

Chapter 12

Coconut

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12.1 Introduction

The coconut palm, *Cocos nucifera* L. is now grown mainly by smallholders but was once the major perennial plantation oil crop widely cultivated in the humid tropics. It has a pan-tropical distribution, occurring in coastal areas between the latitudes 20° north and south of the equator and at altitudes between sea level and 1,200 m. Coconut grows best under conditions of high humidity, at temperatures of 27–30°C and on moderately to well-aerated soils.

Coconut is the most extensively grown and used palm in the world and about 10 million families in over 80 countries rely on coconut as their main source of food and income. Coconut is a smallholders' crop and a major proportion of the production is usually consumed locally. The actual percentage of domestic consumption of coconut in Asian and Pacific Coconut Community (APCC) countries was around 64% in 2001. Coconut is mainly an oil crop, particularly rich (48%) in lauric acid (Jones 1991). Virgin coconut oil (Bawalan and Chapman 2006), expelled under low heat from fresh coconut meat to preserve its natural vitamins and enzymes (Marikkar et al. 2007) is now becoming popular in the pharmaceutical industry and is gaining a significant international market. Coconut as a bio-fuel is also a newly emerging product which would reinstate coconut palm as a valuable oil crop in the not too distant future. Already people on the island of Bougainville in Papua New Guinea are powering up their vehicles and generators with environmentally friendly coconut bio-fuel. In addition, the coconut industry offers a wide range of coconut products such as desiccated coconut, coconut cream, coconut milk powder, defatted coconut, coconut fibre and fibre products, shell charcoal and activated carbon, coconut vinegar and coconut arrack (liquor) etc. for the local and the international markets. Tender coconut as a natural beverage is presently gaining popularity and currently there is also a growing international

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market for fresh coconut water. Fresh coconut water is already widely used as a natural beverage in some coconut producing countries, India being the largest nut water consuming country whilst in Brazil, in the state of Sao Paulo alone, a daily consumption of 100,000 nuts has been estimated. Accordingly there is a vast interest in growing dwarf coconut varieties for water utilization. Coconut oil is also the principal raw material used in the manufacture of soap, glycerine and margarine. The lauric acid from coconut oil is used to manufacture detergents, cosmetics and pharmaceuticals. Locally the trunk is made into furniture, handicrafts and building materials, the fibre from the nuts for mattresses, doormats and ropes. Coconut as a whole plant, particularly the colour forms of dwarf varieties, are a tropical ornamental, much in demand as a signature tropical landscape element (Meerow and Ayala-Silva 2006). Because of the multiplicity of uses of the coconut palm, it is termed 'one of Nature's greatest gifts to man' (Burkill 1966) and also as 'The Tree of Life'.

The estimated total area under coconut in the world in 2001 was 11.8 million ha. The contribution of the major coconut growing countries in terms of land area cultivated with coconut are Indonesia (31%), the Philippines (26%), India (16%), Sri Lanka (4%), Thailand (3%), Tanzania (3%), Malaysia (2%), Brazil (2%), Papua New Guinea (2%), Vietnam (1%), Mexico (1%), and Mozambique (1%). Samoa, Micronesia, Fiji, Solomon Islands, Vanuatu, Palau, Bangladesh, China, Myanmar, Cocos Island, French Polynesia, Guam, Kiribati, Tonga, Comoros, Ghana, Ivory Coast, Madagascar, Nigeria, Tanzania, Colombia, Dominican Republic and Jamaica contribute the other 8% of cultivated coconut lands. More than one half of the coconut production however comes from Southeast Asia, mainly from the Philippines and Indonesia while almost one quarter comes from Asia, mainly from India and Sri Lanka. The remainder comes almost equally from American, African and Pacific regions (Asian and Pacific Coconut Community 1997).

12.2 Origin and Domestication

Cocos nucifera L. is a member of the monocotyledon family Arecaceae (Palmaceae) in the subfamily Coccoideae that includes 27 genera and 600 species and is the only species of the genus *Cocos*. Coconut possesses a diploid genome with 32 chromosomes ($2n = 2x = 32$).

There are conflicting theories regarding the origin and domestication of coconut. A number of theories supported a New World origin of coconut with subsequent dispersal to Asia and Polynesia (Guppy 1906; Cook 1910; Ridley 1930). For example, the centre of origin of Cocoid palms, the closest relative of coconut, is north-western South America. However, a theory for Polynesian and Asian origin has been postulated (Child 1964, 1974; Burkill 1966; Purseglove 1985; Dennis and Gunn 1971) and both Fremont et al. (1966) and Purseglove (1985) have provided convincing evidence of a Southeast Asian

origin and Indo-Pacific domestication for coconut based on ethnological and entomological evidence. Evidence from fossils and archaeological studies argue for a South–West Pacific origin of coconut (Child 1974; Purseglove 1985) while Indian fossils and the Madagascar forest coconut support an Indian Ocean origin (Chiovenda 1921; Mahabale 1976; both cited in Harries 1995). However, at present the origin of coconut is still not fully resolved but reports are available that wild specimens of coconut have been found growing in natural coastal forests in the Philippines and Australia supporting the theory that coconut originated in the Western Pacific. A possible region for coconut domestication was considered to be Melanesia, on the coasts and islands between South East Asia and the Western Pacific approximately between New Guinea and Fiji (Child 1964; Purseglove 1985) but more recently a submerged continental region of South East Asia (Malesia) has been suggested (Harries 1990, 2002). In an effort to explain the presence of close relatives of coconut in the New World, Purseglove (1985) suggests that the ancestral palm, which is likely to have had a fibrous mesocarp and be able to float and to establish itself under suitable conditions, could have been carried by ocean currents from South America to Polynesia in a similar route to that suggested for sweet potato (Purseglove 1965, 1968), and coconut may have evolved from that ancestor as a separate event in the Melanesian region. Harries (1978) describes a possible evolutionary process for coconut based on natural selection and evolution of large-fruited coconut from a small fruited progenitor. Gunn (2004) provides the most recent review on the phylogeny of the *Cocoeae* (*Arecaceae*).

Swaminathan and Nambiar (1961) suggested that dwarf coconuts (coconut palm with short stature, see varietal groups) may have originated as a result of inbreeding among tall coconuts as these show limited self-pollination, but this was not supported by subsequent cytological studies by Raveendranath and Ninan (1974). Purseglove (1985) states that dwarfs are probably mutations of tall types. However, Harries (1978) suggests that some characters of dwarfs (i.e. early germination, precocity, nut shape, different and bright fruit colours, the proportion of husk and for some dwarf forms the high resistance to lethal yellowing disease) indicate that domestication is more likely since dwarf populations could never survive in the wild (Harries 1995).

Coconut has been distributed to all parts of the tropical world including Central and South America, East and West Africa, South and Southeast Asia and the Pacific islands. From its putative centre of origin, coconut has been disseminated both east and west by floating in the sea and by human dissemination (Ohler 1984), particularly by the ancient Polynesian sea voyagers, who carried coconut as a source of food and drink on long sea voyages (Harries 1978). Whitehead (1976) also suggests that the spread of coconut from its putative centre of origin to Central and South America was the end result of the dissemination process and once established in a new vicinity, human activity accounted for further dissemination beyond the initial distribution range.

It is accepted that the coconut palm has been present on the Atlantic coast of Africa and South America and around the Caribbean for less than 500 years (Child 1974; Purseglove 1972) as there were no coconuts in those regions at the time of Columbus's voyages. There is, however, evidence that coconuts were on the Pacific Coast of Panama in pre-Columbian time (i.e. before 1492), either by early Polynesians carrying them or by ocean currents naturally distributing them. Harries (1978) observed a great similarity in West and East African coconuts pointing to a common source of coconuts for those regions. Coconuts in the East African coast were once thought to have either been brought there by ancient Arab traders or to have floated from India in the tenth century where they had grown for 2000 years, but according to more recent studies (Schuiling and Harries 1992; Krain et al. 1993), the presence of coconut palms could pre-date human activity. It is also possible that Malaysian sea-rovers, who reached Madagascar in the first century AD, took coconut with them to Madagascar and the Comoro islands (Lebrun et al. 1998). From there coconut subsequently reached the coast of East Africa. Coconut reached Cape Verde, West Africa only after 1500 AD through the Portuguese (Harries 1977; Purseglove 1985), probably from East Africa or India, and was then taken to the Caribbean and Atlantic Coast of America. European explorers after 1492 contributed to further dissemination of coconut by transporting them from Asia and East Africa to West Africa, the Atlantic coast of South America and the Caribbean region (Purseglove 1972). Zizumbo-Villarreal (1996), reviewing the history of coconut in Mexico, reported that the first introductions of coconut to the Atlantic Coast of Mexico were from West Africa and the Caribbean islands around 1549. He further reports that the introductions to the West Coast of Mexico originated from Panama around 1539, from the Solomon Islands around 1569 and from the Philippines from 1571 onwards by the Spanish during the Spanish colonial period. Plantations were developed throughout the tropics by the end of nineteenth century. Coconut populations that are now considered endemic to the Atlantic Coast of Africa, America and around the Caribbean region are basically the same as the coconuts in East Africa, India and Sri Lanka (Harries 1977) while coconuts in the Pacific Coast of America are related to the Pacific islands and Southeast Asian coconuts based on fruit component analysis data (Harries 1978; Vargas and Blanco 2000; Zizumbo-Villarreal et al. 2005).

12.3 Varietal Groups

The classification of coconut has been highly non-standardized, resulting in different authors in different countries using different terminology of coconut. However the major classification of coconut is based on stature and breeding behaviour which groups coconut broadly into two groups or types: tall (also termed *typica*) and dwarf (also termed *nana*), but Menon and Pandalai

(1958) were quoting Narayana and John (1949) who included *javanica* as another type of dwarf in India. Liyanage (1958), working in Sri Lanka, used similar *typica-nana* terminology, but discarded *javanica* and described *aurantiaca* as a new group. Neither of these South Asian classifications includes the Niu leka dwarf from the South Pacific. Tall types are the most commonly grown commercially exploited group and grow to a maximum height of about 20–30 m. They are predominantly allogamous (cross-pollinating), although a limited degree of autogamy (self pollination) has been reported for some tall groups (Bourdeix 1988; Bourdeix et al. 1990). The dwarf types in contrast attain a maximum height of about 10–15 m and are predominantly autogamous. Despite this higher degree of autogamy, dwarfs cross-pollinate with one another and with tall. The major differences between tall and dwarf coconuts are given in Table 12.1.

