

Chapter 9

Physiology and Biochemistry



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Abstract Coconut palms are grown in diverse environments in different tropical regions of the world. Palms experience several cycles of different stresses during their life period and respond to external factors at morphological, anatomical, physiological, biochemical and molecular levels. Significant developments are made in unravelling the physiological and biochemical mechanisms underlying the productivity performance of coconut in various agroclimatic conditions. Delineating the seedling and adult palm growth, dry matter partitioning, compositional changes in developing nuts, oil and fatty acid profile in germplasm, drought tolerance mechanism, in situ drought-tolerant palms, responses to root (wilt) disease, drought management strategies, response to climatic parameters and climate change impact and adaptations are important milestones in this area of research. Further efforts eventually led to the development of InfoCrop-COCONUT model for simulating growth, development and yield, opening new vistas in research programmes for improving coconut management for higher yields. Since climate change is projected to have positive and negative impacts on coconut yield depending on the region, it is important to use advanced technologies for harnessing positive impacts while countering measures for overcoming the negative effects. This chapter summarizes the major research understandings in physiology and biochemistry of coconut palms.

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9.1 Introduction

Physiological and biochemical studies in coconut deal with the plant physiological and biochemical aspects that regulate the production potential of coconut palms. The productivity of coconut depends on the biological efficiency and is mainly dependent on dry matter production and partitioning towards the economically important parts. This in turn is regulated by genetic makeup, agroclimatic conditions, management as well as soil characteristics. The literature available on biological efficiency of coconut is comprehensive, generated through exhaustive experimentation. There exists substantial gap between potential nut yield and actual realized yield which is mainly due to low inputs, limited management, poor soil conditions, climatic stresses, nutrient deficiencies and biotic factors. Further, coconut plantations face vagaries of nature, quite often due to their perennial nature, flowering behaviour and long life span. Stable dry matter production, efficient use of inputs, tolerance to abiotic stresses, resilience to climatic stresses and improved harvest index (HI) are the key factors for sustained growth and yield. For achieving these, an in depth understanding of physiology and biochemistry of the crop is essential. In this chapter, the physiological and biochemical processes that regulate the crop growth and development starting from seed germination through early seedling growth, flowering and post-fertilization stages culminating in the nut yield are dealt with.

9.2 Growth and Development

9.2.1 *Physiological and Biochemical Changes During the Early Phase of Germination*

The coconut palm is a monocotyledonous palm with the fruit (drupe) having a thick epicarp, fibrous mesocarp and a hard endocarp (shell) lined by solid endosperm. Both the epicarp and mesocarp together constitute the husk (Juliano 1926). The fruit has a single embryo enveloped by the liquid endosperm (nut water). The embryo is embedded in the solid endosperm at one end of the endocarp. The embryo starts germinating when the mature nut comes into contact with moisture for sufficient duration. The nut contains all essential nutrients, hormones and carbon sources required for the germination and growth of the embryo.

9.2.1.1 Germination

Mature nuts (11–12 months old) are suitable for sowing (Nelliath et al. 1976), and storage of seed nuts in the shade for 1 month (seasoning) is essential for breaking the dormancy (Fremond and Lamothe 1966). Soaking the nuts in water or in a

solution of 0.01 M potassium nitrate and 0.02 M sodium carbonate for 48 h (Thomas 1974), chopping the husk from both ends of the nuts, injection of different hormones (Liyanage 1952; Deshpande and Kulkarni 1962) as well as major and minor nutrients (Menon and Pandalai 1960; Sumathykutty Amma 1964) hasten the germination process. Nuts sown horizontally give rise to better seedlings than those planted vertically (Espino 1923; Lumige 1969) due to constant contact of nut water with the embryo. Please refer to Chap. 7 for details on nursery management.

The first morphological sign of germination is the enlargement of the embryo and protrusion of the apical mass around the shell (Kartha 1981). For this, the dwarfs require 10 days, hybrids 15 days, while the slowly germinating tall require an average of 20 days (Wuidart 1981). In the agronomic context, emergence of plumule out of the husk is considered as germination. As per this, the nuts of tall variety take 11–12 weeks to germinate, and the percentage of germination reaches the maximum between the 17th and 18th week.

The embryo commences to grow in two directions. The plumule moves towards the soft eye to develop as shoot, and the other end of embryo develops into an absorbent spongy growth known as the haustorium, which consists of loosely connected thin-walled cells with interspaces (Selvaratnam 1952; Child 1964). The haustorium absorbs food materials from the nut water as well as kernel and supplies to the growing plant. Physiological and biochemical changes during the early phase of germination include the solubilization of stored food material and its utilization, which is influenced by various factors like absorption of water, activity of enzymes and hormones.

Absorption of Water During the early phase of germination, there is a gradual increase in the amount of water absorbed by the nut which is higher in tall as compared to early germinating dwarfs. Seed reserves support the growth and development of haustorium and emergence of root and shoot. Dry matter of haustorium is more than that of shoot and root, implying the essential role of haustorium in the early phase (Manjula 1990). The volume of haustorium differs among the tall (~315 cm³), dwarfs (~155 cm³) and hybrids (~205 cm³).

Solubilization of Seed Reserves During Germination Coconut endosperm comprises mainly of lipids (68–70%), sugars (6–7%) and protein (6–9%) (Nathanael 1967). The major reserve food material is, thus, lipid which gets solubilized faster, during the very early stage, i.e. 28 days and 42 days after sowing, respectively, in the case of Dwarfs and Tall. This is evident from a decrease in the oil content in the kernel, with a concomitant increase in the major lipid solubilizing enzymes, i.e. lipase. There is a threefold increase in the activity of lipases in dwarfs with a comparatively higher reduction in the oil content (4.1–4.8%) than the tall and hybrids (2.3–3.2%) which explains the early germination in dwarfs.

Kernel sugars are composed mainly of mannans (Balasubramaniam 1983) which are broken down by β -mannosidases. During the development of haustorium, total soluble sugars and reducing sugars decline in kernel, along with decreased activity of hydrolytic enzymes, viz., amylase and invertase. These products are absorbed by

haustorium up to 13 weeks. Thus, there exists a pool of soluble sugars in the haustorium, formed by the activities of β -mannosidases and β -amylases. From this pool, sugars are supplied to the growing embryo. Seedlings utilize the soluble carbohydrates, and excess are stored as starch to be utilized for growth (Balasubramaniam et al. 1973). Up to the formation of haustorium, protein content increases gradually and then declines rapidly thereafter. The protease activity, in general, remains parallel with the protein levels (Manjula et al. 1993). In coconut, the liquid endosperm, i.e. nut water, serves as a rich source of nutrients between kernel and developing embryo. Up to the time of haustorium development, the sugars and amino acids increase in the nut water due to the dissolution of material from the kernel. These compounds decline with the corresponding development of embryo. Breakdown products of lipids, carbohydrates and proteins from kernel are dissolved in liquid endosperm, which then act as a *via media* for transferring the components to the growing embryo (Manjula et al. 1995). By about 22 weeks after germination, with the appearance of green leaves, the seedling gradually becomes autotrophic.

9.2.2 Seedling Growth

Growth Characters The development of the seedling occurs in two phases. In the first phase (up to 4 months), the relative growth rate (RGR) falls from $72 \text{ g } 100\text{g}^{-1} \text{ week}^{-1}$ to $7.5 \text{ g } 100 \text{ g}^{-1} \text{ week}^{-1}$ and thereafter remains constant during the second phase (5–15 months). Till the 4th month, the plant is entirely dependent upon the endosperm for its growth, while at 15th month, it becomes fully autotrophic (Foale 1968). The first leaf unfolds at 2 months after germination. Leaves produced up to 4th month are quite small with total leaf area (LA) of 8 dm^2 . As the seedlings grow from 6th month to 12th month, there is a steady increase in LA, typically, from 19 dm^2 to 51 dm^2 and shoot dry mass (SDM) from 41g to 133 g. Leaf area index (LAI) reaches 5.6 at the 12-month stage (Kasturi Bai and Ramadasan 1990). The rate of leaf production remains fairly constant and is an important characteristic feature showing positive correlation with earliness of flowering.

Measurement of Seedling Growth and Vigour Seedling selection for high vigour is of paramount importance in establishing a stand of superior yielders (Table 9.1). Conventionally, selection of vigorous seedlings is done on the basis of a few easily measurable morphological characteristics such as girth at collar, total number of leaves, plant height, length and breadth of leaves or leaflets and early splitting of leaves.

