipules at their bases, forming a fibrous tissue that more or less surrounds the whole stem. As the leaf becomes older, the stipules dry and fall away. In young palms, the stipules persist till the leaf dies.

The progression of leaf development from the minute bud to the adult leaf takes several years. On an average, the time taken from inception to final abscission of the leaf is almost 5 years. Different workers have explained the stages in development of the leaf (Patel 1938; Padmanabhan 1963), formation of leaflets (Venkatanarayana 1957) and sequence of events involved in differentiation of leaf primordia into adult leaf (Periaswamy 1965). The leaf primordium is differentiated almost 28–32 months

prior to its emergence from the leaf sheath. Under favourable conditions, the leaves of good bearing palms remain on the crown for 3–3.5 years after emergence. Generally, the life span of leaves is lesser in poor bearers than medium and heavy bearers (Patel 1938). In addition, the season and also soil conditions affect leaf shedding. Satyabalan (1993) observed that high yielders bear higher number of leaves on the crown indicating the longevity of the leaf as well as the drought tolerance of the palm. In regions where the seasons are more marked, there is a considerable cyclic variation in the rate of leaf opening which appears to be more dependent on the temperature rather than the rainfall. Generally, 1-year-old seedlings contain seven to nine leaves, with majority of the seedlings having eight leaves. The number of leaves on the crown increases to 30–35 during maturity, and an adult palm on an average bears about 30 leaves.

The length of the leaf varies from 4 m in dwarfs up to 7 m in tall, depending on variety, growing condition and age of the palm. The petiole accounts for about one-fourth of the total length of the leaf but varies with the variety. The petiole continues as the midrib of the leaf. A short and stout petiole is able to better withstand vertical pressure exerted by the developing bunch in its axil. The leaflets are borne on either side of the midrib and have differential length based on their position in the leaf. The first leaflets at the base are short, followed by a gradual increase in length of the subsequent leaflets with the maximum length being achieved at about one-third of the midrib followed by a graded decline in length towards the top of the leaf. The smallest leaflets at the tip are about 25 cm in length, while the largest leaflets measure about 80–120 cm. The number of leaflets in a mature palm leaf ranges from 200 to 250.

The leaves in a coconut palm are so arranged as to ensure maximum light availability to each leaf. They are arranged in five spirals, running either in the clockwise or anticlockwise direction, and spirality in a palm can either be right-handed (bunches hang towards the right of the petiole) or left-handed but remains the same throughout the life of the palm. Based on the phyllotaxy, the 6th leaf is positioned over the first leaf, the 11th leaf over the 6th and so on. The two types of spirals are distributed almost equally in a population, with a slight preponderance of the left spiral (Davis 1962; Louis and Chidambaram 1976).

Patel (1938) reported that the number of leaves in the unopened cabbage is 1 to 1½ times the opened leaves on the crown of the palm. Leaf primordium differentiation occurs 28–32 months prior to the emergence from the leaf sheath as a small indistinct protuberance on the side of the growing point. Within a month, it undergoes repeated periclinal and anticlinal cell divisions and develops into a seven to ten cell-layered fingerlike structure having three layers of primary meristem, viz. the outermost dermatogen, the middle three cell-layered periblem and innermost layer plerome. In the succeeding month, the rapidly growing protuberance assumes the shape of a hollow cone enclosing the next younger leaf and the growing point. At this stage, procambial initials, which subsequently form the vascular bundles, appear in the plerome. The developing leaf initially contains only the petiole portion, and differentiation of the leaflets occurs 8 months later, in approximately the seventh rudimentary leaf from the growing point. Venkatanarayana (1957) observed

the formation of 18-layered rectangular mass of cells united at the margin that develops into leaflets, followed by subsequent longitudinal split in the middle of this tissue, forming the sides of the leaflets. The epidermis of the leaflets, both upper and lower, is derived from only the perome tissue and not from the dermatogen. The inception of plications and the separation of leaflets in palm leaves is on the basis of vertical and transverse growth stresses (in the expanding and elongating lateral faces of the rachis) acting at the base of the nonplicate lamina which bears alternating lines of weaker parts between parallel rows of provascular strands whose cells elongate at right angles to the forces of vertical stress and resist them (Padmanabhan 1984).

The procambial strands of the leaflets are formed after the xylem vessels of the first formed vascular bundles of the petiole and the main rachis have thickened. Within the leaflet, the procambial strands of the midrib are formed first, followed by those of the sides 2 months later. This is followed by the formation of the cross veins. In a mature leaflet, there is a strong central midrib from which slant down the two sides of the leaflet. The epidermis is observed on either side with a thick outer cuticle. The lower epidermis is thinner than the upper epidermis. Below the upper epidermis are two layers of hypoderm that serves as water storage tissue, while beneath the lower epidermis is a single broken layer of hypoderm. Below the upper hypoderm and spreading almost to the lower hypoderm is the broad palisade tissue comprising of thin walled, elongate and closely packed cells. Below the palisade tissue is a scanty spongy parenchyma. The chloroplasts are formed in the mesophyll just prior to the emergence of the leaf. Each leaflet contains about 20–25 vascular bundles running all along its length and occupying the entire thickness of the leaflet from the upper to lower hypoderm. Of these, five to six bundles are big while the rest are narrow. In between two large vascular bundles and just above the lower hypoderm are three small vascular bundles made up of a few tracheids, three to four phloem elements and a small group of fibres. The top of the petiole contains as many as 500–1000 diminutive vascular bundles alternating with small group of fibres, which provide additional mechanical strength to the leaf. The upper epidermis is highly cutinized. On the lower epidermis, numerous multicellular, dark brown, short-stalked scales containing tannin (trichomes) occur at regular intervals in small depressions. In addition, bundles of crystals of raphides are seen all over the lower epidermis. The stomata are first formed about a year prior to the emergence of the leaf and are initially confined to the margin of the leaflets away from the midrib, while the vast majority of stomata are formed just about 3 months prior to the emergence of the leaf. The stomata are confined to the lower surface of the leaflets and are distributed all along its length in two to four longitudinal rows in between every two vascular/fibre bundles. The stomata are elliptic with two guard cells containing large starch grains and a small opening. The guard cells are bordered by subsidiary cells, and a small square cell at either end of the stoma joins these subsidiary cells. The stomata are fairly large with a dimension of $38 \mu \times 19 \mu$, extending to $38 \mu \times 40 \mu$ along with the subsidiary cells. Normally, a leaflet contains about 170–220 stomata mm^{-2} . However, stomatal density is a varietal character. Dwarf varieties, in general, have higher stomatal density than tall (Satyabalan

1993; ICAR-CPCRI 2015). The mature stomata are tetracytic, with both the polar and the lateral subsidiary cells cut off by the neighbouring protodermal cells. Each lateral subsidiary cell is the result of a longitudinal division of a trapezoid cell formed by two oblique divisions of a lateral protodermal cell. The ontogeny of stomata conforms to the perigynous type with nonintersecting oblique division (Ghose 1979).

The midrib of the leaflet is a very strong structure with a central ring of seven to eight vascular bundles enclosed within a fibrous sheath formed by two to three rows of thickened cells. The outer epidermis is highly cuticularised and is continuous with that of the sides of the leaflets. Between the epidermis and the fibrous sheath are two layers of hypoderm (continuous with the upper hypoderm of the sides of the leaflet) followed by two to three layers of parenchyma. The attachment of each half of the leaflet to the midrib is narrow and tapering, but the place of attachment is strengthened by a group of fibres. There is also a special motor tissue bordering the inner epidermis that is continuous with the lower epidermis of the leaflet. Behind the motor tissue are a vascular bundle and a patch of sclerenchyma. In young leaflets, this motor tissue is nonfunctional and comprises of smaller, much compressed, thin-walled elongated cells. By the time the leaflets are about to open, the motor tissue develops considerably and consists of two rows of big cells. These cells absorb water supplied by the vascular bundle behind it and become turgid, thereby causing a lateral push to be exerted along the sides of the leaflet, which gets separated from its oppressed position in the bud and remains at an angle. The bundle of fibres at the base of the attachment of the sides act as a pivot on which the side moves. However, as the epidermal folds are highly cutinised, sudden movements are checked. The outer margins of the sides of the leaflets are peculiarly folded somewhat like a hook; one margin is folded on the upper epidermis and another on the lower so that both point towards the same direction. At the bend of the fold, the epidermis is in short folds, and immediately behind the fold is a motor tissue similar to the one at the base of the sides of the leaflets. The cells in the motor tissue are initially narrow, elongated and much compressed but are developed at the time of unfolding of the tissue. When the cells become big and turgid, they exert an outward pressure, and as a result, the fold is straightened, and the interlocked margins are released, thereby helping the leaflets to unfold. This motor tissue at the margin of the leaflets persists in some of the older leaves, while in others it is lost and the epidermal folds straighten out and therefore the margin becomes a truncate structure instead of a bent one. In addition to these two motor tissues, two other motor tissues are seen at the base of the leaflet. Of these two, one is located at the angle made by the inner or upper half of the leaflet on the main rachis and helps to spread out the leaflet as a whole, while the other located on the inner side of the outer half of the leaflet at the place of attachment on the main rachis helps keep the outer half of the leaflet in position. Thus, there are four different motor tissues in the leaflet – one pair running the whole length of the midrib, one at the margins and two at the base.

The petiolar sheath is first visible as a soft wing on either side of the petiole, about a year after the leaf is differentiated. The young sheath is made up of a mass

of parenchyma forming the ground tissue in which are scattered a few procambial strands. As the leaf matures, these strands develop into vascular bundles of considerable size and length with a broad mass of sclerenchyma, like those in the stem. In addition to the vascular bundles, isolated groups of fibres occur all over the sheath, especially towards the periphery. A narrow cortex is also visible in the young sheath. The old sheath consists of closely woven fibres and vascular bundles with a mass of sclerenchyma and without much of the thin-walled ground parenchyma. The importance of the mechanical tissue of the petiole sheath is evident, as at an early stage it encircles the stem and partly bears the weight of the leaf in the developing bud, and as the petiole of the other young leaves enclosed in the sheath develops, it is gradually torn up. The thickness of leaf sheath, fibre of weft and warp strands has relevance to adaptation, geographical affinity, pollination system and taxonomic forms (Arunachalam et al. 2005).