Table 12.1 Contrasting features of tall and dwarf coconuts

Character	Tall (<i>typica</i>)	Dwarf (<i>nana</i>)
Stature	Tall (about 20–30 m)	Short (about 10–15 m)
Bole formation at base of stem	Yes	No
Time till flowering	6–8 years	3–4 years
Economic life span	Long (about 80–100 years)	Short (about 40 years)
Bearing nature	Continuous	Seasonal
Nuts/palm/year	Average 40	Average 80–100
Copra amount and quality	200 g/nut, good quality	80–100 g/nut, poor quality
Growing conditions	Variable	Sensitive to climate changes
Breeding habit	Out-breeding	In-breeding

In addition to the tall and dwarf groups, a few intermediate groups, sometimes referred to as semi-talls or semi-dwarfs are also found. King coconut in Sri Lanka (Liyanage 1958), and to the understanding of the authors, Gangabondom in India (Menon and Pandalai 1958) and Niu Leka Dwarf in Fiji (Powell 1868; Bourdeix et al. 2005a) are examples of such intermediate groups. However the King coconut which has been classified as *aurantiaca* by Liyanage (1958) is totally different from the Niu Leka, and they cannot be classified in the same group.

As tall coconuts are predominantly cross-pollinated, they are highly heterogeneous and consist of unique individual genotypes. However, many coconut varieties (or cultivars) within the main group of tall exist that show certain general morphological resemblance within the variety but very slight dissimilarity or, in certain cases, contrasting dissimilarity between them. When there is dissimilarity it is generally attributed to fruit traits (size, shape and colour) and the proportions of the components of fruit (percentage weight of husk, shell, nut water, meat etc.) though in certain instances traits such as soft husk, sweet nut water, resistance to particular diseases (e.g. Vanuatu Tall

resistant to foliar decay virus and Sri Lanka Green Dwarf resistant to lethal yellowing disease in Ghana) also contribute to the differences. These cultivars often have different geographical origins and carry a prefix to the cultivar name of the country of origin, or the region of origin within a country, where they are originally and naturally grown. Earlier there had been no proper standardized nomenclature for coconut, whereas now each variety is given a unique international name, usually consisting of the group, whether it is a tall or dwarf, to which a geographical or cultural reference is added; for varieties of uniform colour, for instance, the different colour forms of the dwarf group, that colour information is also added. Examples of cultivars are West African Tall, Sri Lanka Tall, Mozambique Tall, Malayan Tall that originated from different countries and San Ramon, Tagnanan Tall, Markham Valley Tall that originated from various regions within a particular country. Examples of such cultivars in the dwarf group are Cameroon Red Dwarf, Sri Lanka Green Dwarf, Malayan Yellow Dwarf and Madang Brown Dwarf (Madang is a village in PNG). Furthermore, germplasm collections, field gene-banks and the Coconut Genetic Resources Network (COGENT) database have certain other entries termed as populations or accessions for the collections of coconut populations within a particular coconut cultivar, identified in different geographic locations. Examples of such populations are Panama Tall Monagre and Panama Tall Aguadulce, and West African Tall Mensah and West African Tall Akabo, Sri Lanka Tall Ambakelle and Sri Lanka Tall Kasagala. They are also sometimes referred to as ecotypes if the particular accession or population was a result of an environmental selection over several generations. In these populations or accessions the morphological differences are either not noticeable or very slightly detectable, but their adaptability for particular ecological niches or for a particular pest or disease resistance cannot be predicted from morphology.

Within the main varieties, numerous groups of coconut do exist which Liyanage (1958) referred to as forms of coconut and Bourdeix et al. (2005a) referred to as variants that are phenotypically highly distinctive. Some examples are Bodiri, Nawasi, Dikiri pol and Pora pol in Sri Lanka (Liyanage 1958), Laccadive Micro Tall in India (Bourdeix et al. 2005b), Spicata in different countries, Makapuno in the Philippines and Nim in Thailand.

Instead of the above varietal groups, Harries (1978) proposed two main types of tall coconuts; one that has large, long, angular, thick-husked and slow-germinating nuts with less free water content, the 'Niu kafa type' or wild coconut, that evolved naturally and was disseminated by ocean currents, and another that has more spherical nuts with an increased proportion of endosperm, reduced husk thickness, early germination and resistance to disease, the 'Niu vai type' or domestic coconut, that was selected under cultivation for increased nut water content and was disseminated by humans. Harries (1978) further suggests that introgression of these two types and further selection and dissemination by man gave the wide range of varieties and pan-tropical distribution of coconut seen today.

Whichever terminology is adopted, the authors are of the view that many of the named varieties, cultivars or populations reported in coconut literature were the result of either the vernaculars being used by local people and differences in the regions where they come from or because of slight morphological differences. For example, Whitehead (1966) has shown that coconut palms in Pacific islands are designated by several local names which do not always refer to distinct cultivars, but to small morphological differences. It is also possible that there could be some duplication of varieties in different coconut growing areas that are known by different names and hence classified as different varieties or populations. Therefore, until they are studied in detail by systematic morphological and molecular investigations, the true differences between varieties and populations remain unresolved.

12.4 Genetic Resources

In coconut, *Cocos nucifera* L., being the only species in the genus *Cocos*, there are no closely related wild relatives known. Although it is now generally assumed that truly wild type coconuts do not exist any longer, their characters are present in modern populations. Buckley and Harries (1984), Gruezo and Harries (1984) and Leach et al. (2003) reported wild types of coconut on uninhabited coral atolls, on small isolated islands or on remote mainland beaches. The domestic coconut is found associated with isolated or previously isolated human settlements and dwarf coconuts can be included in the domestic group, as they cannot survive in the wild. Present day coconut consists of a mixed complex of wild and domestic characteristics, depending on which of these forms predominated when cultivation began in each region.

Many different coconut genetic resources have been described by different authors (Narayana and John 1949; Gangolly et al. 1957; Menon and Pandalai 1958 and references therein; Liyanage 1958, Bourdeix et al. 2005a). There is a great diversity in fruit characters within and between populations for size, shape and the colour of the fruit and proportions by weight of fruit components viz. husk, shell, endosperm and water. Ashburner et al. (1997a) conducted a survey on diversity in fruit components of South Pacific coconut, and reported great diversity for fruit morphology in a range from populations exhibiting wild type characters to populations displaying domestication characters. Variation in fruit shape varies from near-spherical to short and long angular with different degrees of expression of a pear shape (Foale 1991). It is also observed that there is a great deal of variation in frond morphology, orientation of the crown, number and length of bunch, number of female flowers and number of nuts per palm even within populations (personal observations of the authors). It has been reported that there is more morphological diversity in Southeast Asia than there is in South Asia, Africa or South America (Benbadis 1992; Whitehead 1976). As a consequence, more named varieties are found in Southeast Asia relative to other areas.

Coconut genetic resources are currently threatened by a high rate of genetic erosion all over the world, mainly due to industrialization, urbanization, infra-structure development, changing use of agricultural land for high-value cash crops, and natural disasters such as cyclones, tsunamis, droughts, pests and diseases. Moreover, coconut development programmes involving the replanting of existing areas in regions of greatest diversity with fewer numbers of high yielding hybrids or improved varieties with a narrow genetic base threatens to displace older populations resulting in a further reduction of the genetic base. Therefore, collection and conservation of coconut biodiversity was nationally and internationally recognized as an important objective, as future breeding is based on collected material. As a result, the Coconut Genetic Resources Network (COGENT) was established in 1992 as a global network under the auspices of International Plant Genetic Resources Institute (IPGRI) with the objective of strengthening national programmes to conserve and utilize coconut genetic resources (<http://www.cogentnetwork.org>). Under this programme, COGENT, with funding from the Asian Development Bank (ADB) assisted by 13 Asia-Pacific countries in 1996 initiated the collection of coconut genetic resources and in 1997 extended support to Mauritius, Madagascar, Seychelles, Sri Lanka and Vietnam to collect and conserve threatened or useful coconut biodiversity. The COGENT participants also set up an international Coconut Genetic Resources Database (CGRD) in 1992 with the objective of construction of a computerized catalogue of accessions representing a large number of coconut cultivars spread throughout the coconut growing regions in order to gain an understanding of coconut diversity and thereby promote coconut germplasm exchange (Hamelin et al. 2005). The CGRD database was designed to provide passport, characterization and evaluation data for the coconut accessions in the database, and the number of accessions in the database by the year 2003 increased to 1426 compared to 500 in 1994. These 1426 entries included 599 tall cultivars, 111 dwarf cultivars and 1 semi tall cultivar, some cross-pollinating dwarfs and populations within cultivars. However, results obtained by molecular studies on 33 coconut populations in Sri Lanka, revealed a very low level of population differentiation (2%) indicating very close relationships between those populations (Perera et al. 2001). This poses the question whether same genotypes carry different accessions/codes in the collection, and this has become an issue to be resolved urgently. The recent book on 'Coconut Genetic Resources' (Batugal et al. 2005) published by IPGRI and the CGRD database provide a comprehensive coverage on the coconut genetic resources available throughout the world. COGENT has also initiated the establishment of four large multi-site international coconut gene-banks in Indonesia, India, Papua New Guinea and Ivory Coast as well as 28 national genebanks in 24 countries, in addition to the existing small international collections in Tanzania, Ivory Coast, the Philippines and India.