Since growth is a function of LA development and dry matter (DM) production, they are used as criteria for selection of superior seedlings (Liyanage 1953; Menon and Pandalai 1960). Several regression equations have been developed for non-destructive estimation of LA and DM production (Foale 1968; Ramadasan et al. 1980; Satheesan et al. 1983; Shivashankar et al. 1986). Since these equations differ

Table 9.1 Correlation of seedling characters with nut yield of palm

Character (1-year-old seedling)	6-year-old palms	
	Cumulative yield	Female flower production
Girth	0.65**	0.69**
No. of leaves	0.55**	0.61**
Leaf area	0.73**	0.83**
SDM	0.62**	0.72**

**Significant at $p = 0.01$

based on the morphology of seedling and cultivar variations, it is necessary to define growth conditions of seedlings to ensure accuracy of estimations.

$$\text{Seedlings' dry weight (g)} = -112.5 + 12.6G + 0.23H + 5.6N + 0.02T$$

where G = Girth at collar (cm), H = height (cm), N = no. of leaves, and T = Total leaf area = $27.4 + 0.61 X$, where X = length (cm) \times breadth (cm) of individual leaves

Among the various seedling characteristics, though height of seedlings and number of leaves are correlated with dry weight of shoot in WCT, their direct bearing on the dry weight of the shoot is negligible. On the other hand, LA and girth at collar significantly influence the shoot dry matter (SDM). Thus, the important determinants of the vigour of seedling are LA, girth at collar and SDM (Ramadasan et al. 1980). The LA of 6-month-old seedlings is correlated with SDM of 12-month-old seedlings ($r^2 = 0.55$) (Kasturi Bai and Ramadasan 1990), implying that the vigour of the seedlings can be determined before the attainment of complete autotrophy. Coconut seedlings show a gradual change in the leaf morphology from pinnate to bifurcate leaves with advancing age and as such the applicability of regression equations is limited to the age of the plant, especially in the first few years of growth.

In many crop plants, the hybrid vigour and yield are correlated with the activity of nitrate reductase (NR). Since NR plays a key role in the utilization of nitrate and consequently DM production, NR activity in coconut seedlings is significantly correlated with the leaf area development and DM production (Shivashanker et al. 1985). Heterotic hybrid seedlings of COD \times WCT had higher NR activity than the intermediate and dwarfs, and it was significantly correlated with dry matter accumulation ($r^2 = 0.55$).

9.2.3 Leaf and Crown

Young coconut seedlings have pinnate type of leaves, which are not split into leaflets. These initial leaves act as the source of photosynthates to the developing seedling and subsequently emerging leaves start splitting (called as frond). As palms grow, the size of newly emerging fronds also becomes bigger. Every palm has a crown of leaves orientated at the top of the trunk consisting of opened leaves and

those in the bud in various stages of development. The number of leaves in the crown varies depending on the age and the conditions prevailing, viz., climatic conditions, methods of cultivation, cultivar and management. The leaves are produced in spiral succession, generally at one leaf month⁻¹. In highly productive well-grown palms, the number of leaves is about 30–42, and one inflorescence emerges in the axil of each leaf. At any given time, generally 12–15 spadices can be seen. There are generally 3 sets of leaves in a coconut canopy, (i) above inflorescence bearing leaves, (ii) inflorescence bearing leaves and (iii) leaves below inflorescence bearing leaves (Naresh Kumar and Kasturi Bai 2009a). Leaves in coconut canopy are arranged in 3 shapes, viz. oval, X shape and semicircle shape. Leaf orientation is most suited for proper light interception by all leaves in oval-shaped canopy (Naresh Kumar and Kasturi Bai 2009a).

Development and Structure of the Leaf The primordium of the leaf is first differentiated about 30 months prior to its emergence from the leaf sheath. In the beginning, the leaf primordium is a small indistinct protuberance at the base and on the side of the growing point. By periclinal and anticlinal divisions of the cells, the protuberance, in about a month's time, increases in size and assumes a finger-like shape with 7 to 10 layers of cells. At this very early stage, the 3 primary meristems, viz. the dermatogens, the periblem and the plerome, can be distinguished in the growing point. The outermost layer of cells forms the dermatogen which is continuous with the growing point. The 3 layers of cells below the dermatogen form the periblem, and the plerome is innermost in the growing point. During the succeeding month, the size of the protuberance considerably increases and assumes the shape of a hollow cone enclosing the next younger leaf and the growing point. At this stage, the initial cells of the procambial strands, which will ultimately become the vascular bundles, first make their appearance in the central tissue or plerome of the base of the second leaf from the growing point of the stem. The procambial strands consist of elongated cells actively dividing along their length lying in the middle of the leaf, where they are in 5 to 6 rows, while along the margins, they lie only in one central row. The number of strands later increases as the leaf develops in size. The young leaves are without laminae, and they consist of only the petiole portion at the apex of which is a growing point with the primary meristems. The leaflets are first differentiated at the tip of the seventh leaf from the growing point in about 8 months after it originated. The differentiation of the leaflets occurs first below the top of the young petiole on either side of it.

Leaf area and Dry Weight Non-destructive methods to estimate the LA and leaf dry weight were developed (Ramadasan et al. 1985; Ramadasan and Mathew 1987). Regression equations were developed taking into account all the absolute values derived from the base, middle and top 3 pairs of leaflets from a single leaf. Total area and dry weight of the leaf can be determined with ease by estimating the dry weight of middle 6 leaflets and by leaflet count of the same leaf. Once the leaf is completely unfolded, there is no perceptible increase in LA and dry weight.

The length of the leaf (including the rachis) normally ranges from 4 to 6 m, while the rachis length varies from 1 to 1.5 m (Kasturi Bai 1993). The LA of individual leaf ranges between 3.8 and 5.1 m², whereas the dry weight ranges from 0.97 to 1.36 kg. Differences in area and dry weight between leaves of the same age in a palm are low. Thus, the area and dry weight of leaves produced per unit time can be estimated by multiplying the estimated LA or dry weight of a single leaf by the number of leaves produced in a year. Variations exist in the LA and dry weights among the cultivars. Equations for non-destructive estimation of the total LA based on the area of 12 leaflets and the total number of leaflets per leaf (Jayasekara and Mathes 1992) and for the determination of the dry weight of the leaf by measuring the width and length of the petiole (Friend and Corley 1994) were developed.

$$\text{Leaf dry weight} = -3.14 + 0.0197X_1 + 0.0202X_2$$

where X_1 = dry weight of six leaflets (g) and X_2 = no. of leaflets

Leaf Anatomy Besides leaf area and dry weight, leaf anatomy has also been recognized as an important component of productivity. Cultivar differences have been observed in leaf thickness and tissue density (Ramadasan and Satheesan 1980). Hybrids have been found to possess higher tissue density than the WCT palms. However, in coconut, the leaf tissue density, in general, is low as it contains more air space volume which is characteristic of all C₃ species as against high tissue density and low air space volume in C₄ species.

Leaflet mean thickness is 341 μm with bottom portion of the leaflet being thicker and tapered towards tip portion. Epidermal cells are closely attached to form a compact layer devoid of intercellular spaces. The upper epidermis is thicker with large-sized cells than lower epidermis. Cuticle on upper epidermis is twofold thicker than the cuticle on lower epidermis (2.49 μm). Cuticle is even thicker at midrib and at edges of leaflet. Coconut leaflets are hypostomatus. The guard cells have hook-like protuberances at both ends, a characteristic typical to Palmae. Elongated epidermal cells surround the guard cells along their entire length. These cells are larger than guard cells. On the lower epidermis, multicellular, shortly stalked scales occur at regular intervals in short depressions. These scales contain tannins (Menon and Pandalai 1960; Naresh Kumar et al. 2000a). This distribution of palisade and spongy parenchyma makes the leaflet dorsiventral (Naresh Kumar et al. 2000a).