3.4.4 *Inflorescence*

The coconut palm is monoecious with distinct male and female flowers borne on the same inflorescence. The inflorescence emerges from the leaf axils, and in adult palms under favourable conditions of growth, one inflorescence is produced every month from successive leaf axils. The age at initial flowering varies with the variety as well as the growing conditions and ranges from 3 to 7 years after planting the seedlings in the main field. Dwarfs in general commence flowering earlier than the Talls. The inflorescence, referred to as a 'spadix', is initially visible as an oblong flat structure enclosed by a double sheath called spathe and when fully mature becomes more cylindrical. Due to the pressure exerted by the growing inflorescence, the spathe ruptures along a longitudinal groove and exposes the inflorescence.

The length of the inflorescence ranges from 60 to 200 cm and has about 8000–10,000 male flowers and 0–400 female flowers, depending on the variety, cultural conditions, season and age of bearing (Patel 1938; Menon and Pandalai 1960; Niral et al. 2008). The central inflorescence axis, referred to as rachis (peduncle), bears about 30–35 branches, the spikelets. The spikelets carry numerous male flowers, with few female flowers (generally 1 to 2, sometimes none and occasionally up to 5) borne near the base of the spikelets. Occasionally a few hermaphrodite flowers are seen alongside the female flowers in some cultivars. All the flowers are sessile/subsessile.

The flower primordium is formed about 4 months after the initiation of the leaf primordium and about 32 months before the opening of the spathe. The male and female flowers are differentiated about 12 months prior to the opening of the fully grown spadix. Generally, the male flowers begin to form a month later than the females and mature a month before the stigma is receptive. The ovary is differentiated 6–7 months before the opening of the spathe. About 75% of the total growth in the length of the inflorescence occurs during the period of about 6 months before the opening of the spathe. Soon after the opening of the spadix, the male flowers com-

plete their life cycle, while the female flowers have a longer history as it takes another 12 months for the nuts to fully ripen.

The development of the inflorescence has been studied and described by Juliano (1926) and Patel (1938). The inflorescence arises in every leaf axil, and the rudimentary inflorescence primordium is formed at almost the same time as the subtending leaf, and therefore the inflorescence initials are present in the axils of the young rudimentary leaves near the growing point. The inflorescence primordium is a minute cone-like protuberance about $77 \mu \times 107 \mu$ found in the axil of the fourth leaf from the growing point, about 32 months prior to the opening. The whole inflorescence cluster consists of a central axis (the rachis), from which the rachillae arise in spiral succession. The rachillae at their apices bear the male flowers (either singly or in pairs) in the axils of tertiary bracts (floral bracts), with female flowers at the base. The inflorescence initially begins as a minute protuberance at the end of two clasping bracts, one of which is situated towards the cabbage and the other between the petiole and the inflorescence initial. The first primary bract envelops the second primary bract, and these later outgrow the whole floral cluster and form the outer and inner spathes enveloping the growing inflorescence. The enclosed inflorescence primordium has at its apex a ring of actively dividing cells, which shows signs of formation of the primary inner bract which later develops into a persistent inflorescence envelope. After the spathes have completely enveloped the growing point of the inflorescence, secondary bracts make their appearance as minute lateral protuberances. The lower secondary bracts tend to elongate more rapidly than those at the apex, so that their tips are nearly as long as the apex of the main rachis of the inflorescence.

The next stage in the development of the inflorescence is marked by the appearance of the primordia of the rachillae, in the axils of the secondary bracts. These primordia rapidly elongate vertically and lateral to the main rachis leaving behind the subtending secondary bracts. The main rachis always terminates with a single rachilla almost similar to the lateral branches. In the rachillae, tertiary or floral bracts appear, and in the axil of these floral bracts, there is a zone of actively dividing cells, which form the initials of the flower primordium.

3.4.4.1 Floral Morphology

Male Flowers The male flowers outnumber the female flowers in a spadix. The number of male flowers varies depending on the length of spikelet-bearing portion and the number and length of spikelets in an inflorescence. The male flower comprises of three sepals, three petals and six stamens, which are about 8 mm in length and are arranged in a single whorl with a rudimentary/abortive pistil in the centre. Anthers are yellowish in colour and attain a bluish-green tinge on maturity. Opening of the male flowers commences from the apex of the spikelets and extends downwards and occurs throughout the day, with maximum blooming during 8–10 AM. The interval between the opening of the first male flower and the shedding of the last male flower is termed as the male phase, which lasts for 18–22 days.

The number of male flowers varies with the variety, age, as well as environment. Nampoothiri (1970) reported that the proportion of male flowers at the distal, middle and proximal portion of the inflorescence was constant from tree to tree in the case of tall varieties, while in the case of dwarf varieties, the ratios of male flowers in the three positions were found to vary from palm to palm.

Female Flowers The female flowers are comparatively few in number, as compared to the male flowers. They are larger having a diameter of 13–25 mm, globular in structure and are bracteolate. They contain six rounded, concave, imbricate perianth with a staminodal ring at the base and a short style with three stigmas at the centre. Ovary is tricarpellary, syncarpous with a single anatropous ovule in each carpel. However, only one ovule is fertile. Two to five male flowers, referred as accessory or axillary male flowers, accompany each female flower. Generally, the female flowers become receptive 3–4 weeks after the opening of the spathe, by which time the male flowers in the spadix would have shed their pollen. Each female flower remains receptive for 1–3 days. The interval between the receptivity of the first female flower and the last female flower is termed as the female phase, and it lasts for 5–7 days, depending on the variety and growing conditions.

3.4.5 Pollen, Pollination and Fruit Set

The male and female flowers being separate, transmission of the pollen from the male flower to the female flower is through wind or insects (Sampson 1923; Patel 1938; Louis and Chelladurai 1984). The possibility of both self and cross-pollination exists in coconut, depending on the time interval between the opening of the male flower and the receptivity of the female flowers, and varies with the variety as well as cultural and environmental conditions. In general, there is a gap of at least 2–3 days between the end of the male phase and commencement of the female phase in an inflorescence (Ratnambal et al. 1995, 1999), and hence pollination is effected through pollen from neighbouring palms (cross-pollination). However, in majority of the dwarf populations, self-pollination is observed (Jack and Sands 1922), due to overlapping of the female and male phases in an inflorescence (Ratnambal et al. 1995, 1999). Self-fertilisation can also occur through overlapping of the male and female phases of successive inflorescences, during certain seasons like summer months in India (Patel 1938), as well as rainy season in the Philippines (Copeland 1931) and in Sri Lanka (Petch 1913).

The pollen sacs burst and shed their pollen before the opening of the male flower or simultaneously with splitting of the perianth lobes. The fresh pollen grains are smooth and spherical in shape and measure about 0.063 mm in length and 0.02 mm in breadth. The coconut pollen retains its viability for up to a week at room temperature. The viability period is enhanced when pollen is stored at low temperatures and/or in the desiccators. Nampoothiri (1970) observed differential fertility of pollen within an inflorescence, with pollen from male flowers at the proximal end of the inflorescence being the most sterile, while at the distal end, the pollen sterility was the least.

3.4.6 *Fruit Development: Endosperm, Embryo*

The fruit starts developing upon fertilisation of the female flowers. Even though an inflorescence produces many female flowers, only a few develop into mature fruits, while the rest are shed during the course of development. The coconut fruit contains an internal endosperm (kernel) with embryo embedded in it and protected externally by a thick pericarp. The fruit of the coconut palm, commonly referred to as the 'nut', is botanically a drupe. The pericarp has three distinct regions, the exocarp/epicarp (tough fibrous outermost layer, with varying shades of green, brown, red or yellow colour, depending on the variety), mesocarp (husk portion immediately beneath the epicarp) and endocarp (shell). In the tender fruit, husk is fleshy and has an astringent taste, which becomes more fibrous as the fruit matures. The thickness of the mesocarp is dependent on the variety and varies from 2 to 15 cm. The shell, on its basal side, has three pores (eyes) representing the three carpels of the ovary. One of the eyes is soft, while the other two are quite hard. the embryo is protected by the shell and is present beneath the soft eye. The thickness of the endosperm ranges from 0.8 to 2.0 cm, depending on the variety. In between the endocarp and the albuminous endosperm is a thin layer of testa/seed coat. The testa is brown in colour and adheres to the endosperm. in the middle of the endosperm is a cavity filled with sweet water, also referred to as the liquid endosperm. In the immature fruit, this central cavity is completely filled with water. However, the quantity of liquid endosperm reduces gradually during development and on storage for a few months after harvest. If the nut water is completely exhausted, the fruit loses its ability to germinate (Menon and Pandalai 1960).

The young embryonic fruits are initially yellowish in colour, but turn green, yellow or red (depending on the variety) on exposure to light. On reaching complete maturity (10–12 months after fertilisation), the fruits turn brown. Juliano (1926) observed that after fertilisation, the fruit develops with the pericarp developing more rapidly at the basal region which appears whitish and soft till almost maturity. The endocarp is differentiated even before fertilisation and appears as a soft creamy white structure. As the fruit develops, the embryo sac increases in size leaving a large vacuole at the centre. The young fruits initially grow more in length than width, and later, there is a greater increase in width rather than length, and finally the fruits in most of the varieties are wider than long.