12.5 Major Breeding Achievements

As in many crops since early agricultural times, the coconuts grown all over the world were derived by mass selection and open pollination, using criteria determined informally by farmers themselves. The earliest selection of coconut dates back 8,000–14,000 years (Harries 2002) during which time coconut had been selected and domesticated for large round fruits rich in water as a source of sweet uncontaminated water for seafarers travelling from island to island. However, after commercialization of coconut during the nineteenth and twentieth centuries, the yield of copra per palm or one of its correlates have been the major criteria for selection of seed palms by farmers. The efficiency of mass selection of mother palms based on desirable characters has been studied extensively, and the progeny trials established in Sri Lanka occupied the most prominent place in early coconut breeding research and generated much information for developing criteria for selection of seed coconut palms. Most prominent of these is the estimation of heritability values for a number of useful characters in coconut (Liyanage and Sakai 1960) as effective criteria for selection of seed palms (Liyanage et al. 1988). The progenies resulting from open pollinated seeds are the basis of an improved population. For instance, the response to selection for de-husked nut weight by open pollination was a yield gain of 14.4% by selecting the best 5% of the population (Liyanage, 1972). Current seed palm selection criteria in Sri Lanka and elsewhere are developed from such observations. Early studies on coconut also provided information on some useful correlates between seed characters, period to sprouting and flowering, and initial yield and copra outturn. Seeds that sprout early promote seedling height, leaf and root number leading to a shorter flowering period and higher production of copra (Liyanage and Abeywardena 1957; Liyanage et al. 1988). Coconut nursery management practices all over the world adopt this concept for culling weak seedlings from nursery beds, i.e. rejection of late germinated seeds at a given period of time depending on the cultivar and removal of weak seedlings again after keeping in the nursery for a fixed period of time.

From the same progeny trials it was found that open pollinated progenies of certain coconut palms are uniformly high yielding giving a mean yield of about 35–40% more copra than the population mean. That phenomenon was explained as possessing of sufficient dominant yield traits in those palms to pass on to their offspring despite having been indiscriminately pollinated by unknown palms. Such palms were described as prepotent palms (Harland 1957). However, their identification is laborious and time consuming and relatively few palms prove to be prepotent from a large number tested, thus the quantity of seed nuts collected from them for the industry is negligible. With the assumption that progenies arising from artificial pollination using pollen of a prepotent palm as the male parent will be equally high yielding as the natural progenies of prepotent palms, seed production through artificial pollination of selected high

yielding mother palms from pollen of prepotent palms had been practised for the genetic improvement of coconut. Raising an enormous quantity of improved seeds demanded by farmers either by artificial pollination or stringent mass selection is impossible, so seed gardens were designed specifically for mass production of improved coconut genotypes. Since improved genotypes are produced by controlled natural pollination the concept of isolated seed gardens was well appreciated for mass production of superior genotypes (Liyanage 1954, 1961a). The Sri Lanka Tall \times Sri Lanka Tall named as Ambakelle Tall or CRIC60 from the Isolated Seed Garden (ISG) at Ambakelle is an excellent example of such improvement attempts, which surpassed the yield of ordinary Sri Lanka Tall coconut (Liyanage et al. 1988).

Despite inherent constraints, the inter-varietal hybridization has shown the greatest gains in coconut breeding, demonstrating the usefulness of heterosis in coconut. The beginning of scientific coconut breeding came when the first controlled hybridisation was made in Fiji in 1926 between Malayan Red Dwarf and Niu Leka Dwarf (Marechal 1928). In India, the first hybridisation between tall and dwarf (West Coast Tall \times Chowghat Green Dwarf) was attempted in 1930, with the intention of combining the quality of copra from the tall parent and the high productivity as well as early flowering from the dwarf parent. Sri Lanka initiated studies to test coconut hybrids in 1949 by assessing the cross between Sri Lanka Tall and Sri Lanka Green Dwarf (Liyanage 1954, 1972; Liyanage et al. 1988) and the productivity of this hybrid was remarkable – recording over 20,000 nuts per ha after 12 years from transplanting (Manthiriratne 1971, 1972, 1978). Most of the hybrid tests were conducted between 1940–1960 and involved dwarf \times tall (inter-varietal) and tall \times tall (intra-varietal) crosses and in these studies the superiority of dwarf \times tall over local tall cultivars was well established. But it was not until the mid-1970s that coconut F_1 hybrids became widely available in commercial quantities. After the first successful attempt (Harries and Romney 1974), many dwarf \times tall hybrids have been produced utilizing different tall and dwarf cultivars originating from different geographical regions. The crosses Malayan Dwarf \times Panama Tall (Maypan), Malayan Yellow Dwarf \times West African Tall (PB121 or MAWA), Cameroon Red Dwarf \times Rennell Island Tall (Maren), Malayan Red Dwarf \times Tagnanan Tall (Matag or PCA15-2), Sri Lanka Green Dwarf \times Sri Lanka Tall (CRIC65), Sri Lanka Green Dwarf \times San Ramon Tall (Kapruwana) are examples of some of the most promising present day hybrids between dwarf and tall used in a wide range of environments. More details on recommended and preferred hybrids in different countries are described by Batugal (2005) and Bourdeix et al. (2005b).

Recently it has been shown that tall \times tall hybrids, crosses between tall of different origins are high yielding though they are not promising in terms of early flowering (Bourdeix et al. 2005b). It must be noted that these crosses are different to Sri Lanka Tall \times Sri Lanka Tall crosses which are combinations between superior palms of the same variety. The Sri Lankan experience between tall \times tall hybrids using Sri Lanka Tall \times San Ramon Tall was that they were

highly promising in terms of copra per nut as well as total copra production per unit area (Everard 2002) though they produced equally in terms of nut number as local tall selection CRIC60, but less than 40% of nut number as the dwarf × tall hybrid CRIC65. Some of the other famous tall × tall hybrids are West African Tall × Rennell Island Tall (PB213 or Waren) and West African Tall × Vanuatu Tall (PB 214 or Wavan).

Although the first coconut hybrid tested in the world was a dwarf × dwarf hybrid (Marechal 1928), they are still the least exploited hybrids. However, the authors strongly believe that dwarf × dwarf hybrids are ideal trees for home gardens in urban areas to grow them as ornamental palms while meeting the daily coconut requirement if they show hybrid vigour for meat content per nut and the quality of copra. In Sri Lanka currently there is a demand for coconut varieties with short stature from people living in urban areas as palm height is a problem in small home gardens and picking is difficult in tall varieties. Though no follow up of Marechal's work has been documented, a success story of a cross between Malayan Yellow Dwarf and Malayan Red Dwarf varieties (PB332) produced in 1971 at the 'Marc Delorme' centre in Ivory Coast is reported by Bourdeix et al. (2005b), but no dwarf × dwarf hybrids have yet been widely distributed to farmers.

In terms of breeding for resistance to biotic and abiotic stresses, the intercrossing of resistant/tolerant germplasm with adapted high yielding materials has been the strategy. All colour forms of Malayan Dwarf have been identified as lethal yellowing disease resistant cultivars and the hybrid Malayan Dwarf × Panama Tall (Maypan) is therefore in particular demanded for areas where the lethal yellowing disease phytoplasma occurs. Further, two Pacific coast tall cultivars have been identified as highly resistant to this disease known as amarillamiento letal in Mexico (Zizumbo-Villarreal et al. 1999). Other disease resistant types include Vanuatu Tall, identified for tolerance to the coconut foliar decay virus, and Sri Lanka Green Dwarf, for Cape St. Paul wilt tolerance (also caused by phytoplasma) in Ghana. In India breeding for root wilt disease is of high priority in the coconut breeding programme. Chowghat Green Dwarf and Malayan Green Dwarf have been identified by the Central Plantation Crop Research Institute (CPCRI), India as resistant varieties, showing a higher level of resistance to root wilt disease compared to other coconut varieties. The cross between Sri Lanka Yellow Dwarf × Sri Lanka Tall has been identified as a tolerant cultivar for *Aceria* mite by evaluating five commercially cultivated coconut cultivars in Sri Lanka in a severely mite affected area (Perera 2005, 2006). Sri Lanka Yellow Dwarf and Gon thembili cultivars have also recently been identified as tolerant cultivars to coconut *Aceria* mite (Perera 2006).

Drought is a serious constraint to coconut production in many countries as coconut is mainly a rain fed plantation crop. Hence breeding for drought tolerance has been given high priority in many coconut breeding programmes. In Sri Lanka, a selection based on mean yield and genotypic adaptation to changes in climate of the Sri Lanka Tall cultivar, correlating 15 years of individual palm yield data with 15 years rainfall data has identified a new

cultivar released under the name of Ambakelle Special (Wickramaratne 1987a,b). In Ivory Coast PB-121 was identified as a drought-tolerant hybrid (Bourdeix et al. 2005b), while much work has been done in India to assess and measure the degree of drought tolerance, resulting in the identification of several tolerant varieties (Rajagopal et al. 2005).

Studies on clonal propagation of coconut have been in progress in many coconut growing countries and also in European laboratories since the 1970s, but have not generated a protocol which can be applied to coconut breeding yet (Oropeza et al. 2005). Successful *in vitro* culture of coconut embryos has been developed as a tool for safe exchange of germplasm and to rescue embryos of Makapuno coconut, a coconut variety which has high commercial value in the confectionary industry but does not germinate when intact in the nut (Carandang 2002; Rillo 2004).

12.6 Current Goals of Breeding

Coconut breeding objectives are still primarily focused on high yield. The definition of yield in terms of yield improvement in coconut is complex. It is yield in terms of nut number that is attractive to the grower who sells coconut on numbers basis whereas it is the size of the nut or the weight of meat or copra that is demanded by the manufacturer or the processing sector. However, as the number of nuts per bunch and size of the nuts is negatively correlated in coconut, one cannot enhance both traits simultaneously by improving naturally occurring coconut varieties by selection alone. On the other hand, in terms of national production targets of a country it is the total meat or copra content per unit planted area that is important. The breeding programmes aiming at a higher nut number have succeeded through the production of dwarf \times tall hybrids that surpass the yield of tall coconut cultivars by over 45% (Perera 2005) when hybrids are agronomically well followed up. The low copra content in the hybrid is more than compensated for by the number of nuts produced. As copra content per hybrid nut is generally low compared to tall nuts, at least in the context of Sri Lanka and India according to the experience of the authors, hybrid nuts are less in demand by manufacturers due to greater labour requirement during processing. In the contrary, the tall \times tall coconut hybrid (CRISL98) in Sri Lanka is less demanded by the growers though it produces about 40% more copra per nut, but is slightly lower in number of nuts per palm. This is despite its producing more copra per unit area than the dwarf \times tall hybrid compensating through the high copra content per nut. It is a fancy hybrid for manufactures as well as for large scale coconut growers who sell their nuts on a weight basis. Hence, the current breeding goal is the development of hybrids that produce a large number of nuts carrying thick kernel by carefully manipulating the parent palms in the breeding programme. This has been achieved by the hybrid Kapruwana in which parents are large

fruited San Ramon that originated in the Philippines and Sri Lanka Dwarf Green which is a prolific bearer. Kapruwana produces as equally well as CRIC65 in nut number and with high copra content per nut comparable with the hybrid CRISL98.