Anatomical features of leaflet vary among the cultivars. Leaflets are significantly thicker in WCT, FMS (405 and 363 μm, respectively) with thick cuticle on both adaxial and abaxial side of leaflet compared to other cultivars in which the leaflet thickness ranges between 308 and 339 μm. However, GBGD and MYD have very thin cuticle on both sides. Upper epidermal cell size, guard cell size, xylem tracheid lignification, sub-stomatal cavity size and hypodermal cell size also vary among the cultivars (Naresh Kumar et al. 2000a). Further, they reported that the parenchyma cells (spongy and palisade) are significantly bigger in WCT and FMS compared to other cultivars. Palisade parenchyma cells are the smallest in WCT x COD, while PHOT has smaller spongy parenchyma cells than other cultivars. Xylem tracheids

in vascular bundles have scalariform thickenings ranging from 2.85 μm in MYD to 3.38 μm in WCT. Water cells also are significantly bigger in WCT and FMS. The indigenous cultivars had extreme values for all the traits related to leaflet anatomy (WCT had maximum values, and GBGD and COD x WCT had minimum values). However, the exotic cultivars had medium values thus indicating the possibility of using some of these parameters to identify ecotypes in coconut.

9.2.4 Stem

The trunk of coconut grows erect to a height of 10–24 m. The annual growth of stem is recognizable by ‘scars’ (mark of leaf base). As the new leaves are added, the old ones are shed leaving the scars of leaf base which correspond to a year of growth of the palm. Since the trunk just below the crown mainly contributes to the growth of the stem, dry matter production of this apical portion is used for estimation.

In general, coconut palm produces 12–14 leaves annually, and the data on these segments is sufficient to estimate the quantity of dry matter produced by way of stem growth annually. Besides, any differences in the stem growth rate due to variation in environment variables will be reflected in this portion of stem. Increment in stem height can be easily determined by marking the stem portion just below the crown and taking the measurement after a period of time, typically 1 year. Coconut stem is the main reservoir of carbohydrates which are mainly stored in soluble form, largely as sucrose, while roots have no storage function (Mialet-Serra et al. 2005). Canopy pruning did not influence stem reserves showing a very low phenotypic plasticity of coconut (Mialet-Serra et al. 2008). The increment in stem height year⁻¹, ranged between 23 and 37 cm, varies significantly between cultivars and hybrids. Talls, Dwarfs and hybrids differed for stem DM production between 1.7 and 7.3 kg palm⁻¹ year⁻¹ (Kasturi Bai et al. 1996a). The density of stem decreased gradually from just below canopy (0.32 g cm⁻³) to base (0.8 g cm⁻³) with a mean density of 0.517 g cm⁻³ (Naresh Kumar et al. 2008a).

A non-destructive method was developed to estimate the standing stem biomass (Naresh Kumar et al. 2008a).

Standing stem dry weight (kg) = Length (in m) \times girth² (in m, at 1.5 m above ground level) \times 41.14142.

For annual stem dry matter estimation (Ramadasan et al. 1985), the equation is

$$Y = -113.44 + 93.67 \times \text{Length of three leaf scar segments}$$

9.2.5 Flowering

Commencement of flowering in coconut is noticed by the appearance of first inflorescence (spadix) in the leaf axil. The initiation of inflorescence primordium occurs in the 10th to 14th leaf axil, and the flowering in the Tall variety takes place around

the age of 5 years or at the 45th leaf stage of growth or beyond (Patel 1938; Pillai et al. 1973). Genotype x environment influence on spadix initiation is evident from their higher production during March to September when average day length is more (Wickramasurya 1968). WCT seedlings responded to long-day treatment in terms of chlorophyll fractions, vigour and early initiation of inflorescence primordium. The primordial initiation took place in the 10th leaf axil in the long-day treatment palms and in the 14th leaf axil, in the controls. Although inflorescence primordial growth is initiated in the 10th to 14th leaf axil, all these in most instances are aborted until the 45th leaf stage after transplantation (Pillai et al. 1973).

Factors Influencing the Onset of Flowering In fruit trees, a high carbohydrate reserve in the stem is an essential prerequisite for early initiation of flowering. In coconut, seasonal and cultivar variation exists in the carbohydrate fractions. Hybrids are superior to Tall (WCT) in their efficiency of mobilization of carbohydrate fractions to inflorescence primordium (Kasturi Bai and Ramadasan 1983). The inflorescence from the primordial stage takes about 26 months to emerge out of the leaf axil (Patel 1938). In juvenile palms, the emergence of first inflorescence is noticed during the months of August to October. This period coincides with the decrease in the insoluble carbohydrate fraction (starch) as against an increase in the non-reducing sugar fraction (Kasturi Bai and Ramadasan 1978). Increased productivity in irrigated condition can be due to the assured availability of soluble carbohydrate fractions for the initiation and the development of inflorescence.

Stem carbohydrate reserves significantly differ between the flowered and non-flowered palms. In 8-year-old WCT palms, a higher ratio of carbohydrates to nitrogen (C/N ratio) as well as higher leaf number is observed in palms that have commenced flowering over those which have not (Ramadasan and Mathew 1977). Not only the development of inflorescence but also the female flower production is regulated by the carbohydrate metabolism. In Kerala, India, maximum female flower production occurs during the period of March to May (Menon and Pandalai 1960), whereas in Sri Lanka it is up to September (Abeywardena 1968). Concomitant with the increase in female flower production from March to May, there is an increase in the insoluble carbohydrate fraction in stem and leaf and a decrease in soluble fraction. Insoluble fraction is positively correlated with female flower production, whereas the sugar content is negatively correlated (Kasturi Bai and Ramadasan 1982). The derangement of the carbohydrate metabolism due to Mg and P deficiencies leads to an impaired nitrogen metabolism and delays the initiation of flowering (De Silva et al. 1973). Glucose, free amino acid, total nitrogen, protein nitrogen and nonprotein nitrogen were lower in the laminae of nonbearing coconut palms than in the bearing palms of similar age (Balasubramaniam et al. 1974).

Hastening the age of flower production is of particular interest in palms which do not flower even after 5 or 6 years. Though exogenous application of gibberellin and kinetin (500 ppm and 1000 ppm) enhanced only the elongation of the petiole of the youngest leaf, injecting 1000 ppm gibberellin into the trunk of 2-year-old seedlings could induce flowering in the 36th leaf axil instead of 45th leaf axil. Thinning of immature bunches at 4 months of maturity and extraction of the inflorescence sap increased female flower production (Mathes 1984).

Coconut Inflorescence Sap Coconut inflorescence sap is the phloem sap collected from the unopened spadix. The sap collected by traditional method (called *neera*) is prone to microbial fermentation. A simple technology developed at ICAR-CPCRI ‘coco-sap chiller’ for the collection of sap under low temperature keeps it fresh and unfermented during collection (Hebbar et al. 2013, 2015a, b). The sap, thus, collected can be stored for prolonged time under refrigerated condition (-1 to -3 °C). It tastes sweet and is delicious with no alcohol and devoid of contamination, as it is collected in an aseptic condition. This fresh, hygienic and unfermented sap (called Kalparasa) is slightly alkaline (pH 7–8) and golden brown in colour, while neera is oyster white in colour, with a pH 6 or below and an astringent smell. Kalparasa also contains amino acids, total phenols, flavonoids and antioxidants 2.5, 1.5, 4.6 and 1.8 times higher than neera, respectively (Hebbar et al. 2015a). It is also rich in vitamins C, E and Niacin. Further, the products of Kalparasa such as sap concentrate and sugar were also found to be rich in amino acids, polyphenols, flavonoids, vitamins and antioxidants (Hebbar and Chowdappa 2016). Extracting the sap before the nut production is advantageous in terms of energy production (Hebbar et al. 2015a; Hebbar and Chowdappa 2016). However, a balance between sap production and nut production must be maintained for yield sustainability of the palm.

9.2.6 Nut Development

The ovary development in coconut from the time of initiation of inflorescence primordium to full maturity of the nut can be divided into two major phases, i.e. pre-fertilization phase taking about 32 months and the post-fertilization phase continuing for another 12 months. The growth of the fruit begins immediately following fertilization, with a rapid development of the pericarp at the basal region which remains soft and white until the fruit is nearly mature. The endocarp is already differentiated as a soft, creamy white structure long before the time of fertilization. During the development of fruit to maturity, the embryo sac increases in size, leaving a large cavity at the centre.