The developing nut attains its maximum size and weight around 8 months after fertilisation and remains so for another 2 months. Subsequently, there is a drastic reduction in nut weight along with a slight decrease in the size. In the final stages of ripening, there is loss of water from the liquid endosperm. Abraham and Mathew (1963), based on their studies on cytology of coconut endosperm, reported that the development of the solid endosperm (kernel) in the fruit becomes visible 6 months after fertilisation as a thin jellylike coating around the periphery of the large embryo-sac cavity. The endosperm tissue is thicker at the antipodal end. The thickness of solid endosperm reaches its maximum around ninth month. The rate of oil deposition in the endosperm peaks at this stage and continues well after the fruits have turned brown (Menon and Pandalai 1960).

Jayasuriya and Perera (1985), based on their studies on the growth, development and dry matter accumulation in coconut fruits, reported four distinct growth phases, viz. initiation, pre-pollination development, post-pollination development and finally maturation and senescence. They reported commencement of husk, shell and endosperm growth in the first, fifth and sixth months, respectively, with simultaneous growth of all the three components from 5 to 8 months after fertilisation. The rapid growth phase of the husk, shell and endosperm is extended from 3 to 7 months, 5 to 9 months and 6 to 10 months, respectively. The weight of the nut and the individual nut component traits are influenced by the variety as well as growth conditions (Patel 1938; Harries 1978; Satyabalan 1993; Niral et al. 2009).

3.4.6.1 Fruit Maturity

The fruits mature 10–12 months after fertilisation. In tall varieties, it generally takes 11–12 months for the fruits to mature, whereas in dwarf varieties, nuts will mature in 10–11 months after emergence of the inflorescence. On maturity, the outer surface of the fruit (the exocarp) starts turning brown. At this stage, the fruits, in certain varieties, tend to detach from the fruit stalk and fall. However, in certain varieties, especially some of the dwarf varieties, the attachment to the fruit stalk is strong, and the mature fruits do not shed from the palm even after the fruits have turned completely brown. In such cases, if mature fruits are not harvested regularly, the endosperm tends to dry and get spoilt inside the nut.

3.4.6.2 Morphology

Structure of the Fruit A mature embryo is cylindrical in shape and approximately 0.8 mm in length. The embryo is in the endosperm just below the germ pore, seen as a dark circular spot on the endocarp. The plumule and radicle can be distinguished within the proximal end of the embryo. In cross sections, the plumule shows a central meristematic zone surrounded by the scaly leaf primordia, which in turn are enclosed by the coleoptiles. The radicle is situated opposite to the plumule and within the apical mass of meristematic cells. The proximal part of the embryo is separated by a small constriction from the cotyledon which develops into the haustorium (apple) during germination of coconut seed nuts.

On germination, the embryo simultaneously develops in two directions, from proximal end, the apical part forces its way out through the germ pore and the plumule and radicle then grows outside the endocarp and from distal end of the embryo, the cotyledon expands to form a pear-shaped haustorium inside the central cavity of the fruit. Haustorium is mainly an absorptive and storage organ which supports the growth of the embryo by providing the products of endosperm hydrolysis till the seedling becomes self-sustaining. Compared with various other tissues within a haustorium, the surface tissues are markedly different, having an undulating structure which is closely attached to the degrading endosperm, with starch

grains and oil droplets. It accumulates relatively high amounts of sucrose and starch, with considerably higher activities of phosphoglucomutase and phosphoglucose isomerase, and plays a key role in absorption of oil reserves released from degraded endosperm as well as in the conversion of sugars (Sugimura and Murakami 1990). López-Villalobos et al. (2001) studied the changes in germinating coconut over a four month period and reported continuous and proportionate growth of haustorium, plumule and radicle during coconut seed germination, with haustorium increasing to 45 g nut⁻¹ and weighing four to five folds higher than the other two tissues. The vascular bundles run in parallel to the haustorium surface, extending from shoot apex to the distal tip of the haustorium, and the combined strength of these strands of vascular tissue passing through the soft eye prevents the breakage of the growing seedlings' attachment to the haustorium. Various biochemical changes occur in the developing fruits. For details, please see Chap. 9 on Physiology and Biochemistry.

3.4.7 Propagation

Coconut palms are propagated only by seeds. The mature, husk dried nuts containing the seeds germinate on sowing, and the time taken for germination is influenced by the variety and season (Whitehead 1965b; Nampoothiri et al. 1972; Satyabalan 1993; Niral et al. 2006). Natural regeneration also occurs widely in favourable environments if the fallen nuts are left in the field as such. Although the seed nuts are sown either vertically or horizontally keeping the broader surface of fruit facing up (as in commercial nurseries), the seeds can germinate mostly in all directions. In a natural fall from the palm, mostly the seeds settle on the ground with the broader surface touching the ground. Generally, seed nuts of tall varieties germinate from 60 to 200 days after sowing and those of dwarf varieties germinate from 30 to 95 days after sowing. There are some exceptional varieties too with still earlier germination and also showing viviparous germination.

3.4.7.1 Seed Germination, Growth and Development of Seedlings

During germination, the sprout appears as a spear out of the nut and the lamina unfurl upon growth and development after producing a couple of scaly leaves without lamina. The laminae of the first few leaves are fused. The length of the leaves increases from few centimetres in scale leaves and up to 2 m in sixth leaf stage depending on the cultivar and growing conditions. Generally, the seedlings are taken for planting at six to seven leaf stage with at least one leaf showing splitting to leaflets.

3.5 Cytology

Santos (1929) was the first to study the cytology of *C. nucifera* who reported the chromosome number as $n = 16$. In India, the chromosome number ($n = 16$) was first reported by Janaki Ammal (1945) and Venkatasubban (1945) followed by other workers (Ninan et al. 1960; Abraham et al. 1961). These studies and those of several others (Nambiar and Swaminathan 1960; Swaminathan and Nambiar 1961; Raveendranath and Ninan 1973) have confirmed the somatic chromosome number of $2n = 32$.

3.5.1 Karyomorphology

The gross features of chromosome complements of tall (WCT) and dwarf (CGD, COD) varieties have been studied in India. Raveendranath and Ninan (1973) observed the presence of secondary constrictions on the long arm of chromosome VI in tall and long arm of chromosome III in dwarfs. However, these differences were not consistent, and additional satellites were observed on chromosome II (long arm), chromosome I (short arm), short arm of chromosome XII (Raveendranath and Ninan 1973), long arm of chromosome XII (Thankamma Pillai et al. 1983) and IX (Nambiar and Swaminathan 1960) in tall and in chromosome VI (long arm) in dwarfs (Raveendranath and Ninan 1973). Nambiar and Swaminathan (1960) observed that in tall, majority of the chromosomes had submedian centromeres, with two pairs of chromosomes much longer and three pairs relatively short. On the other hand, Raveendranath and Ninan (1973) observed that tall as well as dwarf had a preponderance of chromosomes with median centromeres, with four submedian chromosomes (II, IV, VII, XIV) in WCT, three (chromosome II, VII, XII) in COD and only one (chromosome II) in CGD. In higher plants, karyotypic evolution has been from complete symmetry to asymmetry (Stebbins 1950). From this angle, WCTs show a more evolved karyotype than COD and CGD. Total chromatin content is found to be greater in CGD than WCT (Raveendranath and Ninan 1973). The total chromatin content is more in wild species than cultivated ones. Therefore, CGD appears to be the most primitive among the three accessions studied. However, evidences from morphology, breeding system and meiotic behaviour support the possible evolution of dwarf from tall.

3.5.2 Meiotic Studies

The different varieties of tall and dwarf (both open pollinated and inbred populations) show significant differences in their meiotic behaviour. The dwarf are reported to show less stable meiosis than tall, and it has been proposed that

ancestral types show more stable meiosis (Lindquist 1960). In general, microsporogenesis is more regular in open pollinated than inbred progenies. Nambiar et al. (1970) studied cytological behaviour in five tall accessions, viz. Laccadive Ordinary (LCT), Philippines Ordinary (PHOT), Andaman Ordinary (ADOT), New Guinea (NGT) and Cochin China (CCNT), and observed that microsporogenesis was relatively regular in both inbred and open-pollinated progenies of LCT, while comparatively higher frequencies of chromosome aberrations and pollen sterility were observed in inbred as well as open-pollinated progenies of CCNT and NGT and inbred progenies of PHOT and ADOT. The lack of inbreeding depression only in LCT could either be due to differences in intensity of inbreeding and selection between these geographically distinct varieties or due to the LCT being comparatively less sensitive to inbreeding.

Nambiar and Swaminathan (1960) observed many meiotic irregularities in Apricot from Strait Settlements (SSAT) and Dwarf Red forms, which are derived from the Dwarfs, while meiosis was regular in LCT. Consequently, higher pollen sterility occurred in these two dwarf derivatives in comparison with LCT. Thankamma Pillai et al. (1983) studied meiosis in nine cultivars and hybrids and indicated that the percentage of abnormalities was highest in CGD and COD, while chromosome abnormalities and sterility were very low in $D \times T$ and $T \times D$ hybrids. They concluded that the higher degree of inbreeding in dwarfs might be the reason for higher chromosome aberrations and sterility in them. Cytological studies on *Spicata* palms (Ninan et al. 1960; Ninan and Satyabalan 1963) indicated irregular meiosis with inversions, translocations and many other abnormalities. *Spicata* palms, being predominant outbreeders, are believed to have arisen from tall through mutation. Further, cytological studies have been undertaken on abnormal palms, bulbiferous palms and root (wilt) disease-affected palms.

Nambiar and Prasannakumari (1964) studied microsporogenesis in root (wilt) disease-affected palms and reported low frequency of cytological aberrations, high pollen fertility and seed set. Thankamma Pillai and Vijayakumar (1972) studied the course of microsporogenesis in a palm bearing defective nuts (self-pollinated progeny of NGT) and observed that the aberrant meiosis and sterility in this palm was attributed to inbreeding. Raveendranath et al. (1975) found no appreciable karyological differences between the normal (Talls) and abnormal palms producing bulbils (in the place of normal inflorescences) and opined that cryptic structural changes or genetic mutations might be responsible for this abnormality.