As the vegetative phase of the commercially grown tall coconut varieties is long taking about 8–10 years, precocity in flowering is still a current goal in coconut breeding. Significant progress has been achieved in precocity in the coconut breeding programme by combining early flowering behaviour of dwarfs with commercially grown tall coconut cultivars, but breeders still see scope of shortening the time till flowering in hybrids by incorporating some dwarf germplasm such as Salak Dwarf from Indonesia, which is exceptionally early in flowering. Breeding for oil content or for an oil rich in a particular fatty acid is in the early phase as an objective in coconut breeding.

With the global climate change, droughts have become frequent in many coconut growing countries and hence they become a constraint in coconut production. Therefore, in the recent past, breeding for drought tolerance has become a breeding goal in the coconut breeding programmes of many coconut growing countries. Selection of cultivars and individual genotypes in the fields prone to droughts has been given high priority with the objective of selecting parents for breeding programmes or improvement of local varieties through selection.

Though many major and minor coconut pests that damage coconut palms exist, efficient and effective chemical and biological control methods are in place to control them. However, all chemical and biological control measures field tested so far under experimental conditions have either been unsuccessful or not practical to adopt to control the coconut mite; *Aceria guerreronis*, a microscopic coconut pest that lives beneath the perianth of the nut causing damage to developing nuts. Hence breeding for tolerance to *Aceria* mite is a current breeding goal in the coconut breeding programme in Sri Lanka and India (Perera 2005, 2006). Screening of coconut varieties for tolerance to *Aceria* mite is in progress and some initiatives have been taken to develop hybrids involving crosses between tolerant parents (Perera 2006). Similarly breeding for disease resistance has also been a current breeding objective given the situation that in certain countries lethal disease of coconut destroys millions of coconut palms. Among them, breeding for lethal yellowing disease in the Caribbean and Latin American countries and for root wilt disease in India has been given priority, where these phytoplasma diseases occur and spread.

Nowadays coconut farmers prefer to cultivate short stature palms because of the unavailability of trained pickers or climbers and hence breeding for short stature is also a current breeding objective.

12.7 Breeding Methods and Techniques

The coconut is the sole species of genus *Cocos* and as such present and past breeding work of this crop is limited to the intra-specific level. Furthermore the long generation interval, high heterozygosity, the lack of a reliable method of

vegetative propagation and the limited number of seeds produced per year, all limit the use of many traditional breeding methods employed in other crops. Obtaining a pure line from heterozygous coconut remains an unrealistic expectation because of the long vegetative phase. Thus coconut breeding is confined to mass selection of phenotypically superior parent palms, and to inter-varietal hybridization.

Mass selection is the most fundamental method for coconut breeding (Liyanage 1955). Palms displaying superior agronomic traits such as stout straight trunk with even growth with closely spaced leaf scars, well spread crown with 25–30 healthy fronds, well packed with all stages of inflorescences and developing bunches and palms with short bunch stalks are initially selected from high yielding populations. Then the number of nuts produced per year, average weight of husked nut and tolerance to adverse weather conditions and to pests and diseases of the selected palms are assessed over a period of 3–5 years. Based on these data only the best 5–10% of the palms are selected as seed palms and seeds collected from these palms are distributed as mother palm seeds (Liyanage 1966).

However, as the number of seed nuts collected from mother palms was insufficient to meet the growers demand, a programme called plus palm selection was introduced in Sri Lanka in 1980 which was very much a stop-gap measure to produce a seed that was, in quality, similar to a mother palm seed, but was not exactly so. In adopting this programme, the actual genetic quality of the seed may have been compromised to a degree due to the extent of the seed requirement at that time.

Plus palms are superior palms selected from high yielding blocks of selected estates based on good agronomic features, but quantitative data are assessed just for a single harvest. The plus palms are selected in two stages: (a) Selection of high yielding blocks from suitable estates based on yield figures for the past five consecutive years, and (b) selection of plus palms within the high yielding blocks. The high yielding blocks must satisfy the criteria that the minimum size of the block should be 2 ha, mean block yield should be at least 8,400 nuts/ha/year and the mean yield per palm should be at least 60 nuts/year, the block must have at least 132 bearing palms/ha, the palms must be in the age range of 15–45 years, and the block must be free of pest and diseases. During the selection of plus palms, 100 palms distributed randomly over the block are harvested, and the mean number of nuts/palm of the block is estimated. Then the number of nuts harvested from each palm is recorded and only the palms that record yield above the estimated mean for the block are selected. Palms selected on the above criteria and with satisfactory agronomic characters are then tested for nut weight. Three ripe nuts are taken at random from each palm, husked and weighed, and if the total husked nut weight of 3 nuts is more than 2.1 kg, they are selected as plus palms. The harvesting of nuts of the marked plus palms is done separately to avoid mixing of nuts in handling. The percentage of selection following this method averages to about 20–24%. In order to obtain steady improvement in the quantitative traits it is important to repeat the method

adopted in mother palm selection and plus palm selection to their progenies from generation to generation.

Since the gain from mass selection through open pollination is limited, seed production by artificial cross pollination between high yielding parent palms has been another breeding method in coconut (Liyanage 1954, 1966). Parents are either selected based on phenotype or based on the progeny performance in order to increase the response to selection. However, seed production through this method is limited and therefore setting up of isolated seed gardens was the answer (Liyanage 1961b). In these seed gardens natural assisted pollination occurs between selected elite palms in current mass production of improved coconut seeds. The isolation of the seed garden is achieved either by a forest barrier around the seed garden that is thick enough to prevent pollen arriving from outside (Liyanage 1955) or through 12 or more guard rows of the same coconut variety. The latter is another technique widely practiced currently in the establishment of seed gardens (Liyanage and Azis 1983). This technique was designed after studying the movements of the honey bee, which is also a carrier for the pollination mites.

For inter-varietal hybridization, different crosses between genetically diverse varieties are made using hand pollination. Then the crosses are evaluated in the field in comparison with recommended cultivars as controls, preferably in different agro-ecological zones and in different soil types in order to select new coconut hybrids and hybrids suitable for particular environments or soil types. Once a suitable cross is identified, parent palms are multiplied in a seed garden and seeds are produced by natural controlled pollination. The coconut palm is monoecious and its inflorescence (a compound flower termed a spadix) contains both male and female flowers. The inflorescence protected by a thick sheath is called a spathe. The spathe naturally splits open to expose the emerging inflorescence which consists of a central axis or rachis with up to 40 lateral branches. Each lateral branch is densely set with numerous (200–300) male flowers and fewer (<50) female flowers. The principle of hand pollination focuses on emasculation of the inflorescence followed by isolation of the female flowers by means of a cotton bag (Liyanage 1954). When the female flowers become receptive, selected pollen is artificially introduced. The close supervision of emasculation determines the rate of success and the legitimacy of the hybrid seed nuts.

Since production of seeds by inter-varietal crosses is laborious and time consuming and generates only a very few seeds in relation to the general demand for improved seeds, the isolated seed garden concept is also adopted for production of inter-varietal hybrids. The two parent varieties, usually one tall and one dwarf type or sometimes two tall types are planted in a given proportion based on which variety is emasculated to serve as the maternal parent. The mother parent is then emasculated and the female flowers of this variety are allowed to be pollinated naturally by the other variety. Sometimes only a single variety is planted in the seed garden where pollen collected from another outside parent is blown on to the receptive emasculated inflorescences

of the palms in the seed garden. This method allows to change the hybrids produced within the same seed garden by changing the pollen source.

12.8 Integration of New Biotechnologies in Breeding Programmes

Although conventional coconut breeding programmes using standard breeding techniques based on phenotypic selection have been relatively successful, the inherent constraints in coconut breeding as described previously make the potential use of new biotechnologies highly attractive. Application of molecular genetics in coconut breeding, particularly molecular markers began in the early 1990s and their application in coconut have been diverse, ranging from assessing genetic diversity to creating genetic linkage maps. Initially the studies were aimed at assessment of coconut genetic diversity and genetic relatedness at the DNA level using universal marker techniques such as RAPD (Ashburner et al. 1997b; Duran et al. 1997; Everard 1996; Dasanayake 2003; Dasanayake et al. 2003), RFLP (Lebrun et al. 1998, 1999), AFLP (Perera et al. 1998; Teulat et al. 2000) and ISTR (Duran et al. 1997; Rohde et al. 2000). Later on the need for coconut specific markers was felt and accordingly in 1999 two sets of microsatellite markers were isolated by two groups of scientists independently using the cultivars Sri Lanka Tall (Perera 1999; Perera et al. 1999) and Tagnanan Tall (Rivera et al. 1999). Microsatellites as co-dominant markers have been particularly useful in analyzing highly heterozygous coconut for genetic diversity and genetic relatedness estimates, germplasm characterization and development of collections (Perera et al. 2000, 2001, 2003; Teulat et al. 2000; Dasanayake et al. 2003; Meerow et al. 2003), hybridity testing (Perera et al. 2004), detecting somaclonal variation in coconut tissue cultures, and for construction of genetic linkage maps (Herran et al. 2000; Lebrun et al. 2001; Baudouin et al. 2006). A microsatellite kit comprising 14 primers and an associated software for data analysis has also been developed (Baudouin and Lebrun 2002) standardizing the techniques across laboratories for comparable results, efficient detection of diversity and identification of varieties. More recently DArT markers for coconut have been developed and used for diversity studies (Perera 2005). Among these markers, SSRs have been the most widely and extensively used in analyzing coconut.