The coconut water (liquid endosperm) is formed in small quantities in the third month of development of the nut and reaches maximum in the eighth month and declines thereafter as the nut ripens. The endosperm of the coconut develops as a coenocytic liquid, containing many free nuclei and some cells (Cutter et al. 1955; Bhatnagar and Johri 1972). The cells coalesce towards the periphery of the embryo sac. Additional cells are formed when free nuclei adhere resulting in the formation of cellular endosperm. In the mature coconut, the liquid, which is of cytoplasmic origin, does not contain free nuclei or free cells. The shell begins to form during the fourth month of nut development and continues to grow up to the twelfth month. The kernel is the last component to form in the seventh month and its growth continues up to the eleventh month when the maximum value of dry weight is reached. The reddish testa, which assumes a brownish tint when matures, is laid down before the formation of the kernel. Total nut production $\text{palm}^{-1} \text{ year}^{-1}$ shows great variation

among cultivars/hybrids, but bunch production or spikelet bunch year⁻¹ does not vary significantly among them. However, female flower production varies significantly among cultivars/hybrids (100–400) with higher production observed in hybrids than in the cultivars (Kasturi Bai et al. 1996a).

9.2.6.1 Biochemistry of the Developing Nut

The liquid endosperm plays a vital role in fruit development by acting as a reservoir of precursors for the synthesis of fruit constituents. The major constituents of the liquid endosperm are sugars and minerals, while fat and nitrogenous substances form a minor fraction (Kamala Devi and Velayudham 1978).

Changes in Carbohydrates Reducing sugars form the major part of immature nuts. Sugars in liquid endosperm of immature nuts (3–4 months) are almost entirely reducing sugars, which increases to a concentration of about 5% by seventh month. During this period of fruit development, sugar (sucrose) in inflorescence phloem sap entering the fruit is completely converted to glucose and fructose by the action of invertase present in the stalk (Balasubramaniam 1983; Balasubramaniam and Alles 1989). With the formation of solid endosperm (kernel) at about seventh month, non-reducing sugars appear and increase in concentration both in kernel and in nut water, while the levels of reducing sugars and total sugars decrease (Balasubramaniam 1983). Simultaneously, polysaccharides in kernel increase following a sigmoid pattern. The initial lag phase of polysaccharide synthesis continues until the establishment of the jelly-like endosperm on the entire surface area of nucellus. This is followed by a logarithmic phase in which the endosperm gradually thickens and turns hard. Stationary phase is characterized by the formation of a hard solid endosperm in which almost all cell wall polysaccharides are laid down. Fat content of the kernel increases during the same period indicating that the glucose of the liquid endosperm is converted to sucrose and to the polysaccharides of the kernel, besides being utilized as a precursor for the synthesis of fats (Naresh Kumar and Balakrishnan 2009). The total carbohydrate content of the kernel increases from 31.9% in the 6 month to 44.9% at maturity, during which time free sugars increase from 11.3% to 23.6% (Sierra and Balleza 1972). Sucrose contributes to the synthesis of nearly 20% of the lipids stored in the endosperm and a large number of polysaccharides including cellulose stored in its pericarp (Van die 1974).

Composition of Carbohydrates in Nut Water Coconut water contains mainly monosaccharides, viz. glucose, fructose and sucrose, and traces of trisaccharide raffinose (galactose-glucose-fructose) and tetrasaccharide stachyose (glucose-galactose-glucose-fructose). A polysaccharide (an arabinogalactan) was isolated from the liquid endosperm of mature coconut (White et al. 1989). It has a molecular weight exceeding 500 kDa and is composed of galactose and arabinose with minor amounts of mannose and glucose. Two smaller polysaccharides containing significant amounts of xylose or mannose and lesser amounts of arabinose and another polysaccharide, composed exclusively of uronic acid residues, have also been reported.

Carbohydrate Composition of Kernel Galactomannans and galactoglucomannans are the major polysaccharides of mature coconut kernel and copra meal, respectively (Rao et al. 1961; Kooiman 1971; Balasubramaniam 1976). The copra meal contains substantial amounts of cellulose, minor amounts of arabinoxylogalactan, galactomannan and traces of arabinomannogalactan and galactoglucomannan (Saitagaroon et al. 1983). Primary cell wall of immature cells is formed of cellulose, polysaccharides and galactomannans. The mannans are absent in the kernel of 5- to 6-month-old nuts, while the mature nut consists chiefly of mannans, containing at most a few per cent of galactose residues (Balasubramaniam 1976), and during fruit maturation, the galactomannans (galactose to mannose 1:7) increase (Balasubramaniam et al. 1974). During the transition of the endosperm from the hydrated gelatinous phase to the dehydrated solid mature state, most of the galactose groups are removed from the cell wall (Kooiman 1971). This process is catalysed by the enzyme D-galactosidase present in the endosperm (Mujer et al. 1984a, b).

Changes in Amino Acids The developing fruit contains a variety of nitrogenous substances, of which free amino acids constitute a major part. During nut maturity, the total nitrogen and nonprotein nitrogen (NPN) progressively increase although percentage levels decrease marginally on whole nut basis. The NPN content remains above 60% at all stages of maturity (Jayalekshmy et al. 1988). In the maturing nut, the free amino acid content in the coconut water increases from 4 mg to 16 mg 100 ml⁻¹, whereas concentration of bound amino acids does not show any marked change. The first traces of α -amino butyric acid appear in liquid endosperm with the formation of kernel at about 5–6 months after the fruit set and subsequently increases with maturity. The α -alanine and β -aminobutyric acid are present in large quantities in the endosperm of the immature nut. Proline content is the highest in the immature nut and decreases with maturity leaving only a trace in the water of the mature nut. In the immature nut water, about 70% of the free amino acids are made up of glutamine, arginine, asparagine, alanine and aspartic acid, while alanine, α -amino butyric acid and glutamic acid constitute about 75% of the free amino acids of mature nut water. With increasing age of the fruit, aspartic acid and glutamic acid increase slightly, while alanine increases markedly, whereas other amino acids do not show much change (Baptist 1956). In coconut kernel, amino acids such as methionine, tyrosine, tryptophan and phenyl alanine are present in high levels (Hagenmaier et al. 1972).

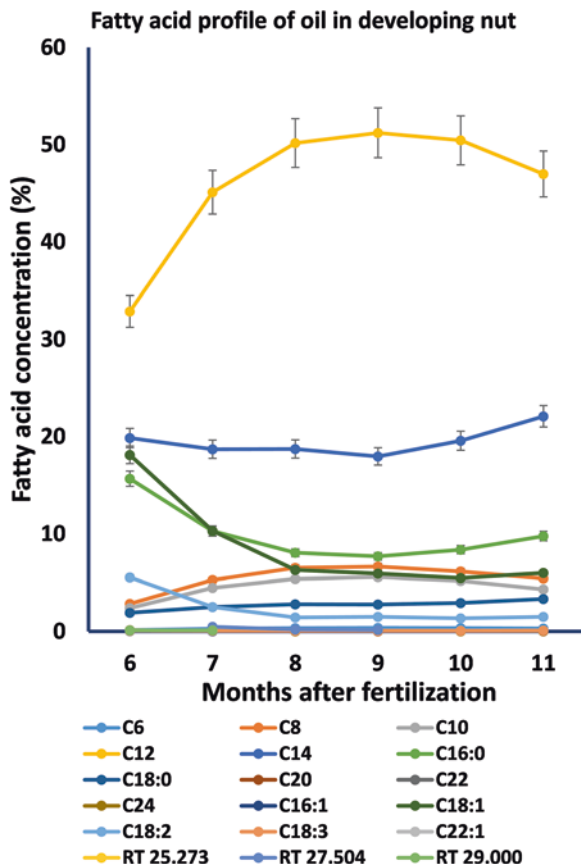
Changes in Protein The protein content of nut water increases from 0.13% to 0.29%, while it decreases in the kernel from 8.3% in the fifth month to 6.2% at maturity. The coconut proteins have been classified according to their solubility behaviour, amino acid content and heat denaturation. About 84% of the coconut proteins are of high molecular weight (150 kDa), and the rest belong to low molecular weight class (24 kDa). Based on solubility studies, it was identified that 90% protein could be classified as albumins and globulins.

Changes in Lipids Fatty acid biosynthesis starts at about fifth month, when the kernel begins to form and increases up to 12th month. The fat content of the nut water increases up to 10th month and rises gradually thereafter reaching maximum in the 12th month. At the same time, the fat content of the kernel also increases, and the oil content per nut is at its maximum in the 12-month-old nuts. In coconut dry kernel, oil is present in the range of 57–70% depending on cultivar/hybrid. In coconut oil neutral lipids form major fraction (~94%) followed by the glycolipids (3.5%) and phospholipids (2.5%) (Naresh Kumar et al. 2000b). Lysophosphatidylethanolamine comprises about 23% of all phospholipids in coconut kernel. The rest of the phospholipids are composed of phosphatidylinositol, phosphatidylserine, phosphatidylcholine, phosphatidylethanolamine and other unidentified phospholipids in equal abundance (Monera and del Rosario 1982).