3.5.3 Cytology of Endosperm and Embryo

Abraham and Thomas (1962) reported free nuclear divisions in coconut water (liquid endosperm). Abraham and Mathew (1963) and Abraham et al. (1965), based on their studies on 6-month-old fruits, observed that size of nuclei varied considerably in the developing endosperm. They found that the tissues adjacent to endothelium were normally triploid ($3x = 48$), less frequently hexaploid ($6x = 96$) and still less

frequently dodecaploid ($12x = 192$) and proposed that higher ploidy levels arise by C-mitosis. They also recorded an inverse relationship between ploidy and percentage oil content, with the inner part of the endosperm having the highest ploidy level and lowest oil content (Abraham 1963; Abraham et al. 1965). In tall variety, the percentage of oil content in the outer, middle and inner layers of endosperm was 75.7, 54.1 and 41.4, respectively. Abraham et al. (1965) recorded higher ploidy levels (48x and above) in buttery endosperm (Philippine makapuno coconuts), which they felt arose through amitosis and nuclear fusion. Unlike the endosperm, the young coconut embryos are diploids and divide by normal mitosis. Raveendranath and Ninan (1973) studied karyomorphological features of somatic chromosomes from 6-month-old embryos and observed an essential uniformity in relative chromosome length from root tip (Nambiar and Swaminathan 1960) and embryo cells of WCT palms. Ninan and Raveendranath (1965) reported occurrence of a haploid embryo in a WCT palm.

3.6 Genetic Resources

Before, we deal with the genetic resources in coconut, it is important to understand some of the terms commonly used to describe coconut diversity. There are diverse perspectives in the understanding of taxonomical terminology used in coconut. Most non-scientific observers and stakeholders do not differentiate between the terms in vogue, which confuses the readers. Even in many scientific papers, the terms cultivar, variety, ecotypes, variants, types and forms are loosely used. The traditional taxonomists consider variety as the last entity in classification, which leads to the indiscriminate coining and use of different terms with no uniformity and specific definition.

After many attempts in earlier years, the coconut breeders seem to have come to the conclusion that it is almost impossible to classify coconuts perfectly, in view of the range of variability for most of the characters. While largely agreeing to this, there is a necessity to remove the chaos existing in the nomenclature among the coconut workers based on some consensus. Taking in the wisdom of the present and earlier coconut workers, a coconut nomenclature is suggested below with the hope that it will guide future workers.

3.6.1 Variety

A variety can be defined as a group of palms having similar traits that can be reproduced from generation to generation. From the taxonomical point of view, the term variety is ranked just below the level of species, but above subvariety and form and hence in coconut, *typica* and *nana* can be considered as botanical varieties. Variety *typica* would represent varieties with tall plant habit with all the associated features

of typical talls such as in Indian West Coast Tall, West African Tall, Malayan Tall, Rennell Tall, etc. Variety *nana* would represent varieties with dwarf plant habit and all the associated features of typical dwarfs such as in the Malayan Yellow Dwarf, Chowghat Green Dwarf, Malayan Orange Dwarf, Rangiroa Red Dwarf, etc.

However, this taxonomical grouping does not include *intermediate* varieties having certain features of *nana* and some features of *typica*. It will be desirable to have at least four varietal groups in coconut, as has been suggested by Bourdeix and co-workers (Bourdeix et al. 2017). Therefore, in addition to dwarfs *nana*, which are predominantly self-pollinating, there could be another varietal group of dwarfs, viz. *Javanica*, to accommodate the compact dwarfs, which are predominantly cross-pollinating as in the case of *typica* but with dwarf plant habit as in the case of *nana*. The Niu Leka Dwarf, with dwarf plant habit but has nonoverlapping male and female phases, facilitating cross-pollination, will fall in this category. The *Aurantica* could be the fourth group, encompassing coconut palms with semi-tall plant habit and with variable reproduction modes (cross/self-pollination) as is seen in the tall \times dwarf and dwarf \times tall hybrids. The King Coconut and Navasi Thembili of Sri Lanka are classical examples of the fourth varietal class.

3.6.2 *Cultivar*

It is an assemblage of palms which is distinct, comparatively uniform and stable, having been purposely selected for a particular character or a combination of characters, cultivated for centuries, and is capable of reproducing its characters from one generation to the next in nature. The name “cultivar” comes from a combination of two words: cultivated and variety. Cultivars, therefore, represent cultivated varieties that have evolved due to purposive and continued selection. Examples include the Malayan Yellow Dwarf, Malayan Orange Dwarf, Chowghat Green Dwarf, San Ramon Tall, Laguna Tall, etc. Some coconut researchers suggest that all conserved coconut accessions can be referred to as cultivars, arguing that almost all the coconut palms are selected and planted by mankind, the only exceptions being coconut palms growing naturally in remote/uninhabited islands.

3.6.3 *Ecotype*

Ecotypes are groups of palms or populations within the same variety that are adapted to certain climatic and edaphic conditions and survive as a distinct group due to environmental selection or geographic isolation. Ecotypes are generally named or known by the location where they are grown. However, it is very difficult to identify distinct ecotypes in coconut, except in the instances of geographical isolation, as in isolated atolls. Coconuts in the Cocos (Keeling) Islands of the Indian Ocean and along the Northern Coast of Australia are some such examples. Vanuata Tall, with

resistance to foliar decay virus, is an example having ecotype status (Bourdeix et al. 2005a). Ecotypes, having developed adaptive features for particular environmental conditions over a period of time, can serve as a rich source of valuable genes for coconut breeding. In India, the Laccadive and Andaman ecotypes evolved because of their isolation have provided better sources for coconut breeding such as Lakshadweep Ordinary Tall, Lakshadweep Micro Tall, Andaman Ordinary Tall and Andaman Giant Tall which resulted in release of improved varieties. Despite the involvement of human selection process, Kuttiyadi coconut can also be considered as an ecotype, as it got adapted and evolved in the hilly tracts of Malabar region of Kerala, India.

3.6.4 Form or Morphotype

These can be used to refer to smaller groups of palms within the cultivar/ecotype, which are different from each other for a few distinct characters. The variation could be for colour/size of fruits, taste of tender nut water, etc., such as the Thailand Aromatic Dwarf. Purposive selection of these forms/morphotypes, over a period of time, could result in their progression into the domain of cultivars.

3.6.5 Variant

The term variant can be applied to refer to a group of plants with some special morphological features found in different ecotypes or cultivars. This would include variants arising due to single mutations in a cultivar and are mostly considered abnormal. A classical example of variant is the *Spicata*, wherein the inflorescence is unbranched, with numerous female flowers borne directly on the central axis and with very few male flowers. This variant has been encountered in many cultivars and from countries as distant as the Philippines, India and Samoa and referred to as Spicata Tall, Spicata Red Dwarf, Standard Kudat, etc. Another typical example is the soft endosperm coconut, found in different regions and referred to as makapuno/kopyor/coco gras/dikiri/thayiru thengai. The male coconut tree would also fit into this category as would many other freaks observed in natural populations.

3.6.6 Population

Population refers to any subgroup located in a restricted location, such as an island, atoll or continuous strip of coastline. It could be a mixture of diverse varieties/cultivars/forms. Hence, population could also refer to the coconut palms in a location,

whether highly heterozygous, as are most tall populations or homozygous, as in the self-pollinating dwarfs. For instance, in India, coconuts in the west coast will be one population, and the ones in the east coast will be another population. The term population is also commonly used to refer to a group of individuals obtained from a cultivar. For example, WAT 06, West African Tall *Ouidah* from Benin, is a population of the West African Tall cultivar, and MYD 01 refers to a population of Malayan Yellow Dwarf collected from Kulasekharam in Tamil Nadu, India.

3.6.7 Subpopulation

A subset of a population that shares one or more characters is referred to as a subpopulation. In coconut, subpopulations within a coconut population can be delimited based on morphological traits as well as genetic markers. For example, a group of palms producing high number of medium-sized nuts within a population of Indian West Coast Tall would represent a subpopulation.

3.6.8 Accession

Accession refers to the basic working unit of conservation in the gene banks and is not a taxonomic entity. The conserved genetic resources could represent a cultivar or form/morphotype, etc. Accessions are generally assigned numbers for their precise identity and are unique to a particular gene bank and tend to continuously increase numerically, as new collections are added to the gene bank. For example, in the case of coconut, “IND006” refers to the accession Andaman Giant Tall (AGT) planted in 1940 at the ICAR-Central Plantation Crop Research Institute in India and “SMD NJM R2” designates Malayan Yellow Dwarf planted in 1981 at the Marc Delorme Research Station in Côte d’Ivoire. The [list of coconut accessions](#) conserved in the gene banks of COGENT country members has been documented (Bourdeix et al. 2010) and is available at COGENT website.

In order to create public awareness about coconut genetic resources and to facilitate dissemination of information among the various stakeholders, COGENT/Bioversity International initiated a project to develop an international coconut genetic resources database (CGRD), in the year 1994. The CGRD (Hamelin et al. 2005) was released into the public domain in 1999 and is hosted on the COGENT website. In the CGRD, data on coconut accessions are divided into two main parts – passport data and priority characterisation and evaluation data – taking into consideration the [standardised descriptors](#) for coconut palms and the methods detailed in the [STANTECH manual](#). Presently 725 accessions are listed in the CGRD.

With advances in biotechnology, the term accession is also used in the context of conserving DNA/genomic resources. Considering that coconut is a cross-pollinated

crop with inherent heterozygosity, the DNA of individual coconut palms is conserved separately, and hence the term 'accession' in a DNA gene bank refers to the DNA of a single palm.

3.6.9 Genotype

A group of palms can be referred to as a genotype if their specific parents are clearly known, for example, a hybrid between two known palms or offspring of a single known palm.