12.8.1 Genetic Diversity Analysis

A high level of genetic diversity in coconut has been observed by Perera et al. (2000, 2003) using microsatellites in a collection of 130 coconut individuals representing 51 tall coconut varieties and 49 dwarf coconut varieties sampled across the entire geographic range in the world. The mean genetic diversity values based on Nei's (1987) unbiased statistic observed by Perera (1999) was

0.647 (± 0.139). Perera (1999) also found a reduced number of alleles in dwarf coconut group compared to tall coconut group, comparable with a reduction in the amount of genetic diversity in dwarfs. The results of Rivera et al. (1999), who analyzed 20 coconut varieties, mainly from Southeast Asia and the Pacific and Teulat et al. (2000), who studied 31 individuals of coconut comprising 14 coconut varieties were comparable with those of Perera (1999). Perera (2005) also reported that heterozygous loci were evident not only in cross pollinating talls (30%), but at lower frequency (2.5%) in dwarfs as well. The distribution of genetic diversity between varieties within the tall group was observed to be higher than that within the dwarf group. This finding has since changed the germplasm collection strategies for dwarf and tall groups. The genetic diversity study conducted for coconuts in Sri Lanka (Perera 1999) led to the finding that the genetic base of Sri Lanka coconut is narrow. This has resulted in the change of the breeding strategies of the Sri Lanka coconut breeding programme and led to the importation of exotic coconut varieties and their incorporation in the country's breeding programme. Moreover, these studies identified redundancies in the germplasm collection. Ashburner et al. (1997b) reported the use of RAPDs to study the genetic diversity of 17 distinct South Pacific coconut populations. They observed approximately 60% within population diversity in general and noted two geographically cohesive groups and two single populations in a dendrogram. From the results, they concluded that there had been a low but variable rate of gene migration between South Pacific populations with possible founder effects and subsequent human selection. They proposed that germplasm collection in the South Pacific region should focus on populations rather than individuals because of the highly significant level of variation observed between populations. Perera et al. (2001), who analyzed 33 coconut populations belonging to Sri Lanka Tall variety using SSRs across the island representing different geographical regions concluded that there was no population differentiation (between population variation was only 5%) within Sri Lanka Tall.

12.8.2 Genetic Relatedness

Perera et al. (2003) have constructed a phenetic tree diagram showing the genetic relationships among 51 tall coconut varieties and 49 dwarf coconut varieties across the world. Instantly this phenetic tree divided all tall coconuts into two main groups, the first group comprising all the tall varieties from Southeast Asia, the Pacific and the west coast of Panama and all dwarfs in a sub-cluster within the tall cluster. The second group consisted of talls from South Asia, East Africa and West Africa. Interestingly, none of the dwarf coconuts grouped with the second main tall group. The results of Teulat et al. (2000), based on cluster analysis according to UPGMA using the similarity matrix based on the proportion of shared alleles, confirmed those of Perera

(1999). Results on genetic relationships based on microsatellite markers generally agree with the results using other molecular techniques such as ISTR markers (Rohde et al. 1995) or RFLP markers (Lebrun et al. 1998). Rohde et al. (1995) studied 17 different coconut varieties from different geographical regions and identified groupings of African coconut with Indian Ocean coconuts and Panama Tall coconut from the west coast of Panama with Pacific and Southeast Asian coconuts. Lebrun et al. (1998) reported the use of RFLPs in coconut from various geographical regions. Lebrun and co-workers studied nine cDNA clones and one mitochondrial DNA (mtDNA) clone (*CoxI*) from rice and one ribosomal DNA (rDNA) clone from wheat that were hybridized to genomic DNA from 100 individuals of coconut palms representing 10 tall and 7 dwarf coconut varieties. Two main groups of coconuts were identified, one comprising varieties from the Far East and the Pacific and the other comprising varieties from India, Sri Lanka and West Africa. Higher levels of diversity in Far East and Pacific coconut varieties were observed compared with the other material. Clustering of Panama Tall originating from the Pacific Coast of Panama with coconuts originating from the Pacific and the clustering of West African tall with coconuts originating from the South Asia and Indian Ocean group were also observed. These results were in good agreement with the theory of Harries (1978) on the evolution and dissemination of coconuts. Results from all these studies finally led to the conclusion that *Cocos nucifera* is divided into two large genetic groups, the Southeast Asia and Pacific group and the Indo-Atlantic group.

According to Harries (1978) naturally evolved coconuts, characterized as Niu Kafa type, predominate in South Asia, West and East Africa, the Caribbean and the Atlantic coast of Central America while coconuts selected under cultivation, characterized as Niu Vai type, predominate in Southeast Asia, some Pacific islands and the west coast of Central America. It is generally accepted that the coconut palm has existed on the Atlantic coast of Africa, South America and around the Caribbean region for only about 500 years (Child 1974; Purseglove 1972), and that there is a great similarity between these coconuts and those coconuts in East Africa, India and Sri Lanka (Harries 1978). The grouping of Mozambique Tall, which Harries (1977) suggested as the main original source of coconuts to West Africa and to the Atlantic coast of America, with Cameroon Kribi Tall, West African Tall, Sri Lankan Tall and Andaman Ordinary Tall from the Indian Ocean, appears in a single cluster in the phenetic tree of Perera et al. (1999, 2003) and others (Teulat et al. 2000) thus supporting the validity of Harries's (1977) theory of Portuguese-assisted coconut germplasm dissemination from the Indian Ocean to the Atlantic after 1499. Interestingly, the variety Comoro Tall, from East Africa falls in with the Southeast Asia/Pacific main tall group and it seems that this variety originated from Southeast Asia coconuts, the Niu Vai type. Lebrun et al. (1998) noted that the variety Comoro Tall took an intermediate position between Southeast Asian coconut populations and the Indian Ocean populations, based on RFLP markers. The Thailand Tall varieties, Thai Tall,

Pak Chok, Talai Roi mainly group with the South Asia/Africa Tall group while Kalok variety groups with the Southeast Asia/Pacific tall group. The results of a detailed study on varieties of coconuts in Thailand by Harries et al. (1982) based on fruit component analysis of coconut suggested that both Niu Kafa type and Niu Vai type of coconuts are present in Thailand, with the Niu Kafa type present on the Indian Ocean coast of the country. Harries included the variety Kalok with other large fruited forms such as varieties San Ramon and Tagnanan Tall in the Philippines, Bali Tall in Indonesia, Rennell Tall in the Solomon Islands and Panama Tall and Peru Tall from the Pacific coast of America. He also suggests that variety Malayan Tall probably shares common ancestry with variety Kalok. In contrast, he further observed that variety Pak Chok could be compared with other talls that have Niu Kafa type characteristics, for example the talls from Sri Lanka, India, Mozambique, West Africa, and the Caribbean and Atlantic coasts of America. Rattanapruk (1970) also stated that the variety Pak Chok found growing along the coast of Indian Ocean resembles coconut from Sri Lanka. Interestingly, the variety ecotype Kalok in Perera et al. (1999, 2003) is grouped with varieties San Ramon Tall, Tagnanan Tall, Bali Tall, Rennell Tall and Malayan Tall in the Southeast Asia/Pacific group of coconuts. Similarly, the variety Pak Chok is grouped with those from Sri Lanka, Andaman Islands in the Indian Ocean and Mozambique.

The grouping of Panama Tall (varieties Panama Manarge and Panama Aguadulce, both from the Pacific coast of Panama) with Southeast Asian and Pacific talls is in agreement with Whitehead's (1976) observation of an eastward movement of coconuts from Southeast Asia to the Pacific region and subsequently from there to the Pacific coast of America. These results are largely in agreement with the results from ISTR analysis (Rohde et al. 1995), which grouped Panama Tall with Polynesian varieties/populations of coconuts. Results of all these studies finally support the conclusion that *Cocos nucifera* is divided into two large genetic groups, the Southeast Asia and Pacific group and the Indo-Atlantic group.

The grouping of all dwarf forms from different geographical regions in a single cluster within the main South Asia and Pacific group and the Niu Vai type of coconuts and the loss of allelic richness observed in dwarfs suggest that dwarfs have a common origin and evolved from the Southeast Asia/Pacific group of talls in the Southeast Asia/Pacific region. The results of Teulat et al. (2000) strongly support a common origin of dwarf varieties.

Attempts to investigate the genetic lineages in coconuts using three coconut specific chloroplast microsatellite primers developed by sequencing and isolating mononucleotide microsatellite motifs observed in the PCR amplified chloroplast regions of intergenic spacers between *trnT* and *trnL*, *trnS* and *trnT*, and *trnC* and *trnD*, on a set of 130 coconut genotypes from all over the world, failed to show any chloroplast variation, thus indicating a very close ancestral relationship between coconut groups (Perera 1999, 2002).

12.8.3 Hybridity Testing and Variety Identification

Perera et al. (2004) reported the successful use of microsatellite markers to uniquely identify seed parents in the Sri Lanka coconut breeding programme and the resulting hybrids. This is very important for confirming the identity of varieties and their hybrids in the most likely events of mixing of seed-nut lots, mislabeling of seeds in nurseries and checking the legitimacy of hybrid seedlings. Two SSR primers have exhibited the potential for distinguishing between coconut varieties Sri Lanka Tall, Sri Lanka Green Dwarf and Sri Lanka Yellow Dwarf used as parents in Sri Lanka. This has led to the unique capability of conformity and hybridity testing of two commercially grown coconut hybrids, Sri Lanka Green Dwarf \times Sri Lanka Tall and Sri Lanka Yellow Dwarf \times Sri Lanka Tall. Similarly Bandaranayake et al. (2005) have developed markers specific to the San Ramon variety for identification of uncontaminated materials for multiplication in a seed garden.

12.8.4 Somoclonal Variation in Coconut Plants

Application of microsatellite markers to study any possible somaclonal variation in a limited number of clonal plants of coconut regenerated from various explants through somatic embryogenesis and their successful field planting in Sri Lanka have been reported by Fernando et al. (2004). The microsatellite markers have confirmed the absence of genetic variants among plants within clones (Fernando et al. 2004).