Changes in Fatty Acid Composition of Endosperm In the developing fruits, the pattern of variation of fatty acids in both kernel and nut water appears to be similar, although significant deviations in the relative abundance of component fatty acids have been found (Oo and Stumpf 1979; Padua - Resurreccion and Banzon 1979; Jayalekshmy et al. 1988; Naresh Kumar et al. 2004; Naresh Kumar 2007; Naresh Kumar and Balakrishnan 2009). In general, the relative proportions of fatty acids increase up to C 14:0 during maturation, while a corresponding decrease in the high unsaturated fatty acids occurs (Fig. 9.1).

The most characteristic feature is that the content of lauric acid (C 12:0) in kernel rapidly increases with maturity up to 42.4–52.5% and that of myristic acid is maintained at about 18–23% of the total in the mature nut, while the content of most other fatty acids remains far below 20% (Naresh Kumar and Balakrishnan 2009; Naresh Kumar 2011a). Palmitic acid decreases from 14% to 9% and oleic acid from 23% to 6% from 6-month-old tender nuts to mature nuts. Linoleic acid gets reduced from 5% to 1% during nut development. Palmitoleic and linolenic acids are found in low quantities in 6-month-old nuts, and their percentage decreases with nut maturity. Four of the fatty acids in nut water, C14:1, C15:0, C16:1 and C17:0, which are present in the early stages, disappear as the nut matures, whereas the content of the short-chain fatty acids, C6:0, C8:0 and C10:0, which are present in the negligible levels initially, rises with maturity both in water and kernel. The long-chain fatty acids C18:3 and C22:0 have been found at all stages of fruit growth in nut water but not in kernel. The concentration of long-chain fatty acids is more in 5-month-old nuts as compared to the mature ones. In the mature nut, saturated fatty acids, mostly of short- and medium-chain length, like caprylic (C 8:0), lauric (C 12:0) and myristic (14:0) acids, comprise nearly 83–89%. Concentration of long-chain unsaturated fatty acids in developing coconut kernel is high at 5 and 6 months after fertilization and decreases towards maturity. Concentration of fatty acids also varies during growth (Naresh Kumar and Balakrishnan 2009). Fatty acids degrade in stored oil due to photooxidation, chemical reactions and microbial activity. During storage, the small- and medium-chain fatty acids are degraded to form the free fatty acids (FFAs). Additives such as citric acid (100 ppm) or common salt (NaCl at 1%) prolonged shelf life with least increase in FFAs (Naresh Kumar and Balakrishnan 2012).

Fig. 9.1 Fatty acid profile of a developing coconut. (Modified from Naresh Kumar and Balakrishnan 2009)



Growth Regulators in Developing Fruits Coconut contains numerous growth promoting compounds, and to date several growth promoters have been isolated in pure form from various parts of the coconut fruits. 1,3-diphenylurea, gibberellin, myo-inositol, scyllo-inositol, sorbitol, phyllococcosine and auxin-gibberellin-like substances were identified from liquid endosperm. Zeatin and zeatin ribosides were identified both in mature fruit and liquid endosperm. Purine-like substances and 9-D-ribofuranosyl zeatin were identified only in mature endosperm (Van Staden and Drewes 1975; Dix and Van Staden 1982).

Other Constituents The developing coconut contains many other compounds having specific biochemical roles. Among these, shikimic acid and quinic acid found at all stages of fruit growth are possibly involved in aromatic biosynthesis. Buttons and green variety contain leucocyanidin and leucopelargonidin, while the red dwarf contains small amount of flavonoid pigments in addition to leucoanthocyanidins. Mature coconut contains a number of vitamins in which ascorbic acid is the major component. Coconut water contains an RNA in the soluble form and is found to be

not associated with any cell organelles. Phytin is reported to be present in coconut water and plays a role in supplying phosphate for the synthesis of nucleic acid.

Activity of Enzymes The endosperm, being a site of active metabolism, contains a large number of enzymes. The onset of cellular differentiation in the developing coconut coincides with a rapid rise in acid phosphatase activity. Acid phosphatase activity in the kernel reaches a minimum when the maturation is complete and remains so even during germination. The activities of pyrophosphatase 3' nucleotidase, ribonuclease and deoxyribonuclease also remain similar in the kernel of mature and germinating coconuts. Isolation of RNA polymerases from coconut nuclei (Mondal et al. 1970) of immature coconuts suggests the existence of transcriptional process in them. The enzymes present in coconut include acid phosphatase (immature kernel, nut water), decarboxylases, aspartate amino transferase, RNA polymerase (in immature kernel), pyrophosphatase 3'-nucleotidase, ribonuclease, glycerol dehydrogenase, amylase, lipase, phospholipase and deoxyribonuclease, mannan synthetase, GDP mannose, pyrophosphorylase, esterase (in mature kernel), carbonic anhydrase (1- to 2-month-old fruit) and CAMP-dependent protein kinase (nut water) and invertase (6- to 7-month-old fruit stalk and mesocarp) (Padmaja et al. 1980; Balasubramaniam 1983; Balasubramaniam and Alles 1989; Manjula 1990). Peroxidase is present in 7- to 12-month-old normal and makapuno nuts, while a D-galactosidase and tryptophan aminotransferase are present in 12-month-old nut and kernel (Mujer et al. 1984b).

9.2.7 Variability in Coconut Germplasm for Oil and Fatty Acid Profile

In general, oil content is high in tall than in dwarfs. Among the Talls, Laccadive Micro Tall has the highest oil content, while Green Dwarf has the highest oil content among dwarfs. Lipid fraction content also varies with cultivar. The neutral fraction is maximum in WCT, TCT, MYD x WCT, JVT, FIJT and PHOT. Hybrids have lower concentrations of neutral lipids (90–94%) (Naresh Kumar et al. 2004). Analysis of fatty acid profile of oil from 60 Talls, 14 Dwarfs and 34 hybrids, which included collections from coconut-growing areas of 13 countries as well as from the indigenous ones, indicated wide variation (Naresh Kumar 2007, 2011a). Variability in the saturated to unsaturated fatty acid ratio (6.32–17.6) and contents of lauric acid (42.4–52.5%) and other fatty acids are reported. Further, coconut germplasm also significantly varied for concentration of long-chain unsaturated fatty acids followed by that for long-chain saturated fatty acid and small- and medium-chain fatty acids (Naresh Kumar 2011a). Seasonal variations exist for fatty acid profile except myristic acid which did not vary significantly. The concentration of linolenic acid was the highest in nuts harvested during October. Small- and medium-chain fatty acids were high in nuts collected during January which gradually decreased up to October

(Naresh Kumar and Balakrishna 2009). Eriophyid mite infested nuts had significantly low concentration of unsaturated fatty acids and further decreased with the intensity of infestation (Sujatha et al. 2006).

9.2.8 Total Dry Matter Production (TDM)

Coconut palm has indeterminate growth pattern, producing an inflorescence at each leaf axil at intervals varying from 25 to 30 days, depending on the environmental conditions and age of the palm. Consequently, at any time, a healthy coconut palm carries 12–14 inflorescences or bunches with varying numbers of fruits at different developing stages. TDM constitute the above-ground and below-ground (root) dry biomass, but generally only above-ground biomass is estimated. Total above-ground dry matter constitutes both vegetative dry mater (VDM) and reproductive dry matter (RDM). The dry weight of stem and leaf together constitutes the VDM of the palms and is a useful character for selection for vigorous palms. Low VDM is associated with high harvest index. Cultivar, crop management and agroclimatic conditions cause variation in annual dry matter partitioning to stem (2–6%), leaf (18–33%), inflorescence (4–6%) and nut (61–70%) (Rajagopal et al. 1989b; Kasturi Bai et al. 1996a, 1997; Siju Thomas et al. 2005; Naresh Kumar 2009) as indicated in Fig. 9.2. Significant variation exists in the VDM between the Tall, Dwarf, and hybrid (Kasturi Bai 1993; Kasturi Bai et al. 1996a). Dwarfs produce less TDM mainly due to the low number and small size of leaves. This leads to small and thin stem with narrow leaf