3.6.10 Plant Variety

This is a non-taxonomic term, applied to an intraspecific rank, usually a cultivar or hybrid. In legal parlance, the term plant variety is used to refer to varieties of plants for which patent protection has been applied for. Plant breeders' rights (PBR), also known as plant variety rights (PVR), are rights granted to the breeder for a new variety of plant that provides for exclusive control over propagating the material of a new variety for a specified number of years. In India, guidelines for the conduct of test for distinctiveness, uniformity and stability (DUS) on coconut have been developed by the Protection of Plant Varieties and Farmers Rights' Authority (PPVFRA 2011), in collaboration with ICAR-Central Plantation Crops Research Institute, and so far six varieties, viz. Kalparaksha, Kalpa Sankara, Kalpa Mitra, Kalpa Dhenu, Kalpa Pratibha and Kalpasree, have been registered in the country.

3.6.11 Naming Coconut Cultivars/Ecotypes

The national researchers working on coconut genetic resources are responsible for naming coconut accessions/cultivars/ecotypes of the respective countries. However, considering the need to guide the researchers, avoid confusion and streamline the naming process, COGENT has developed guidelines towards having a standardised procedure for naming coconut accessions (Baudouin et al. 2010).

The international naming of a coconut cultivar or ecotype comprises of two parts: a cultivar name and an abbreviation. An important consideration in naming is to avoid duplicating any previously recorded name (including synonyms). The cultivar name is to be in two parts, written in English (except possibly for the first part) and not exceeding 30 characters. The first part of the name may include either a vernacular name (Agta Tall – Agta being vernacular for blackish necrotic pericarp), place/region/country of origin (West African Tall), a prominent biological trait of the cultivar (Andaman Giant Tall), an ethnological trait linked to the history of the

cultivar (Raja Tall), fruit colour (only if a cultivar is homogeneous for colour, such as Chowghat Green Dwarf) or a combination of those (Raja Brown Dwarf – a combination of an ethnological trait and a colour).

An international abbreviation of a cultivar should consist of three to four letters, followed by two digit numerical, avoiding duplication of any previously recorded abbreviation. The first part of the abbreviation is linked to the cultivar name, such as EAT for East African Tall, WCT for the Indian West Coast Tall. In giving abbreviation for dwarf cultivars, showing homogeneity in fruit colour, it is suggested to include a letter corresponding to the colour of the fruit (G, Y, R, O or B), with a provision to optionally omit the letter G in the case of green fruits: MYD for Malayan Yellow Dwarf, CGD for Chowghat Green Dwarf and CATD for Catigan Green Dwarf. The abbreviation should indicate the plant habit, using the letters T or D, as applicable: PRD for Pemba Red Dwarf, WAT for West African Tall and RTB for King Coconut (synonym Rath Thembili, semi-tall).

It is suggested that specific populations or variants within a cultivar be referred to by using a population name after the cultivar name and by a number after the abbreviation, such as West African Tall *Ouidah* (WAT06), a population of the West African Tall cultivar from Benin; Malayan Red Dwarf Fiji (MRD04), a population of the Malayan Red Dwarf cultivar from Taveuni; Malayan Red Dwarf Kulasekharam (MRD01), a population of the Malayan Red Dwarf cultivar from Tamil Nadu, India; and so on.

3.7 Germplasm Collection and Conservation

In due recognition of the importance of coconut genetic resources to enhance coconut productivity and to mitigate genetic erosion in native habitats, collection and conservation of coconut germplasm have received considerable attention in the major coconut-growing countries, and ex situ field gene banks have been established especially in the Philippines, India, Indonesia and Sri Lanka in the early part of the twentieth century. Subsequently, considering the dwindling productivity of coconut in traditional coconut communities and the fact that about 96% of the coconut farmers worldwide are smallholders, the International Coconut Genetic Resources Network (COGENT) was formed in 1991 to facilitate research on coconut. COGENT started with 15 coconut-growing countries as members and currently has 39 member countries that are divided into five subnetworks: Southeast and East Asia (China, Indonesia, Malaysia, Myanmar, the Philippines, Thailand and Vietnam), South Asia and Middle East (Bangladesh, India, Pakistan, Sultanate of Oman and Sri Lanka), South Pacific (Cook Islands, Fiji, Kiribati, Papua New Guinea, Samoa, Solomon Islands, Tonga and Vanuatu), Africa and the Indian Ocean (Benin, Côte d'Ivoire, Ghana, Kenya, Madagascar, Mozambique, Nigeria, Seychelles and Tanzania) and Latin America and the Caribbean (Brazil, Colombia, Costa Rica, Cuba, Guyana, Haiti, Honduras, Jamaica, Mexico and Trinidad and Tobago). To provide double security for conserved germplasm in national gene

banks and to promote effective access and safe germplasm movement, five multisite International Coconut Genebanks (ICG) have been established, one in each region: Southeast and East Asia (Indonesia), South Asia and Middle East (India), South Pacific (Papua New Guinea), Africa and the Indian Ocean (Côte d'Ivoire) and Latin America and the Caribbean (Brazil). COGENT in partnership with research institutes has developed numerous research methodologies such as varietal identification techniques using standardised morphological descriptors (IPGRI 1995), safe movement of coconut germplasm (Frison et al. 1993), creation and development of the International Coconut Genetic Resources Database (CGRD) and other dedicated software (Hamelin et al. 2005), strategies for germplasm survey and conservation (Bourdeix et al. 2005b) and the publication of catalogues of coconut varieties (Bourdeix and Batugal 2005; Bourdeix et al. 2010). Presently 24 gene banks from 23 COGENT member countries are conserving 725 unique populations with 1837 living accessions.

In India, germplasm collection began in 1924 with the introduction of cultivars from Fiji, Indonesia, Malaysia, the Philippines, Sri Lanka and Vietnam. The germplasm collection was intensified in 1952, and in 1958 the first indigenous germplasm survey and collection were started. The Central Plantation Crops Research Institute Kasaragod is actively involved in the collection and conservation of coconut biodiversity in the field gene bank for utilisation in the coconut improvement programme. The institute has undertaken exotic collections of coconut germplasm from Pacific and Indian Ocean Islands and from the South Asian countries of Sri Lanka and Bangladesh with funding from ADB/IPGRI. Further extensive prospection and collection of indigenous coconut germplasm from different coconut-growing regions of the country have been undertaken, and distinct accessions have been conserved in the National Active Germplasm Site at the institute.

The Indian coconut population harbours a wide range of diversity. The islands of Lakshadweep and Andaman and Nicobar with their natural coconut populations, some of which have established with no human interference, are reservoirs of vast genetic diversity. Majority of the native populations in the traditional coconut-growing zones belong to the wild type with greater proportion of husk, while some of the evolved types have lesser husk and more endosperm. Further, introgression between the niu kafa and niu vai types in the nature has resulted in the emergence of intermediate types (Thomas and Niral 2010).

Presently, ICAR-CPCRI has the largest collection of coconut germplasm with 455 accessions from 28 countries, representing coconut germplasm of south and Southeast Asia, Caribbean Islands, Indian Ocean Islands, Pacific Ocean Islands and African countries and India. The indigenous coconut germplasm comprises of collections from 12 states as well as from Lakshadweep and Andaman and Nicobar Islands. Germplasm characterisation is being undertaken using the IBPGR descriptor (Anon 1978). The institute has brought out descriptors for 74 coconut accessions (Ratnambal et al. 1995, 1999), and a coconut germplasm database has been developed (Rajagopal et al. 2005). ICAR-CPCRI has also contributed to the development of the world catalogue of conserved coconut germplasm and catalogue of farmers' varieties brought out by COGENT/Bioversity International (Bourdeix et al. 2010).

3.7.1 *Alternate Conservation Strategies*

Plant genetic resources are among the most essential of the world's natural resources, and during the last three to four decades, major advances have been made in conserving them. During the past two decades, there have been increasing efforts to develop improved in situ conservation methods which would permit dynamic conservation of plant populations (Sthapit and Jarvis 1999).

Bourdeix proposed a new experimental approach to coconut genetic resources conservation termed 'Polymotu' concept, as an alternate conservation strategy, combining the ancestral practice of the Polynesians, wherein they planted distinct coconut varieties separately in small islands or insulated valleys (Bourdeix et al. 2011). The Polymotu concept cannot be a substitute to conventional field gene banks but is intended to complement efficiently these gene banks. It is envisaged herein that several coconut accessions could be planted, each in a distinct isolated site, and the geographical remoteness will ensure the reproductive insulation required for true to type breeding of each of the accessions through natural pollination. This in addition to conservation will also facilitate germplasm access to people, considering that conventional field gene banks are mostly used by researchers and institutions wherein the main limiting factor is the huge cost incurred on maintenance of the gene bank and reproduction of the accessions.

In coconut, other complementary conservation strategies include conservation of embryos and pollen, which being amenable for long-term conservation can provide a viable backup to field gene banks. The possibility of long-term conservation of zygotic embryos was first suggested by Bajaj (1984), when embryos were observed to resume growth after freezing at -196°C . Assy-Bah and Engelmann (1992) reported successful cryopreservation of immature embryos of coconut 7–8 months after pollination as well as mature zygotic embryos. In India, cryopreservation of mature embryos after desiccation pretreatments has been reported by Karun et al. (2005). Sisunandar et al. (2010a) reported an improved cryopreservation protocol for a wide range of coconut cultivars from Indonesia. In India, cryopreservation of mature coconut embryos through vitrification has been attempted by Sajini et al. (2011). Coconut plumule (apical dome with three to four leaf primordia) extracted from mature embryos (11–12 months after pollination) was also utilised for cryopreservation, by encapsulation techniques (Nan et al. 2008).

Pollen cryopreservation has been successfully used in a variety of plant species (Towill and Walters 2000). Coconut pollen has a life span of few days (Patel 1938) and can be stored for a few days at room temperature in desiccators. Freeze-drying of coconut pollen for short-term storage has also been reported (Whitehead 1963; Rognon and Nucé de Lamothe 1978). Karun et al. (2014) reported long-term cryopreservation of coconut pollen in liquid nitrogen. For details, please refer Chap. 6 on Coconut Biotechnology.