12.8.5 Linkage Mapping and QTL Identification

Studies on coconut genome mapping have commenced only recently. The first genome map for coconut was developed for an East African Tall \times Laguna Tall F_1 population based on ISTR markers (Rohde et al. 1999). This work was extended with a mapping population developed in the Philippines from a cross between Malayan Yellow Dwarf \times Laguna Tall using AFLP, ISTR, RAPD and ISSR markers. Three hundred and eighty two markers have been placed in the map resulting in 16 linkage groups and leading to the identification of six QTLs for early germination (Herran et al. 2000). Genetic correlations have been established between early germination and early flowering, and early germination and high yield. Thus, this has become the first report of the opportunity for marker assisted selection in coconut. Further, QTL for other traits such as leaf production, girth and height have also been identified for the same mapping population (Ritter et al. 2000). In addition to this, another mapping population in Ivory Coast derived from Cameroon Red Dwarfs and Rennell Island Tall has been used to map 280 markers on 16 linkage groups resulting in several QTLs

related to nut number, number of bunches and traits related to fruit components (Lebrun et al. 2001; Baudouin et al. 2006).

The size of the mapping population and selection of parents for the maximum segregation of traits are critical when producing a genome map of any crop (Bandaranayake and Kearsley 2005). The size of the mapping population is particularly a crucial issue in coconut because obtaining a reasonable number of seed nuts from a particular cross is a difficult task as a result of very low seed production in coconut, i.e. about 100 seed nuts per palm per year. From a simulation study, Bandaranayake (2006) concluded that about 400 individuals represent an effective size of a mapping population in coconut for a consistent map resolution. However both linkage maps described in Herran et al. (2000) and Lebrun et al. (2001) were based on the genotypic and phenotypic scores of less than 65 individuals in their mapping populations. The size of these mapping populations thus would not be sufficient for constructing a reliable map because any mapping population with less than 100 meioses is unlikely to be useful for generating a map (Young 1994). Furthermore, genetic relationship studies in coconut as described above suggests that maximum segregation of traits in coconut can only be obtained by crossing varieties of Southeast Asia and the Pacific group with those from Indo-Atlantic group. However, all the mapping populations mentioned were composed of parents belonging to one genetic group, the Southeast Asia and Pacific group. As a result, about 84% of DNA fragments generated in the Malayan Yellow Dwarf \times Laguna Tall mapping population were non-polymorphic indicating that the two parents share identical alleles at a large number of loci.

Based on the experience and the information already generated, a large mapping population has now been created in Sri Lanka comprising 350 individuals arising from a cross between Sri Lanka Red Dwarf (Southeast Asia and Pacific group) and Sri Lanka Tall (Indo-Atlantic group) to obtain maximum segregation of traits and sufficient number of meioses to analyze. Another mapping population, particularly for segregating for tolerance to *Aceria* mite, is being constructed in Sri Lanka between tolerant Sri Lanka Yellow Dwarf and a highly susceptible Sri Lanka Tall palm (Perera 2006). Generation of new mapping populations including phytoplasma-resistant breeding material is being focused in Jamaica (unpublished).

12.8.6 Synteny Studies

Efforts are being undertaken to investigate the possible synteny of the oil palm and coconut genomes as both palm species are diploid and have the same chromosome number, $2n = 32$ (unpublished). Synteny would possibly speed up research by increasing the marker density on the respective linkage maps through the exchange of DNA markers.

12.8.7 In Vitro Culture

Coconut tissue culture has a long history dating back to the 1970s. Since then the problem of cloning coconut has been addressed in a number of research centers worldwide. Initial attempts were on reversion of floral meristem into vegetative growth but later on, most efforts were concentrated on somatic embryogenesis. During the past decade, the in vitro plant regeneration protocol has been improved, and a limited number of clonal plantlets obtained mainly from zygotic tissues has been produced in a few laboratories (Chan et al. 1998; Verdeil et al. 1999; Fernando et al. 2003). However, success is very limited due to numerous constraints. The regeneration efficiency is far from adequate though a small number of vegetatively propagated coconut palms have been established in the field. Due to very poor response of coconut tissues to in vitro conditions it is classified as one of the most recalcitrant species to regenerate in vitro (George and Sherrington 1984).

12.9 Seed Production

Many farmers still practice selection of their own mother palms for obtaining seed nuts for planting, thus selection of palms is based on farmer's long term observations on the performance of each palm. However, in many countries, improved seeds are produced by government and/or private sector organizations and seedlings raised are sold to farmers. When improved seeds need to be produced on a large scale they are produced in isolated seed gardens. In the case of hybrid seeds, the mother trees are planted in isolated seed gardens and daily emasculation of inflorescences is carried out by removing the upper part of each spikelet that carries male flowers. The remaining female flowers receive pollen by natural means, from male parents inter-planted at low ratio within the seed garden, or artificially from pollination labourers visiting each receptive palm, either by using pole-mounted pollen blowers or by using ladders and hand-pollinating each female flower with small brushes. When improved seeds are produced from mass selected high yielding palms or from paired crosses between selected trees, these are planted in the seed garden and allowed to naturally inter-pollinate. The second generation seeds obtained this way are then distributed to farmers for planting. However, production of improved seed often does not meet the demand from farmers, and hence the balance seed nut requirement is obtained from superior mother palms selected in high yielding blocks from high yielding estates. Seed from those trees results from open pollination.

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References

- Ashburner, G.R., Thompson, W.K., Halloran, G.M. and Foale, M.A. (1997a) Fruit component analysis of south Pacific coconut palm populations. *Genet. Resour. Crop Evol.* 44, 327–355.
- Ashburner, G.R., Thompson, W.K. and Halloran, G.M. (1997b) RAPD analysis of South Pacific coconut palm populations. *Crop Sci.* 37, 992–997.
- Asian and Pacific Coconut Community (Ed.). (1997) *Coconut Statistical Yearbook*. Asian and Pacific Coconut Community, Jakarta.
- Bandaranayake, C.K. (2006) An effective population size for reliable map resolution of Coconut (*Cocos nucifera* L.). *CORD* 22(2), 33–40.
- Bandaranayake, C.K., Fernando, W.B.S., Fernando, A. and Herath, N. (2005) DNA fingerprinting to distinguish the coconut type San Ramon. *CORD* 21(2), 30–36.
- Bandaranayake, C.K. and Kearsey, M.J. (2005) Genome mapping, QTL analysis and MAS: Importance, principle, constraints and application in coconut. *Int. Plant Genetic Resour. Newslett.* 142, 47–54.
- Batugal, P. (2005) Performance of coconut hybrids in some countries of Asia, Africa and Latin America. In: P. Batugal, V. Ramanatha Rao and J. Oliver (Eds.) *Coconut Genetic Resources*. IPGRI, Rome, pp. 302–308.
- Batugal, P., Ramanatha Rao, V. and Oliver J. (Eds.). (2005) *Coconut Genetic Resources*. IPGRI, Rome.
- Baudouin, L. and Lebrun, P. (2002) The development of a microsatellite kit and dedicated software use with coconuts. *Burotrop Bull.* 17, 16–20.
- Baudouin, L., Lebrun, P., Konan, J.L., Ritter, E., Berger, A. and Billottee, N. (2006) QTL analysis of fruit components in the progeny of a Rennell Island Tall coconut (*Cocos nucifera* L.) individual. *Theor. Appl. Genet.* 112, 258–268.
- Bawalan, D.D. and Chapman K.R. (2006) *Virgin Coconut Oil; Production Manual for Macro- and Village-Scale Processing*. FAO, Thammada Press, Bangkok.
- Benbadis, B.K. (1992) Coconut and date palm. In: F.A. Hammerschlag and R.W. Litz (Eds.) *Biotechnology of Perennial Fruit Crops*. CAB International, Wallingford, pp. 383–400.
- Bourdeix, R. (1988) Effectiveness of mass selection on the yield component of coconut. *Oleagineux* 43, 283–295.
- Bourdeix, R., Konan, J.L. and N'Cho, Y.P. (2005b) *Coconut, a Guide to Traditional and Improved Varieties*. Editions Diversiflora, Montpellier.
- Bourdeix, R., N'Cho, Y.P. and Le Saint, J.P. (1990) A coconut (*Cocos nucifera* L.) selection strategy I. Rundown of achievements. *Oleagineux* 45, 359–371.
- Bourdeix, R., Santos, G., Labouisse, J.P. and Baudouin, L. (2005a) Useful definition of terms and nomenclature. In: P. Batugal, V. Ramanatha Rao and J. Oliver (Eds.) *Coconut Genetic Resources*. IPGRI, Rome, pp. 9–10.
- Buckley, R. and Harries, H.C. (1984) Self-sown, wild type coconuts from Australia. *Biotropica* 16, 148–151.
- Burkill, I.H. (1966) *A Dictionary of the Economic Products of the Malay Peninsula*. Ministry of Agriculture and Co-operatives, Kuala Lumpur.
- Carandang, E.V. (2002) Makapuno embryo culture: The Philippine Coconut Research and Development Foundation experience. In: F. Engelmann, P. Batugal and J.T. Oliver (Eds.) *Coconut Embryo In Vitro Culture, Part II*. IPGRI-APO, Serdang, Malaysia, pp. 157–162.
- Chan, J.L., Saenz, L., Talavera, C., Hornung, R., Robert, M. and Oropeza, C. (1998) Regeneration of coconut (*Cocos nucifera* L.) from plumule explants through somatic embryogenesis. *Plant Cell Rep.* 17, 515–521.
- Child, R. (1964) *Coconuts*. Longman, London.
- Child, R. (1974) *Coconuts*. 2nd Ed., Longman, London.
- Chioyenda, E. (1921) La culla del cocco. *Webbia* 5, 199–294, 359–449.