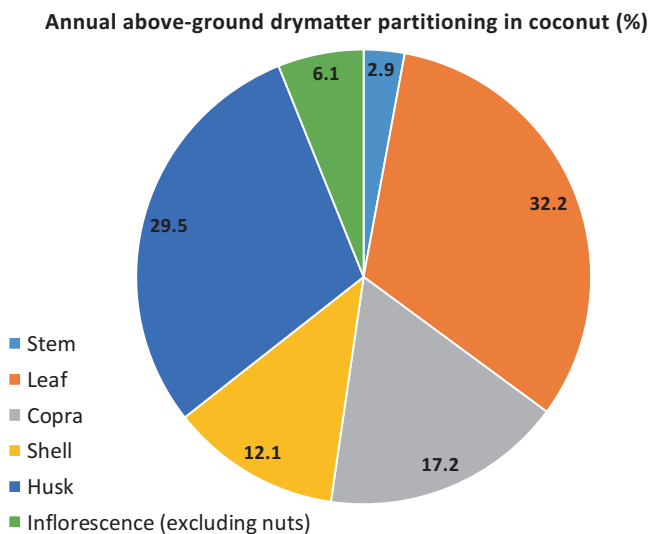


Fig. 9.2 Annual above-ground dry matter partitioning (per cent) in coconut. Values are mean of three tall, one dwarf cultivar and five hybrids

scars. On the other hand, due to big and long leaves as well as more production of leaves, the Talls produce higher TDM, leading to long, sturdy and thicker stem. The increment in stem height year⁻¹ is also higher in Talls as compared to the Dwarfs.

The total dry weight of spathes, bunches and nuts constitute the RDM. Dry weights of the spadices and the spathes constitute about 5% of the total RDM production. Thus, RDM production depends mainly on the nut production and partitioning of nut dry matter towards its components, viz. husk, shell and copra. Based on the dry matter accumulation in the vegetative and reproductive parts, TDM production also greatly varies between the cultivars and hybrids. Kasturi Bai et al. (1996a) reported a TDM production of 17 t ha⁻¹ year⁻¹ in WCT x COD hybrids. However, the highest value reported is 30 t ha⁻¹ year⁻¹ in Dwarf x West African Tall hybrid in Cote d'Ivoire (Corley 1983). Stability of dry matter and yield also varies across locations (Siju Thomas et al. 2005). The potential dry matter production is estimated at 51 Mg ha⁻¹ year⁻¹ (Corley 1983; Foale 1993), while in India, the simulated TDM potential production ranged between 52 and 62 Mg ha⁻¹ year⁻¹ (Naresh Kumar et al. 2008b). Thus, a huge gap exists in the realization of yield and the production potential of coconut palms.

Harvest Index The harvest index (HI) has been considered as an important criterion in biological and economic yield. Because of the limitation in estimating the total biomass including the roots, Ramadasan and Mathew (1987) coined the term 'Annual Productivity Index (API)'. The HI in coconut was estimated by taking into account the annual increment in DM production and expressed as the ratio between dry weight of economic product to TDM production. Being a crop of continuous productivity, API is an appropriate criterion comparable to the HI of annual crops. In coconut, since all the parts are economically important, several values of HI could be calculated. The values of API estimated ranged from 0.4 to 0.5 in a group of palms in which the annual yield ranged from 45 to 91 nuts. Harvest indices are calculated based on the total DM production and its partitioning towards the annual copra out turn (Kasturi Bai et al. 1996a). Hybrids have HI indicating better nut composition than Talls and Dwarfs. The HI based on the copra out turn ranged from 0.13 to 0.23.

9.3 Physiological Basis of Yield Potential

The coconut palm exhibits wide variability in productivity ranging from 30 nuts to 400 nuts palm⁻¹ year⁻¹. This is mainly due to the efficiency of the palms in the dry matter production and partitioning towards yield. The relationship between height of the palm, number of leaves on the crown and the annual yield indicated that leaf area, photosynthetic efficiency and dry matter production are important parameters for high production potential of coconut palms. In addition to management, agroclimatic conditions influence the photosynthetic efficiency, dry matter production and economic yield, thus determining the production potential of palms (Siju Thomas et al. 2005). Significant differences in the number of leaves on crown and

chlorophyll content have been observed between yield groups, and high correlation between these parameters and annual yield of nuts have been reported. Cultivars with high rate of photosynthesis and lower respiration produce higher yields than the cultivars with high respiratory rates. The net assimilation rate, shoot dry weight and chlorophyll concentration have heritability values of 0.64, 0.74 and 0.81, respectively (Ramadasan et al. 1985).

Leaf Photosynthesis Under favourable environmental conditions, coconut develops a profuse canopy with an estimated potential dry matter production of 51–62 Mg ha⁻¹ year⁻¹ (Foale 1993; Naresh Kumar et al. 2008b). In situ measurements of coconut seedling photosynthetic rates indicated saturated photosynthetic photon flux density of about 1400 μ moles photons m⁻² s⁻¹, typical of C3 plants (Naresh Kumar and Kasturi Bai 2009a). Net photosynthetic rates vary between 2 and 15 μ mol CO₂ m⁻² s⁻¹ depending on the age of palm, moisture and nutrient status as well as weather conditions. On the other hand, rate of leaf respiration was relatively similar in young and old leaves –2 to –1 μ mol CO₂ m⁻² S⁻¹. Among C3 plants, coconut has been shown to be relatively less efficient in conversion of photosynthetically active radiation (PAR) energy to biomass. The highest energy conversion of PAR into dry matter in coconut has been estimated to be 1.2–1.4 g MJ⁻¹ (Corley 1983). Within coconut canopy, net photosynthetic (Pn) rates were higher in second to tenth leaves from the top and decline considerably making it a source-limited crop (Naresh Kumar and Kasturi Bai 2009b). A decline in photosynthetic activity of fronds has been observed from 12 to 14 months which is accompanied with a decrease in leaf nitrogen content and decline in incident PAR due to self-shading effect of upper canopy leaves. Canopy shape plays a role in the overall performance of photosynthesis and water use efficiencies and productivity in coconut. Palms with oval-shaped canopy have higher photosynthesis efficiency, water use efficiency and productivity than those with X-shaped and semicircle-shaped canopies (Naresh Kumar and Kasturi Bai 2009b). The photosynthetic nitrogen use efficiency (PNUE) declined with age of leaf (Jeyasekara et al. 1996). Manifestations of water-deficit stress in coconut cause varied responses including low stomatal conductance and water potential that often impair Pn and transpiration (Repellin et al. 1994, 1997; Rajagopal and Kasturi Bai 2002; Naresh Kumar and Kasturi Bai 2009a, b). As a consequence, carbon assimilation rate is impaired in both Tall (Repellin et al. 1997; Prado et al. 2001) and Dwarf cultivars (Gomes et al. 2007) in response to atmospheric and soil water deficit (Naresh Kumar et al. 2002b, 2006a, b; Hebbar et al. 2016b, c). Limited diffusion of atmospheric CO₂ to intercellular spaces due to stomatal closure has been attributed with photosynthetic reductions (Repellin et al. 1994, 1997). Later physiological studies have delineated that non-stomatal factors also contribute to the reduction in Pn both during a period of severe water deficit and during the recovery phase after resuming irrigation (Rajagopal et al. 2000a, b; Gomes and Prado 2007; Gomes et al. 2007). In addition, the photochemical efficiency (FV/Fm) reduced with decreasing water potential suggesting damage to photosynthetic apparatus under stress (Kasturi Bai et al. 2006b). Prolonged exposure to high light intensities caused photo-oxidative stress in coco-

nut seedlings damaging cell membrane, caused leaf senescence and in severe cases resulted in seedling death (Naresh Kumar and Kasturi Bai 2009a). Similarly, zygotic embryo cultured plantlets undergo photosynthetic acclimatization during their growth in *in vitro* condition and during subsequent transfer to acclimation chambers and shade nets (Naresh Kumar et al. 2001).