3.8 Novel Traits and Abnormalities

In addition to the varieties and forms of coconut discussed earlier, a number of variants have been reported by different workers from different coconut-growing regions. These include abnormalities, which are freaks of nature and not distinct varieties, from the botanical point of view. Davis has observed and reported most of the abnormalities in coconut palms, while Menon and Pandalai (1960) have compiled these in their coconut monograph.

3.8.1 *Novelties Associated with Stem*

3.8.1.1 Polyembryony

This is a phenomenon wherein a single nut produces more than one seedling. This has been reported sporadically in different places, and up to five seedlings have been reported to emerge from a single nut. Furtado (1927) was the first to conclude that this phenomenon is due to the development of many embryos from one ovule and not due to polycarpy as was previously believed. Davis (1979) reviewed polyembryony in coconut.

3.8.1.2 Branching

This is a rare phenomenon and has been reported by a number of workers (Ridley 1907; Burkill 1923–25; Furtado 1923–25; Quisumbing 1926–27; Jacob 1935; Davis 1947, 1950, 1956a, Indires 1992; Mao and Lai 1993). Branching is found to take place at all stages of growth and from various regions of the stem. Branching is a commercially important phenomenon as it can help obtain increased yields with less planting space.

Branching in coconut has been attributed to a number of causes. In a young palm, when the growing point is injured, adventitious buds develop and form new growing points from the meristematically active ground tissue of the bole. Branching is also induced when the terminal bud is injured by lightning, fire, storm or as a result of some pest attack. Davis (1950) and Jacob (1935) have reported instances of branching due to dichotomy and stem fascinations, respectively. Davis (1968) and Balaga (1975) were able to induce branching in coconut seedlings but with a very limited success. They observed formation of neomeristems of adventitious origin on making a longitudinal incision in the shoot of young seedlings. Fisher and Tsai (1979) observed formation of a twin shoot, emerging from a single growing tip, while growing isolated coconut embryos *in vitro*. They concluded that this was a case of branching, possibly arising due to an injury to the embryo at the time of dissection and culture.

3.8.1.3 Suckering

This is another rare phenomenon, synonymous to branching, but restricted to the underground portion of the stem (bole). Shortt (1885) reported six shoots in a seedling. In India, Patel (1938) reported as many as 40 suckers arising from the base of a palm. Aiyadurai et al. (1959) reported 18 suckers. Davis (1956b) and Chatterjee (1959) have reported a number of instances of suckering in coconut palms. In India, suckering has been observed in three seedlings belonging to three different varieties as well as in a seedling in a farmer's garden. Suckering is an economically interesting phenomenon as it offers the possibility for vegetative propagation of the palms through stimulation of the suppressed basal buds. However, what exactly stimulates the development of suckers is still unknown. Davis (1960) and Michael and Varghese (1963) were able to induce two to three suckers by causing mechanical injury to the growing point. However, as the number of suckers produced is very much less, this cannot be used for commercial propagation of palms.

3.8.2 *Novelties Associated with Leaf*

3.8.2.1 Plicate Palms

Abnormality in the leaves is rare. Patel (1938) reported fused leaflets in adult coconut palms, wherein the leaflets are fused and do not separate, as in ordinary palms, and attributed it to genetic and environmental factors. Zuniga et al. (1970) grouped these palms under the name 'plicate'. The palms with fused leaflets are referred to as plicate in the Philippines and India and as niu yabia in the Fiji Islands (Satyabalan 1997). Subsequent research workers (Sugimura et al. 1994a; Arunachalam et al. 2001) have observed that plicate palms have reduced leaf length and are poor bearers with a long juvenile period. Moa and Lai (1993) reported sterility in plicate palms. Boron deficiency can also cause the leaflets to remain fused, but in contrast to palms suffering from boron deficiency, the plicate palms do not respond to borax application.

Davis (1956c) described some other abnormalities like forked leaves, twin leaves, fused leaves, multi-leaf, etc. Lilly (1962) observed formation of secondary midribs in some of the leaflets in a leaf of a 10-year-old palm. The secondary midribs were smaller in size than the normal midribs. However, she concluded that this could also be considered as a case of fused leaflets.

3.8.2.2 Chimeras

In palms showing chimera, green and yellow variegations are observed in fruits/leaves. This is due to somatic or bud mutation and has been reported from India and Sri Lanka (Satyabalan 1997). Variations in colour of the fruits can occur within a

bunch or in different bunches of the same palm. A young coconut seedling showing chimera was observed in India wherein part of a leaf was observed to be albino (white/yellowish white) while the rest were dark green. Subsequently produced new leaves also showed this chimeric pattern.

3.8.2.3 Albinos

In coconut nurseries, a few albino seedlings are observed at very low frequencies (less than 1%). These seedlings do not respond to manurial treatment and generally die after producing four to six leaves. Patel (1938) opined that albinism is, due to genetic factors, while Furtado (1926–29) believed that albinism in coconut seedlings was the result of chlorosis due to the absence of ferruginous products in the endosperm. Pandalai and Pillai (1959) based on their experiments with albino seedlings concluded that inadequate availability of iron (due to the inability of the plant to utilise the iron in the leaves) results in the albinic condition. The mobilisation of iron appears to be controlled by recessive gene/genes, since albinism is an inherited character.

3.8.3 *Novelties Associated with Inflorescence*

3.8.3.1 Midget Palm

The terminal inflorescence or hapaxanthic spadix has been reported from India and Indonesia. Here, the inflorescence emerges from the terminal portion and then the palm dies. Davis and Menon (1953) (quoted by Menon and Pandalai 1960) and Davis (1955) first reported the curious phenomenon of coconut seedlings producing inflorescences within 12 months of sowing and referred to them as midget palms.

3.8.3.2 Bulbils

Bulbiferous coconut palms, producing numerous vegetative shoots from spadices, were reported from India by Davis (1948a, b). Venkataraman (1928) recorded a rare instance wherein the buttons/young nuts in a spadix, instead of developing into normal nuts, grew into bulbils somewhat resembling miniature seedlings. This transformation was visible at a very early stage in the development of the inflorescence, even before the spathe had fully opened, as even the unfertilised ovules in the tender inflorescences had started to produce growth primordia. Venkataraman (1928) also referred to this as a case of parthenogenesis. Jerard et al. (2014a) reported a naturally occurring, rare bulbiferous coconut palm among West Coast Tall population, which produced only bulbil shoots in leaf axils in place of normal inflorescence. The identified palm happened to be twins in which both of them

produced only bulbil shoots instead of floral parts. Morphological and molecular studies on these palms revealed that the main palm and their bulbil progenies are genetically uniform. The genetic uniformity of the twin mother palms and their bulbil progenies was confirmed through microsatellite analysis using ten polymorphic SSR primer pairs specific to coconut and has been well demonstrated to differentiate coconut cultivars. The primary and secondary bulbil shoots were found to be capable of growing into independent plants making it possible to use them as propagules to develop a homogeneous clonal population hitherto unavailable in coconut. The bulbils showed axillary growth in 6th–12th leaf axil, which further develop as secondary bulbils indicating the complete vegetative state of the palm. Comparison of shoot apices of a normal seedling with bulbil shoot revealed variation in cell growth pattern. Conservation of bulbiferous palms as a unique genetic resource needs to be taken up to utilise these rare sources for future breeding programmes, provided their seed fertility can be restored.

3.8.3.3 Double Spadix in Leaf Axils

Davis (1957) first reported the occurrence of a double inflorescence. Each of the two spadices was independent with a fully developed spathe and normal spikelets bearing male and female flowers. However, the outer spathe was common to both the spadices. A palm with double spadices in each of the leaf axils was reported in the Indian WCT population indicating the possibility of natural occurrences of such palms.

3.8.3.4 Multi-Spatheate Inflorescence

In a normal inflorescence, only four bracts are visible. The third bract enlarges to form a spathe that encloses the spadix. At the base of spathe and extending a third of its length is the second bract that has transformed to a fibrous sheath to protect the spathe during the early stages of development. At the base of the outer spathe is the first/outer bract, which is about 25 mm long and scaly. The fourth bract is a scaly bract at the base of the spadix. Davis and Menon (1952-quoted by Menon and Pandalai 1960) reported a bispatheate palm wherein all the inflorescences in the palm had two fully developed spathes. In these palms, the fifth/innermost bract develops to the size of the original spathe, and both these spathes completely cover the spadix till its emergence. Subsequently many workers from various coconut-growing countries have reported the occurrence of bispatheate palms. Thomas and Mathew (1960) reported a trispatheate coconut palm. Michael (1963), however, observed a multispatheate coconut palm wherein the inflorescence had five fully developed spathes, the outer spathe enclosing four closely set inner spathes. Here again, the first and second spathes originated from the third and fourth bracts of the inflorescence. However, the origin of the third, fourth and fifth spathes was unclear and was hypothesised to have originated from the rudimentary bracts generally

found at the base of the spadix. The higher number of the spathes offers greater mechanical protection for the spadix and also more protection against insect attacks. Moa and Lai (1993) have reported multispatheate palms at Hainan Island, China.

3.8.3.5 Hermaphrodite Flowers

Normally, the spikelet in a coconut inflorescence has a few female flowers at the base with numerous male flowers towards the top. In between the female and male flowers, occasionally some hermaphrodite flowers are observed (Gopal Rao 1948). Hermaphrodite flowers are bigger than the male flowers, but smaller than the females. Hermaphrodite flower resembles the female flower but shows development of the staminodal ring into stamens. Davis et al. (1954) reported quantitative data on four palms of the tall variety from Kerala, which produce appreciable numbers of hermaphrodite flowers in all the spadices examined. Smit (1970) reported high percentage of hermaphrodite flowers ranging from 10% to 55% between palms of Nias Yellow Dwarf at the Manado seed garden (Davis et al. 1981). Higher occurrence of hermaphrodite flowers in S_1 population of Chowghat Green Dwarf has been reported from India (CPCRI 2014).