- Cook, O.F. (1910) History of the coconut palm in America. Contribution to US National Herbarium 14, 271–342. Cited in: Bruman, H.J. (1944) Some observations on the early history of the coconut culture in the New World. *Acta Americana* 2, 220–243.
- Dasanayake, P.N. (2003) *Use of Molecular Markers for Enhancing the Coconut Breeding Strategy*. Ph.D. Thesis, University of Sri Jayewardenepura, Sri Lanka.
- Dasanayake, P.N., Everard, J.M.D.T., Karunanayake, E.H. and Nandadasa, H.G. (2003) Characterization of coconut germplasm by microsatellite markers. *Trop. Agr. Res.* 15, 51–61.
- Dennis, J.V. and Gunn, C.R. (1971) Case against trans-Pacific dispersal of the coconut by ocean currents. *Econ. Bot.* 25, 407–413.
- Duran, Y., Rohde, W., Kullaya, A., Goikoetxea, P. and Ritter E. (1997) Molecular analysis of east African Tall coconut genotypes by DNA marker technology. *J. Genet. Breed.* 51, 279–288.
- Everard, J.M.D.T. (1996) *Use of Molecular Markers for Breeding of the Coconut Palm* (*Cocos nucifera* L.). M.Sc. Thesis, University of New England, Armidale, Australia.
- Everard, J.M.D.T. (2002) Report of the Genetics and Plant Breeding Division. *Annual Report of the Coconut Research Institute of Sri Lanka*, Lunuwila.
- Fernando, S.C., Verdeil, J.L., Hocher, V., Weerakoon, L.K. and Hirimburegama, K. (2003) Histological analysis of plant regeneration from plumule explants of *Cocos nucifera*. *Plant Cell Tiss. Org. Cult.* 72, 281–284.
- Fernando, S.C., Weerakoon, L.K., Perera, P.I.P., Banupriya, H.D.D., Ambagala, E., Gamage, C.K.A., Santha, E.S., Gunathilake, T.R. and Perera, L. (2004) Genetic fidelity and *ex vitro* performance of tissue cultured coconut plants. In: T.S.G. Peiris and C.S. Ranasinghe (Eds.) *Proceedings of the International Conference to Mark the 75th Anniversary of Coconut Research Institute, Sri Lanka, Part II*. Ceylon Printers, Colombo, pp. 47–57.
- Foale, M.A. (1991) Coconut genetic diversity: present knowledge and future research needs. In: *Papers of the IBPGR Workshop on Coconut Genetic Resources held in Cipanas, Indonesia, 8–11 October 1999*. IBPGR, Rome, pp. 46–53.
- Fremont, Y., Ziller, R. and de Nuce de Lamothe, M. (1966) *Le cocotier*. Maisonneuve and Larose, Paris.
- Gangolly, S.R., Satyabalan, K. and Pandalai, K.M. (1957) Varieties of coconut. *Ind. Cocon. J.* X, 3–28.
- George, E.F. and Sherrington, P.D. (1984) *Plant Propagation by Tissue Culture: Handbook and Directory of Commercial Laboratories*. Exegenetics Eversley, Busingstoke, London.
- Gruezo, W.S. and Harries, H.C. (1984) Self-sown, wild-type coconuts in the Philippines. *Biotropica* 16, 140–147.
- Gunn, B.F. (2004) The phylogeny of the Cocoeae (Arecaceae) with emphasis on *Cocos nucifera*. *Ann. Missouri Bot. Garden* 91, 505–522.
- Guppy, H.B. (1906) *Observation of a Naturalist in the Pacific between 1896 and 1899*. Macmillan, London.
- Hamelin, C., Bourdeix, R. and Baudouin, L. (2005) The international coconut genetic resources database. In: P. Batugal, V. Ramanatha Rao and J. Oliver (Eds.) *Coconut Genetic Resources*. IPGRI, Rome, pp. 282–301.
- Harland, S.C. (1957) *The Improvement of the Coconut Palm by Breeding and Selection*. Bulletin 15, Coconut Research Institute, Ceylon.
- Harries, H.C. (1977) The Cape Verde region (1499 to 1549); the key to coconut culture in the Western hemisphere? *Turrialba* 27, 227–231.
- Harries, H.C. (1978) The evolution, dissemination and classification of *Cocos nucifera* L. *Bot. Rev.* 44, 205–317.
- Harries, H.C. (1990) Malesian origin for a domestic *Cocos nucifera* L. In: P. Baas, K. Kalkman and R. Geesink (Eds.) *The Plant Diversity of Malesia*. Kluwer, Dordrecht, pp. 351–357.

- Harries, H.C. (1995) Coconut (*Cocos nucifera* L.). In: J. Smartt J. and N.W. Simmonds (Eds.) *Evolution of Crop Plants*. 2nd Ed., Longman, London, pp. 389–394.
- Harries, H.C. (2002) The “Niu” Indies: Long lost “home” of the coconut. *Palms* 46(2), 97–100.
- Harries, H.C. and Romney, D.H. (1974) Maypan: An F₁ hybrid coconut variety for commercial production in Jamaica. *World Crops* 26, 110–111.
- Harries, H.C., Thirakul, A. and Rattanapruk, V. (1982) The coconut genetic resources of Thailand. *Thai J. Agric. Sci.* 15, 141–156.
- Herran, A., Estioko, L., Becker, D., Rodriguez, M.J.B., Rohde, W. and Ritter, E. (2000) Linkage mapping and QTL analysis in coconut (*Cocos nucifera* L.). *Theor. Appl. Genet.* 101, 292–300.
- Jones, L.H. (1991) Perennial vegetable oil crops. In: G.J. Persely (Ed.) *Agricultural Biotechnology: Opportunities for International Developments*. CAB International, Wallingford, pp. 213–224.
- Krain, E., Issa, J.A., Kullaya, A. and Harries H.C. (1993) The coconut palm in East Africa, 2. The Pemba Dwarf in Zanzibar. *Palm Enthusiast* 10(1), 9–15.
- Leach, B., Foale, M.A. and Ashburner, R. (2003) Some characteristics of wild and managed coconut palm populations and their environment in the Cocos (Keeling) Islands, Indian Ocean. *Genet. Resour. Crop Evol.* 50, 627–638.
- Lebrun, P., Baudouin, L., Bourdeix, R., Konan, J.L., Barker, J.H.A., Aldam, C., Herran, A. and Ritter, E. (2001) Construction of a linkage map of the Rennell Island Tall coconut type (*Cocos nucifera* L.) and QTL analysis for yield characters. *Genome* 44, 962–970.
- Lebrun, P., N’Cho, Y.P., Bourdeix, R. and Baudouin, L. (1999) Le cocotier. In: P. Hamon, M. Seguin, X. Perrier and J.C. Glaszmann (Eds.) *Diversité Génétique des Plantes Cultivées*. CIRAD, Montpellier, pp. 219–240.
- Lebrun, P., N’Cho, Y.P., Seguin, M., Grivet, L. and Baudouin, L. (1998) Genetic diversity in coconut (*Cocos nucifera* L.) revealed by restriction fragment length polymorphism (RFLP) markers. *Euphytica* 101, 103–108.
- Liyanage, D.V. (1954) Controlled pollination of coconut palms. *Ceylon Cocon. Quart.* 5, 135–138.
- Liyanage, D.V. (1955) Planting materials for coconut. *Ceylon Cocon. Quart.* 6, 75–80.
- Liyanage, D.V. (1958) Varieties and forms of coconut palms grown in Ceylon. *Ceylon Cocon. Quart.* 9, 1–10.
- Liyanage, D.V. (1961a) Report of the Genetics and Plant Breeding Division. *Annual Report of the Coconut Research Institute of Sri Lanka*, Lunuwila.
- Liyanage, D.V. (1961b) The use of isolated seed gardens for coconut seed production. *Ceylon Cocon. Quart.* 12, 121–124.
- Liyanage, D.V. (1966) Planting materials in coconut. *Ceylon Cocon. Planters’ Rev.* 4(2), 27–29.
- Liyanage, D.V. (1972) Production of improved coconut seeds by hybridization. *Oleagineux* 27, 597–599.
- Liyanage, D.V. and Abeywardena, V. (1957) Correlation between seed nut, seedlings and adult palm characters in coconut. *Trop. Agric. (Trinidad)* 113, 326–340.
- Liyanage, D.V. and Azis, H. (1983) A new technique for establishing coconut seed gardens. *Cocos* 1, 1–6.
- Liyanage, D.V. and Sakai, K.I. (1960) Heritabilities of certain yield characters of the coconut palm. *J. Genet.* 57, 245–252.
- Liyanage, D.V., Wickramaratne, M.R.T. and Jayasekera, C. (1988) Coconut breeding in Sri Lanka. *Cocos* 6, 1–26.
- Mahabale, T.S. (1976) The origin of coconut. *The Palaeobotanist* 25, 238–248. Cited in: Harries, H.C. (1995) Coconut (*Cocos nucifera* L.). In: J. Smartt J. and N.W. Simmonds (Eds.) *Evolution of Crop Plants*. 2nd Ed., Longman, London, pp. 389–394.
- Manthiriratne, M.A.P. (1971) Some results of field experimentation with *typica* x *nana* F₁ hybrids. *Ceylon Coconut Quarterly* 22, 107–113.