Gas exchange measurements are linked to water and gas economy of the plants. Coconut palms under the influence of water depletion stress respond with decreased stomatal conductance (g_s , $\text{mol m}^{-2} \text{s}^{-1}$) (Rajagopal et al. 1988, 1989b). Stomatal resistance (r_s) differs during the period of adequate soil water availability and during soil water deficit among the cultivars and hybrids of coconut. During non-stress, r_s shows the least variation among the cultivars, except in WCT x WCT, which exhibited relatively more r_s . However, under stress conditions, where high evaporative demand in the atmosphere prevails, cultivars exhibit differential adaptability through stomatal regulation which is high in Talls and hybrids, whereas, in Dwarfs, it is almost 50% less than that in hybrids (Rajagopal et al. 1990; Naresh Kumar et al. 2002a; Siju Thomas et al. 2008; Hebbar et al. 2016a, b). This indicates the higher transpiration loss of water in Dwarfs than in Talls and hybrids. Among the hybrids studied, COD x WCT had significantly low r_s . Rainfed palms had higher LAVPD (leaf to ambient vapour pressure deficit), leaf temperature (T_{leaf}) and leaf to ambient temperature difference (ΔT), whereas the irrigated palms had higher Pn, Ψ_{leaf} , and transpiration rates (E). The LAVPD and ΔT influenced the g_s and water relations of coconut. Strong stomatal control of plant water status has been demonstrated in mild to moderate water stress (Naresh Kumar et al. 2002a).

9.3.1 Leaf Water Potential (ψ_{leaf})

Leaf water potential (ψ_{leaf}), an indicator of plant water status, has a vertical gradation from middle leaf upwards, the magnitude being higher under rainfed condition. Spindle leaf had significantly higher ψ_{leaf} throughout the day irrespective of rainfed or irrigated conditions (Voleti et al. 1993a, b). Under rainfed conditions, ψ_{leaf} showed a reduction from the spindle to the first leaf. Characteristic midday depression in ψ_{leaf} was evident in both the spindle and the first leaf. The midday depression in ψ_{leaf} was more in rainfed palms than in irrigated ones (Rajagopal et al. 2000a). Variation among the cultivars for ψ_{leaf} also was noted. Seasonal variations in the ψ_{leaf} occur, depending on the weather, type of soil and soil water availability. For example, in rainfed palms, ψ_{leaf} was high in December (-1.10 MPa) and decreased significantly in May (-1.75 MPa) (Shivashankar et al. 1991; Voleti et al. 1993a, b). In general, ψ_{leaf} is lower in palms grown in red sandy loam than those in laterite soil. In irrigated condition, the ψ_{leaf} is maintained at relatively high level corresponding with soil moisture availability even during the non-rainy period (March to May) (Rajagopal et al. 1989b). A rapid screening method was developed based on ψ_{leaf} in excised leaflets (Rajagopal et al. 1988) for easy handling of a large number of cultivars. The

ψ_{leaf} declined with time to different degrees among the varieties, indicating the degree of tolerance. Hence, water requirement of coconut palms depends on many factors such as age, height, stomatal frequency, wax content and stomatal control (Passos and Silva 1990; Rajagopal et al. 1990; Nogueira et al. 1998).

9.3.2 Chlorophyll Index

Foliar chlorophyll content is a good indicator of plant stress and plant health because of its effects on photosynthesis and growth (Datt 1999). Environmental (drought and high temperatures) and nutrient (particularly N) stresses commonly cause loss of leaf chlorophyll content leading to poor photosynthesis, growth, biomass and economic yield. Because chlorophyll is mostly made up of N-containing enzymes and other organic compounds, stress-restricted uptake of N causes early senescence, which is commonly expressed as loss of chlorophyll content and loss of green leaf area. The ability of a plant to maintain chlorophyll content and green leaf area for a longer duration under stress will allow plants to remain photosynthetically active for a longer period of time. Heterotic hybrid seedlings of COD x WCT had higher NR activity as well as chlorophyll and carotenoid concentrations than the intermediate and dwarf types (Shivashankar et al. 1985). Non-destructive method for estimation of chlorophyll in coconut leaves is standardized (Hebbar et al. 2016c).

Chlorophyll Fluorescence Chlorophyll fluorescence is used to evaluate the plant health status, and photochemical efficiency of photosystem II (PS II; Fv/Fm) is routinely used as an indicator of the degree of stress in plants. Estimation of chlorophyll fluorescence as a measure of photosynthetic efficiency in coconut seedlings is a promising indicator to identify potential genotypes that show resistance to drought. The chlorophyll fluorescence PS II efficiency parameter (Fv/Fm), an indicator of extent of physiological stress in leaf, has been found to be higher in irrigated palms compared to the rainfed palms (Kasturi Bai et al. 2006a, b, 2008). Based on PS II efficiency (Fv/Fm) screening, coconut accessions have been classified into high and low groups. Hence, screening of drought-tolerant palms based on yield-related photosynthetic parameters could be achieved effectively by measuring chlorophyll fluorescence (Nainanayake 2007). Coconut seedlings exposed to high light intensities have low Fv/Fm and photochemical quenching than those in shade condition indicating that high light condition causes stress to coconut seedlings implying the need for protection from photo-oxidative stress (Naresh Kumar and Kasturi Bai 2009a).

9.3.3 Osmotic Adjustment

Osmotic adjustment is an important physiological mechanism to combat stress conditions, mainly under water deficit condition. Coconut palms accumulate organic solutes such as sugars and amino acids during stress period as compared to

non-stress period. Cultivar differences were not found significant in sugar accumulation during non-stress and stress periods. Generally, 6.2–16.3% increase in sugar accumulation was observed during stress period compared to non-stress period. Similarly free amino acid accumulation increased by 38% during stress period as compared to non-stress period. Drought-tolerant types accumulated more of these solutes than the susceptible types during severe stress condition (Kasturi Bai and Rajagopal 2000; Kasturi Bai et al. 2006a). Similarly, accumulation of proline, starch and soluble sugars in the leaves of coconut palms subjected to drought stress has been demonstrated. A gradual increase in proline content was observed in coconut leaves under drought though no significant differences could be observed between cultivars. Furthermore, total soluble sugar in coconut cultivars have been shown to cause osmotic adjustment during drought stress (Lakmini et al. 2006).

9.3.4 *Epicuticular Wax*

Epicuticular wax (ECW) from the leaf surface of coconut has served as an important parameter for evaluating genotypes for drought tolerance. Generally, chloroform is being used as an organic solvent for the extraction of ECW from coconut leaf surface, though benzene gives better separation of wax components (Voleti and Rajagopal 1991). A three- to fourfold increase in ECW was observed in coconut forms subjected to drought stress (Voleti and Rajagopal 1991; Kurup et al. 1993). The wax formed in the leaf surface is greatly influenced by the physiological age of palms and leaves. Seedling leaves exhibited low (almost 50% less) ECW than that on the leaves of adult palms subjected to same intensity of moisture stress. Composition of wax content during different stages of palm's growth using TLC showed qualitative differences. Hydrocarbons and esters were formed as major components during non-stress period, whereas alcohols were identified during stress period, and fatty acids were detected during post-stress.

9.3.5 *Water Consumption and Water Use Efficiency*

Evidences of efficient stomatal regulation to maintain plant water status under a mild to relatively high water deficit stress are reported (Naresh Kumar et al. 2002b; Prado et al. 2001; Passos et al. 2003, 2005; Gomes et al. 2007; Gomes and Prado 2007). It has also been documented that water requirement of a palm depends on various factors such as its height, leaf area, soil type, growth conditions, age (Nogueira et al. 1998) and weather factors (Kasturi Bai et al. 1988). Even within the coconut canopy, the lower leaves have low Pn and WUE than others (Naresh Kumar and Kasturi Bai 2009b). Furthermore, Dwarf varieties of coconut consume more water than Tall varieties because of high transpiration rate, stomatal frequency, and limited epicuticular wax on the leaf surface (Rajagopal et al. 1990), as well as a

poorer stomatal control of water loss (Passos and Silva 1990). However, some Dwarf varieties displayed better adaptation strategies to water deficit stress than Talls and hybrids owing to effective control on stomatal transpiration. The WUE has been shown to vary among varieties of Talls and Dwarfs and also among ecotypes of the same variety (Prado et al. 2001; Gomes et al. 2002). The tall genotypes, viz. Kalpadhenu and FMST, had high WUE under 100% field capacity due to their higher root biomass. On the other hand, under water deficit stress, Dwarf maintained higher WUE despite higher stomatal conductance (Hebbar and Chaturvedi 2015).