3.8.3.6 Male Palms

The male coconut palm, also referred to as *Androgena*, produces only male flowers and was first reported from India (John and Narayana 1942). Subsequently, male coconut palms have been reported from China (Mao and Lai 1993), Jamaica and Markham Valley, New Guinea (Whitehead 1966). Ninan et al. (1960) observed meiotic abnormalities such as aneuploidy in a few cells in *Androgena* palms, but no in depth cytological investigations have been undertaken. Male palms are characterised by robust inflorescences with numerous spikelets bearing large number of male flowers. The inflorescence of the male coconut palm is much larger than those of the ordinary palms and also has a much greater number of male flowers per inflorescence than in the ordinary palm. Davis et al. (1955) observed branching of spikes in spadices of male trees and secondary spadices, as well as numerous spathes or highly developed bracts.

3.8.3.7 Spicata Inflorescence

Palms with unbranched inflorescences, referred to as *spicata* (Beccari 1916; Boldingh 1920; Jacob 1941; Davis 1980), though very rare, are reported in about all coconut-growing regions. The inflorescences of the *Spicata* palm have a central spike which is unbranched or rarely with one or two branches, unlike the normal inflorescences that are branched with 30–35 spikelets. The inflorescences of the *Spicata* palms bear a large number of female flowers (125–130) with very few male

flowers (50), in stark contrast to the normal inflorescences, with innumerable male flowers and few female flowers at the base of each spikelet (0–4). However, the fruit setting is low in *Spicata*, with Jacob (1941) observing 10% setting, while Sugimura et al. (1993) reported 4% setting.

The *Spicata* palms cross freely with other coconut varieties. On selfing, John and Narayana (1949) found that only 50% of the progenies breed true to the mother. Whitehead (1965a) on crossing a tall parent with pollen of the dwarf *spicata* observed the resultant hybrids to be intermediate in form and precocity. Whitehead (1966) reported that these hybrids had lesser inflorescence branches and therefore, advocated that the *spicata* character is incompletely dominant or pleiotropic. Ninan and Nambiar (1974) observed that the hybrids from crosses of tall and *spicata* show a low proportion of male flowers per inflorescence, a character associated with *spicata*.

Spicatas are also locally referred to as *KelapaBrol/KelapaBrodjol* in Indonesia, *Spicata-Maure* in the Philippines, *Niu Tuave* in Samoa, *Niu Yalewa* in Fiji Islands, *Ngohard Tapala* and *Niu Toga* in Solomon Islands, *Loholohotahia* in Tonga Islands and *Ma Praew* in Thailand. Whitehead (1966) noted *spicata* palms in many islands of Pacific, with the first report of *spicata* trait in dwarf palms (small red fruited dwarf) in New Guinea. Whitehead also reported the absence of such palms in Jamaica. In India, wide variation has been reported among selfed *spicata* tall progenies (CPCRI 2014), and a yellow *spicata* dwarf population has been developed.

Ninan and Satyabalan (1963) observed meiotic abnormalities and a high degree of pollen sterility in *spicata* palms. Subsequently, Ninan and Raveendranath (1972) undertook further cytological studies in these palms and observed that the 15th pair of chromosomes is heteromorphic (one member has an additional terminal knob). Barring this, the chromosomes of this variety are similar to those of the typical tall variety. This heterozygous condition accounts for segregation following open-pollination of *spicata* into about 50% tall palms having the normal branched inflorescence and 50% *spicata* palms.

Sankaran et al. (2015) identified a rare form of multiple *spicata* from South Andaman, India. Unlike the normal *spicata*, the inflorescence of this peculiar palm contains, in addition to the central spike, 10–15 spikelets of 30–32 cm length, with 23–26 female flowers in each spikelet/rachillae. On an average, each inflorescence produces 330–345 female flowers, but only one or two fruits are produced per bunch, due to high percentage of button shedding.

3.8.3.8 Partial Suppression of Spikelets

This was reported by Davis (1957) wherein about half the spikes towards the basal end of the inflorescence are reduced and in extreme cases represented by one or two flowers only. However, the spikes at the distal half develop normally and bear male flowers. The main axis is extended and bears numerous female and male flowers.

3.8.3.9 Secondary Branching of Spikes

This is generally reported in the male inflorescences of the male coconut tree, wherein the inflorescences bear a larger number of spikelets most of which are branched (John and Narayana 1942). In addition, numerous spathes or highly developed bracts are also seen in such inflorescences. Sugimura et al. (1994b) observed secondary branching of spikes in two of the five inbred lines of Markham Valley Tall but with a normal pre-bearing period.

3.8.3.10 Varied Number of Pistillodes, Astamens, and Perianth

The male flowers normally have three valvate petals and three smaller triangular and valvate sepals, while the female flowers have three huge sepals and three smaller and thinner petals and a bract and a bracteole. Davis observed certain flowers with a larger number of perianths, with one flower having 13 perianths. In one particular female flower, Davis and Menon (as quoted by Menon and Pandalai 1960) observed seven perianth parts and concluded that the seventh perianth was a developed pistillode. They also observed a male flower with six sepals and six large petals with a single ring of 12 stamens with well-developed anthers and six pistillodes. Certain abnormal male flowers having 7/8/10 stamens and 4/5 pistillodes have also been recorded (Menon and Pandalai 1960).

3.8.4 *Novelties Associated with Fruits*

3.8.4.1 Polycarpy

In a normal coconut fruit, with tricarpic ovary, each one has an ovule, but only one embryo develops and produces a shoot. In rare cases, polycarpy has been observed. Jacob (1940) described a two-seeded coconut, wherein the two seeds were separated by a leathery septum while the third ovule was aborted. Davis (1948c) and Daniel Sundararaj (1952) observed a three-seeded coconut with three fertile eyes giving rise to three shoots, one each from each eye. Forbes (1879) reported a nut with 14 carpels, embryos in all of which germinated to produce a palm with 14 stems united at the base.

3.8.4.2 Varied Number of Carpels

A normal female flower has three syncarpic carpels with an embryonic ovule. In rare instances, mono-, bio- and tetracarpic nuts have been reported with the nuts being one-seeded (Davis 1948c). Davis and Menon (1953) (quoted by Menon and

Pandalai (1960) observed that some flowers in the midget palm were bicarpellary. Davis has also observed young coconut fruits having four to ten carpels (Menon and Pandalai 1960).

3.8.4.3 Horned Coconut

A number of workers reported the occurrence of coconut fruits bearing flat horns ranging from one to six. Davis (1965) regarded the production of horns in palm fruits as atavistic. The development of horns in coconut fruits has been attributed to various reasons, like development of the staminodes (Furtado 1926), duplication of the segments of the gynoecium (Petch 1924), apocarpic nature of the ovary (Costerus and Smith 1923; Gadd 1924; Davis and Menon 1953 – quoted by Menon and Pandalai 1960) and enlargement of some perianths (Masters 1869); Nair and Sadanandan (1976) studied anatomically the development of hornlike structures in some coconut fruits from initiation to maturity. The accession, viz. ‘Andaman Horned Cocos’, a coconut germplasm collected from South Andaman, India, and conserved at ICAR-CPCRI, has been registered for this distinct trait of horny nuts (Jerard et al. 2014b).

3.8.4.4 Vivipary

Thomas (1960) described a case of vivipary in coconut and reported viviparous seedlings to be healthier and more vigorous than the normal seedlings. Das and Thakur (1996) in their article on the production and prospects of coconut in Assam have reported the occurrence of vivipary in certain pockets within the state. At ICAR-CPCRI, vivipary has been reported in Malayan and Andaman dwarfs, with fruits germinating on the crown (CPCRI 2013; Shareefa et al. 2014). Viviparous coconuts have been reported from Indonesia also (Satyabalan 1997). Vivipary reported in Andaman Green Dwarf cultivar (Sankaran et al. 2012) was interpreted as an adaptive reproductive strategy that enables seedlings to establish more rapidly and subsequent dispersal by water or other means.

3.8.4.5 Sweet Husk

Menon and Pandalai (1960) have reported certain palms wherein the young buttons have higher sugar content and less tannin content in their pericarp. In normal cases, due to the higher percentage of tannin, the sweetness in the pericarp of young buttons is masked resulting in an astringent taste. In these rare instances, the husk is sweet with less fibre and can therefore be eaten. The nuts of these palms yield very fine white-coloured fibre. The retting period required for these husks is also

comparatively less. Tampake et al. (1982) have reported the occurrence of palms with sweet edible husk in Indonesia. The variety Kaithathali from Lakshadweep, India, is reported to have sweet husk and is chewed by the seafarers as an antidote to seasickness. Sweet-husked varieties have been reported from other coconut-growing countries: Navasi Thembili (Sri Lanka); Kalpa Tebu (Indonesia); Kalpa Logi (Malaysia); Cuyamis, Caumanis, Tabal, Tamisan and Mais (the Philippines); Uta (Rotuma, Fiji Islands); Preug-wan (Thailand); Nu wa or Cocos sucre (New Caledonia); and Cay dua bong (Vietnam). In India, sweet husked-type variants were reported from Lakshadweep as well as Nicobar Group of Islands, wherein the young buttons were sweet to taste, while the mature nuts had less of pale-coloured hard fibres and more of pale or white-coloured coir dust as compared to normal mature coconuts (Niral and Jerard 2017).

3.8.4.6 Soft Husk

Soft-husked types, with less hard husk fibre and more pale-coloured fibres, have been infrequently observed in coconut populations. Niral and Jerard (2017) reported soft-husked types among coconut populations of Lakshadweep Islands and Nicobar Group of Islands, wherein the attachment of the husk to the nut in the dry, mature fruits was observed to be loose and they produce a dull sound when tapped. Such nuts, on complete drying, also tend to show splitting of husk. These are very similar to sweet husk types in fibre colour and texture.