- Manthiriratne, M.A.P. (1972) The performance of dwarfs (*Cocos nucifera* L. variety nana) as a plantation crop in Ceylon. *Ceylon Cocon. Quart.* 23, 92–99.
- Manthiriratne, M.A.P. (1978) Report of the Genetics and Plant Breeding Division. *Annual Report of the Coconut Research Institute of Sri Lanka*, Lunuwila.
- Marechal, H. (1928) Observations and preliminary experiments on the coconut with a view to developing improved seednuts for Fiji. *Agric. J. Fiji* 1, 16–45.
- Marikkar, J.M.N., Jayasundara, J.M.M.A., Prasadika, S.A.H., Jayasingha, C.V.L. and Premakumara, G.A.S. (2007) Assessment of stability of virgin coconut oil during deep frying. *CORD* 23(1), 62–70.
- Meerow, A.W. and Ayala-Silva, T. (2006) Building a better coconut. *Ornamental Outlook* 15(2), 22–24.
- Meerow, A.W., Wissler, R.J., Brown, J.S., Kuhn, D.N., Schnell, R.J. and Broschat, T.K. (2003) Analysis of genetic diversity and population structure within Florida coconut (*Cocos nucifera* L.) germplasm using microsatellite DNA, with special emphasis on the Fiji Dwarf cultivar. *Theor. Appl. Genet.* 106, 715–726.
- Menon, K.P.V. and Pandalai, K.M. (1958) *The Coconut, A Monograph*. Indian Central Coconut Committee, Ernakulam Publishers, India.
- Narayana, G.V. and John, C.M. (1949) Varieties and forms of coconut. *Madras Agric. J.* 36, 349–366.
- Nei, M. (1987) *Molecular Evolutionary Genetics*. Columbia University Press, New York.
- Ohler, J.G. (1984) *Coconut, Tree of Life*. Plant Production and Protection Paper 57, Food and Agricultural Organisation of the United Nations, Rome.
- Oropeza, C., Rillo, E., Hoche, V. and Verdeil, J.L. (2005) Coconut micro propagation. In: P. Batugal, V. Ramanatha Rao and J. Oliver (Eds.) *Coconut Genetic Resources*. IPGRI, Rome, pp. 334–348.
- Perera, L. (1999) *Assessing Genetic Diversity in Coconut using Molecular Markers*. Ph.D Thesis, University of Dundee, Scotland.
- Perera, L. (2002) Chloroplast DNA variation of coconut is opposite to its nuclear DNA variation. *CORD* 18(2), 56–73.
- Perera, L. (2005) Report of the Genetics and Plant Breeding Division. *Annual Report of the Coconut Research Institute of Sri Lanka*, Lunuwila.
- Perera, L. (2006) Report of the Genetics and Plant Breeding Division. *Annual Report of the Coconut Research Institute of Sri Lanka*, Lunuwila.
- Perera, L., Fernando, W.B.S.F., Hearth, N., Fernando, A., Russell, J., Provan, J. and Powell, W. (2004) Use of microsatellite DNA markers for population analysis, variety identification and for hybridity testing of coconut in Sri Lanka. In: T.S.G. Peiris and C.S. Ranasinghe (Eds.) *Proceedings of the International Conference to Mark the 75th Anniversary of Coconut Research Institute, Sri Lanka, Part II*. Ceylon Printers, Colombo, pp. 3–15.
- Perera, L., Russell, J.R., Provan, J., McNicol, J.W. and Powell, W. (1998) Evaluating genetic relationships between indigenous coconut (*Cocos nucifera* L.) accessions from Sri Lanka by means of AFLP profiling. *Theor. Appl. Genet.* 96, 545–550.
- Perera, L., Russell, J.R., Provan, J. and Powell, W. (1999) Identification and characterization of microsatellites in coconut (*Cocos nucifera* L.) and the analysis of coconut populations in Sri Lanka. *Mol. Ecol.* 8, 344–346.
- Perera, L., Russell, J.R., Provan, J. and Powell, W. (2000) Use of microsatellite DNA markers to investigate the level of genetic diversity and population genetic structure of coconut (*Cocos nucifera* L.). *Genome* 43, 15–21.
- Perera, L., Russell, J.R., Provan, J. and Powell, W. (2001) Levels and distribution of genetic diversity of coconut (*Cocos nucifera* L., var. *Typica* form *typica*) from Sri Lanka assessed by microsatellite markers. *Euphytica* 122, 381–389.
- Perera, L., Russell, J.R., Provan, J. and Powell, W. (2003) Studying genetic relationships among coconut varieties/populations using microsatellite markers. *Euphytica* 132, 121–123.

- Powell, T. (1868) On various Samoan plants and their vernacular names. *J. Bot. (London)* 6, 278–285, 242–347, 255–370. Cited in: Harries, H.C. (1978) The evolution, dissemination and classification of *Cocos nucifera* L. *Bot. Rev.* 44, 205–317.
- Purseglove, J.W. (1965) The spread of tropical crops. In: H.G. Baker and G.L. Stebbins (Eds.) *The Genetics of Colonizing Species*. Academic Press, New York, pp. 337–389.
- Purseglove, J.W. (1968) *Tropical Crops: Dicotyledons*. 2nd Ed., Longman, London.
- Purseglove, J.W. (1972) *Tropical Crops: Monocotyledons*. Longman, London.
- Purseglove, J.W. (1985) *Tropical Crops: Monocotyledons*. 5th Ed., Longman, London.
- Rajagopal, V., Kasturi Bai, K.V. and Kumar, N. (2005) Breeding for drought tolerance in coconut. In: P. Batugal, V. Ramanatha Rao and J. Oliver (Eds.) *Coconut Genetic Resources*. IPGRI, Rome, pp. 282–301.
- Rattanaprak, V. (1970) Thailand. In: FAO (Ed.) *Yearly Progress Report on Coconut Breeding*. FAO, Rome, pp. 31–33.
- Raveendranath, T.G. and Ninan, C.A. (1974) A study of the somatic chromosome complements of tall and dwarf coconuts. *J. Plant. Crops* 1, 17–22.
- Ridley, H.N. (1930) *The Dispersal of Plants throughout the World*. Reeves, London.
- Rillo, E.P. (2004) The successful mass production of the Makapuno coconut by embryo culture in the Philippines. In: T.S.G. Peiris and C.S. Ranasinghe (Eds.) *Proceedings of the International Conference to Mark the 75th Anniversary of Coconut Research Institute, Sri Lanka. Part II*. Ceylon Printers, Colombo, pp. 16–30.
- Ritter, E., Rodriguez, M.J.B., Herran, A., Estioko, L., Becker, D. and Rohde, W. (2000) Analysis of quantitative trait loci (QTL) based on linkage maps in coconut (*Cocos nucifera* L.). In: A. Arencibia (Ed.) *Plant Genetic Engineering towards the Third Millennium*. Elsevier, Amsterdam, pp. 42–48.
- Rivera, R., Edwards, K.J., Barker, J.H.A., Arnold, G.M., Ayad, G., Hodgkin, T. and Karp, A. (1999) Isolation and characterization of polymorphic microsatellites in *Cocos nucifera* L. *Genome* 42, 668–675.
- Rohde, W., Becker, D., Kullaya, A., Rodriguez, M.J.B., Herran, A. and Ritter, E. (1999) Analysis of coconut germplasm biodiversity by DNA marker technologies and construction of a first genetic linkage map. In: C. Oropeza, J.L. Verdeil, G.R. Ashburner, R. Cardena and J.M. Santamaria (Eds.) *Current Advances in Coconut Biotechnology*. Kluwer, Dordrecht, pp. 99–120.
- Rohde, W., Herran, A., Estioko, L., Sinje, S., Becker, D., Kullaya, A., Rodriguez, M.J.B. and Ritter, E. (2000) Mapping of DNA markers, homeotic genes and QTLs in coconut (*Cocos nucifera* L.) and synteny studies with oil palm. *Proceedings of the International Symposium on Oil Palm Genetic Resources and Utilization*. Kuala Lumpur, Malaysia, pp. AC1–AC21.
- Rohde, W., Kullaya, A., Rodriguez, J. and Ritter, E. (1995) Genome analysis of *Cocos nucifera* L. by PCR amplification of spacer sequences separating a subset of *copia*-like 16RI repetitive elements. *J. Genet. Breed.* 49, 179–186.
- Schuiling, M. and Harries, H.C. (1992) The coconut palm in East Africa 1. East African Tall. *Palm Enthusiast* 9(3), 22–35.
- Swaminathan, M.S. and Nambiar, M.C. (1961) Cytology and origin of the dwarf palm. *Nature* 192, 85–86.
- Teulat, B., Aldam, C., Trehin, R., Lebrun, L., Barker, G.M., Karp, A., Baudouin, L. and Rognon, F. (2000) An analysis of genetic diversity in coconut (*Cocos nucifera*) populations from across the geographic range using sequence-tagged microsatellites (SSRs) and AFLPs. *Theor. Appl. Genet.* 100, 764–771.
- Vargas, A. and Blanco, F.A. (2000) Fruit characterization of *Cocos nucifera* L. (Arecaceae) cultivars from the Pacific coast of Costa Rica and the Philippines. *Genet. Resour. Crop Evol.* 47, 483–487.
- Verdeil, J.L., Hornung, R., Jacobsen, H.J., Rillo, E., Oropeza, C., Bourdeix, R., N'Cho, Y.P., Hoher, V., Hamon, S. and Sangare, A. (1999) Recent progress on coconut micropropagation through a joined effort involving different countries. In: C. Oropeza, J.L. Verdeil,

- G.R. Ashburner, R. Cardena and J.M. Santamaria (Eds.) *Current Advances in Coconut Biotechnology*. Kluwer, Dordrecht, pp. 391–405.
- Whitehead, R.A. (1966) *Survey and Collection of Coconut Germplasm in the Pacific Islands*. Her Majesty's Stationery Office, London.
- Whitehead, R.A. (1976) Coconut. In: N.W. Simmonds (Ed.) *Evolution of Crop Plants*. Longman, London, pp. 221–225.
- Wickramaratne, M.R.T. (1987a) Breeding coconut for adaptation to drought. *Cocon. Bull.* 4, 16–23.
- Wickramaratne, M.R.T. (1987b) Report of the Genetics and Plant Breeding Division. *Annual Report of the Coconut Research Institute*, Lunuwila, pp. 51–107.
- Young, N.D. (1994) Constructing a plant genetic linkage map with DNA markers. In: R.L. Phillips and I.K. Vasil (Eds.) *DNA Based Markers in Plants*. Kluwer, Dordrecht, pp. 39–57.
- Zizumbo-Villarreal, D., Fernández-Barrera, M., Torres-Hernández, N. and Cardena, R. (1999) Lethal yellowing resistance in coconut germplasm from Mexico. In: C. Oropeza, J.L. Verdeil, G.R. Ashburner, R. Cardena and J.M. Santamaria (Eds.) *Current Advances in Coconut Biotechnology*. Kluwer, Dordrecht, pp. 183–196.
- Zizumbo-Villarreal, D. (1996) History of coconut (*Cocos nucifera* L.) in Mexico: 1539–1810. *Genet. Resour. Crop Evol.* 43, 505–515.
- Zizumbo-Villarreal, D., Fernández-Barrera, M., Torres-Hernández, N. and Colunga-García-Marín, P. (2005) Morphological variation of fruit in Mexican populations of *Cocos nucifera* L. (Arecaceae) under *in situ* and *ex situ* conditions. *Genet. Resour. Crop Evol.* 52, 421–434.