3.8.4.7 Pink-Husked Fruits and Anther Filaments

A few coconut palms bearing pink-ringed fruits, with pink-coloured mesocarp in developing fruits, have been reported (Bourdeix et al. 2010; Niral and Jerard 2017) from different regions of India (in west coast tall population, East Coast tall population, yellow dwarf), the Philippines (Pilipog Green dwarf) and French Polynesia (Tahitian Red Dwarf). A green dwarf with attractive pink mesocarp colour in tender fruits from Fiji has also been reported. At ICAR-CPCRI, Jerard et al. (2016) reported palm-bearing fruits with pink-coloured mesocarp from San Ramon tall population. While the pink colour appeared on all the female flowers (at the base of the tepals) and also in tender fruits, the pink colour was exhibited only in a proportion of male flowers. This is the first report on differently coloured anther filaments in coconut male flowers, one with dark pink and another with normal yellow filament which has the potential in marker-assisted selection, towards development of tender nut varieties with attractive pink husk. Although no morphological differences could be seen on size of male flowers and anthers, the flowers with pink filaments could be easily identified even at unopened stage since the pink tinge can be seen at the bottom of tepals.

3.8.4.8 Sweet Endosperm

A variant with sweet endosperm, referred to as 'Mohachao Narel', has been reported from India (Samsudeen et al. 2010, 2013). The sweet endosperm has very little fibre content, making the kernel palatable as a salad for table purpose. Only a small percentage of the nuts in a bunch express this character. Studies on nut component traits of sweet and normal fruits of this population indicated slightly lesser fruit and husked fruit weight as compared to normal nuts. Though endosperm thickness was similar, endosperm weight, copra weight and copra recovery were more in normal nuts at similar age of maturity. The development of a large population bearing sweet kernel fruits is a challenging task as the inheritance and genetics need further understanding through progeny testing. Among the progenies of Mohachao Narel, conserved at ICAR-CPCRI, the percentage of sweet kernel fruits in a palm varied from 4.5% to 60% (ICAR-CPCRI 2017).

3.8.4.9 Soft or Buttery Endosperm

The endosperm (kernel) of a mature coconut is normally hard, but in certain palms, few of the nuts have a thicker and softer flesh of a buttery consistency with less liquid endosperm which is viscous. Such coconuts with buttery kernel are popularly referred to as makapuno in the Philippines and are used in preparation of specific coconut delicacies and fetch a premium prize. In India, Patel (1938) recorded rare instances wherein the internal cavity of the shell was filled with a jelly-like substance of the consistency of thick curd and locally referred to as 'thairuthengai' (curd coconut). Satyabalan (1953) observed rugged/warty kernel in 10% of the fruits in a Laguna tall palm at ICAR-CPCRI, India. The abnormal kernel was not sweet and had an oily taste/flavour but with lesser fibre content, while the embryos were normal in size and shape. Soft kernel types were collected from Andaman Islands (Jerard et al. 2013) and Kerala (CPCRI 2014), belonging to Andaman and West Coast Tall coconut populations, respectively. The fruit component studies in the soft kernel types indicated that the fresh kernel has lesser fibre, oil and sweetness. The tender nut water from soft kernelled fruits was more viscous due to suspended kernel tissue and recorded higher TSS. Adriano and Manahan (1931) distinguished three different types of endosperm in soft kernel fruits: nuts with a hard outer layer, a soft viscous middle layer and a semi-liquid inner layer of endosperm, nuts with a hard outer layer and a soft viscous middle layer and nuts with one layer of hard endosperm, filling the whole central cavity.

Makapuno is reported to be a single recessive gene mutation (Torres 1937) and has been successfully exploited through controlled pollination among makapuno-bearing palms followed by embryo culture to develop elite populations giving higher percentage of makapuno nuts. Mutants similar to the makapuno type have been reported from other coconut-growing regions, such as Coco Gra of Seychelles, Kopyor of Indonesia, Thairu Thengai or Nei Thengai or Ghee Thengai of India, Dikiri Pol of Sri Lanka, Mapharao Khati of Thailand, Sap of Vietnam, Niu Garuk of Papua New Guinea and Pia of Polynesia.

Zuniga (1953) obtained the expected Mendelian ratios in the progeny of makapuno. However, Cruz and Ramirez (1968) advocated a more complex behaviour, considering the different types of makapuno being found and the differences in nuclear behaviour between various makapuno types. The embryos though normal in size do not germinate under natural conditions, but germinate *in vitro* when cultured in appropriate nutrient media. Cedo et al. (1984) based on their observations from controlled pollination studies, with makapuno palms derived from embryo culture, concluded that makapuno coconuts are homozygous and that pollen produces a xenia effect. Mujer et al. (1983, 1984a, b) based on his biochemical studies on normal and makapuno coconut concluded that the makapuno endosperm occurs due to a deficiency in the activity of the enzyme alpha-D-galactosidase. Samonte et al. (1989) observed that the activity of three galactomannan-degrading enzymes, viz. alpha-D-galactosidase, beta-mannanase and beta-mannosidase, was consistently low during endosperm maturation in the makapuno endosperm as compared to normal endosperm.

3.8.4.10 White Testa

The testa in a normal coconut is brownish in colour, while in rare instances, the testa has been observed to be white (Tampake et al. 1982).

3.8.4.11 Aromatic Types

Aroma, which is released when a tender coconut is cut open, is a novel trait. A few exceptional palms have been reported to produce fragrant endosperm in different countries, such as Klapawangi, aromatic green dwarf, Nam-Hom, etc. The liquid endosperm (tender nut water) in aromatic coconut is characterised by a pleasant 'pandan-like' aroma, similar to the aroma of aromatic rice, which adds palatability in tender nut consumption and fetches a premium price in the market. In Thailand, Saensuk et al. (2016) concluded that the aroma in the liquid endosperm of the popular aromatic green dwarf coconut is due to the presence of 2-acetyl-1-pyrroline (2AP), and this qualitative trait is controlled by a single recessive gene.

3.8.5 *Novelties Associated with Chromosome Number*

3.8.5.1 Haploidy

Whitehead and Chapman (1962) reported a diploid-haploid twin (seedling) in coconut, the haploid being the weaker member of the pair. At ICAR-CPCRI also such diploid-haploid twin (seedlings) has been observed in the coconut nursery, in different varieties, at very low frequencies. Ninan and Raveendranath (1965), during the course of extensive investigations on cytology of embryo and endosperm in

coconuts, encountered a haploid embryo with chromosome number of 16 and nuclear volume of only about a third of that of the diploid nuclei ($2n = 32$), in a West Coast Tall palm. They concluded that the haploid embryo probably resulted from haploid parthenogenesis.

3.8.6 *Novelties Associated with Gross Morphology*

3.8.6.1 Compact Crown

Compactness is an important trait, in development of improved varieties, especially as it is amenable for high density planting. In Fiji, compact dwarfs have been reported in natural populations, possibly having arisen from introgression between the local types. The compact dwarfs are allogamous, but with a very low rate of trunk extension as in the case of dwarfs, but with trunk diameter and flowering behaviour similar to tall but with the crown being more compact than those of tall or the slender dwarfs. The first compact dwarf described in coconut is the Niu Leka Dwarf. Bourdeix et al. (2017) reported the presence of compact dwarfs in French Polynesia and the Cook Islands, some with green, brown, red-orange and yellow fruits, including a compact red dwarf in French Polynesia, with pink mesocarp colour in young developing nuts and hypothesised that some of the compact dwarfs presently available in Polynesia are progenies of the Niu Leka \times Malayan Red Dwarf crosses made in Fiji by Marechal (1926). In India (CPCRI 2010), a dwarf mutant identified in seedling progenies from Lakshadweep coconut population showed extreme dwarfism as compared to the other conserved dwarf accessions. Besides, compact dwarf hybrids of MYD \times NLAD have been developed in India (CPCRI 2013).

3.9 Future Strategy

Coconut, with a long history of domestication and cultivation, has evolved, through the ages, from being an important oil-producing crop to an important food crop, with high nutritive value today. The crop now finds a place in the list of 49 priority crops of global importance in food and livelihood security of the International Treaty on Plant Genetic Resources for Food and Agriculture, wherein country signatories to this treaty agree to make their genetic diversity and related information about the crops stored in their gene banks available to all, to facilitate research, innovation and exchange of information to stimulate sustainable crop production.

The fact that coconut belongs to a monotypic genus with no known wild relatives has been a major handicap in unravelling the origin as well as the evolution of the present-day cultivated coconut. In the absence of experimental studies, our understanding of the origin and domestication has been based on historical accounts, fossil records and some phylogenetical studies. Comprehensive phylogenetic studies

using all related genera, viz. *Attalea*, *Syagrus*, *Parajubaea*, *Jubaeopsis caffra* and *Voanioala*, as well as the species earlier classified under the genus *Cocos* may help to throw light on the evolutionary relationship of *Cocos nucifera*, under the subtribe Attaleinae. Wide hybridisation between these related genera and geographically isolated/remote coconut populations can also be attempted to facilitate better understanding of the evolution of the present-day coconut.

In view of the basic need for a broad genetic base for varietal improvement, especially for developing resistant planting material to combat serious diseases which is a major constraint limiting coconut production in all the coconut-growing countries, intensified efforts are required for collection, conservation and in-depth studies on coconut populations of remote/uninhabited islands in the Pacific Ocean as well as the Indian Ocean, including the Andaman and Nicobar Islands and the Lakshadweep Group of Islands. Activities of COGENT need to be strengthened for this purpose. Simultaneously, new approaches and synchronised global efforts are required to conserve the available variability in the crop, both in situ and ex situ in field gene banks, cryo-genebanks as well as DNA banks, to mitigate loss of biodiversity through genetic erosion, from loss of native habitats, sea level rise, growing urbanisation and replanting of existing coconut plantations.

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