9.3.6 Biochemical Traits

Biochemical response of coconut palms to water deficit stress and information concerning the protoplasmic tolerance to drought stress has led to the conclusion that coconut leaves have efficient biochemical systems that protect cell membranes and their intracellular components. Lipid composition, lipid peroxidation level and the activities of enzymes related to oxidative stress are good indicators of dehydration tolerance in leaves of coconut. Water deficit induced a reduction in total leaf lipid content, mainly that of the chloroplast membranes, an effect particularly expressive in the less drought-tolerant genotypes (Repellin et al. 1994). In addition, an increase in the degree of lipid unsaturation in response to severe drought was also observed, which seems to be related to the maintenance of membrane fluidity, mainly in the chloroplasts (Repellin et al. 1997). Drought-tolerant coconut cultivars showed a lower level of lipid peroxidation and higher activity of catalase, superoxide dismutase and peroxidase than cultivars empirically classified as drought susceptible. Indeed, peroxidation level was negatively correlated ($r^2 > 0.73$) with activity of antioxidant enzymes (Shivashankar et al. 1991; Chempakam et al. 1993).

Hybrids, viz. LCT x GBGD, LCT x COD and WCT x COD, and the Talls, viz. JVGT, FMST, PHOT and CCNT, show higher ECW content than the other cultivars including Dwarfs. The transpiration (E) is inversely proportional to the content of ECW on the leaf surface (Rajagopal et al. 1990). Coconut palms subjected to drought stress have been demonstrated to have efficient enzymatic removal of ROS due to the increased activities of enzymes such as superoxide dismutase (SOD), catalase (CAT), peroxidase (POX) and polyphenol oxidase (PPO) (Kasturi Bai et al. 1996b; Mukesh Kumar et al. 2016) as well as acid phosphatase (APH) and L-aspartate:2-oxoglutarate amino transferase (AAT) in adult WCT palms, while activities of malic dehydrogenase (MDH) and nitrate reductase (NR) decreased (Shivashankar 1990; Shivashankar et al. 1991). Similarly, increased enzymatic activities were observed with PEG induced osmotic stress (Shivashankar 1990). However, the intensity of change was high because of rapid stress induction. Increase of APH and AAT activities in coconut leaves subjected to osmotic stress is correlated with decline in ψ_{leaf} (Rajagopal et al. 1988). Furthermore, enzymatic activity of NR decreases with a little change in relative water content (RWC) of leaves, and the activity loss was found to be high in susceptible cultivars. Besides, a

correlation has been established between thermal stability of NR *in vivo* and drought tolerance in several coconut cultivars (Shivashankar 1992). Membrane integrity studies on coconut subjected to drought stress showed negative correlation between leaf water potential and MDA content (Kasturi Bai et al. 2011). Besides drought, influence of atmospheric concentration of CO₂ and temperature are considered to be major climatic factors that influence the growth, development and productivity of coconuts (Naresh Kumar et al. 2008b). Studies on antioxidant enzymes of coconut seedlings under elevated CO₂ and temperature revealed that specific activities of the enzymes were greatly altered. Elevated CO₂ caused significant increase in the activities of enzymes such as SOD, POX and CAT, whereas elevated temperature levels reduced the POX activity even though increased activities of SOD and CAT were observed. However, the activities of PPO decreased under both elevated CO₂ and temperature conditions. Increased activities of SOD, CAT and POX are pertinent to maintain integrity of the cell. It was also proposed that increased activity of SOD and CAT compensated for the decreased activity of POX in coconut seedlings under high ambient temperature stress (Sunoj et al. 2014). Moreover, low water potential of coconut seedlings under elevated temperature is compensated due to improved antioxidant potential and hence maintained a low growth. This study also identified WCT and COD x WCT as tolerant due to greater membrane stability and lower MDA content, under changing climatic conditions.

9.4 Physiological and Environmental Constraints for Higher Productivity

Weather variables like rainfall, day/night temperature regimes, relative humidity, sun shine duration and vapour pressure deficit play pivotal roles in crop growth, development and yield. Short-term responses of coconut to water stress such as low stomatal conductance, Ψ_{leaf} , net photosynthetic rate and transpiration rate have been demonstrated as mentioned above. As coconut is a source-limited crop (Naresh Kumar et al. 2008b), low Pn rates and mutual shading of leaves in canopy contribute to yield loss, apart from external stresses. The influence of weather on nut yield in coconut starts from inflorescence initiation and lasts till nut maturity (about a 44 month period). Coincidence of dry spell with critical stages, viz. initiation of inflorescence primordium, ovary development and button size nut, significantly reduces nut yield (Rajagopal et al. 1996). See Fig. 9.3 for details.

Earlier studies also indicated relationship between rain fall, other weather variables and nut yield in coconut (Peiris et al. 1995; Peiris and Thattil 1998; Naresh Kumar et al. 2008b, 2009a, b). Longer dry spell affects the nut yield for the next 4 years to follow with stronger impact in fourth year, irrespective of the total rainfall as depicted in Fig. 9.4 (Naresh Kumar et al. 2007b, 2009a).

Climatic extreme events such as tropical cyclones affect coconut palms, and severely affected palms take about 6 years to recover to give satisfactory nut yield

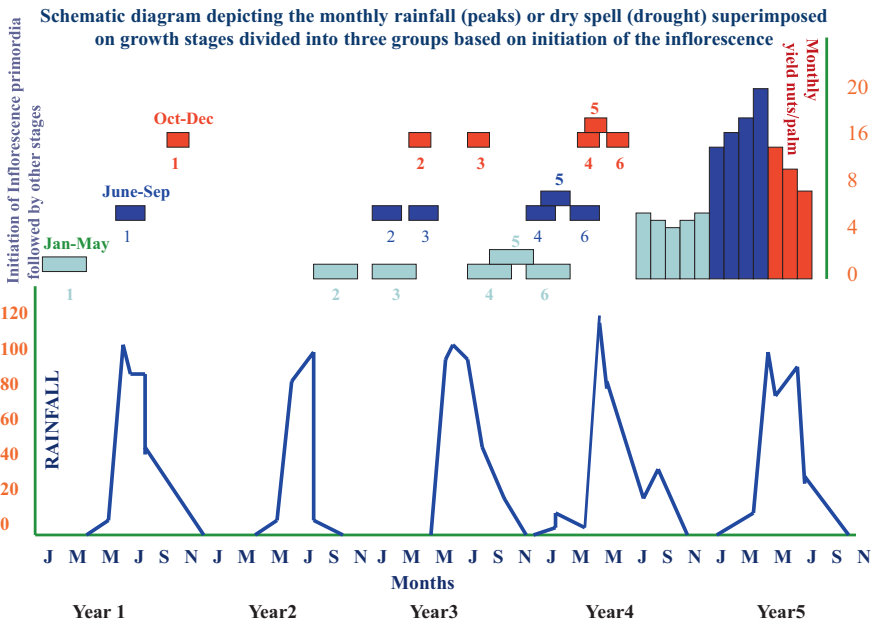
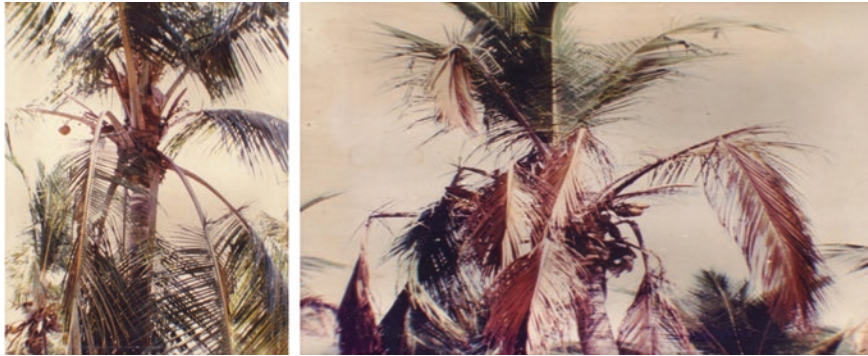


Fig. 9.3 Symptoms of drought stress in coconut palm. Coincidence of dry spell with sensitive stages of inflorescence and nut development and resultant nut yield. (redrawn from Rajagopal et al. 1996)

(Naresh Kumar et al. 2007b, 2009a; Naresh Kumar 2011a). Further, temperatures below 10 °C and above 40 °C affect effective leaf area, nut set and yield (Naresh Kumar et al. 2008b). Thus, unfavourable climatic conditions contribute to yield reduction. Simulation analysis indicated spatial variation and substantial yield gap varying from 34% to 85% depending on management in major coconut-growing regions in India (Naresh Kumar et al. 2008b). In addition to these, the biotic stresses further reduce nut yield. Therefore, genetic improvement for tolerance to biotic and abiotic stresses, as well as development of improved agronomic management to mitigate these stresses are needed for reducing yield gap.

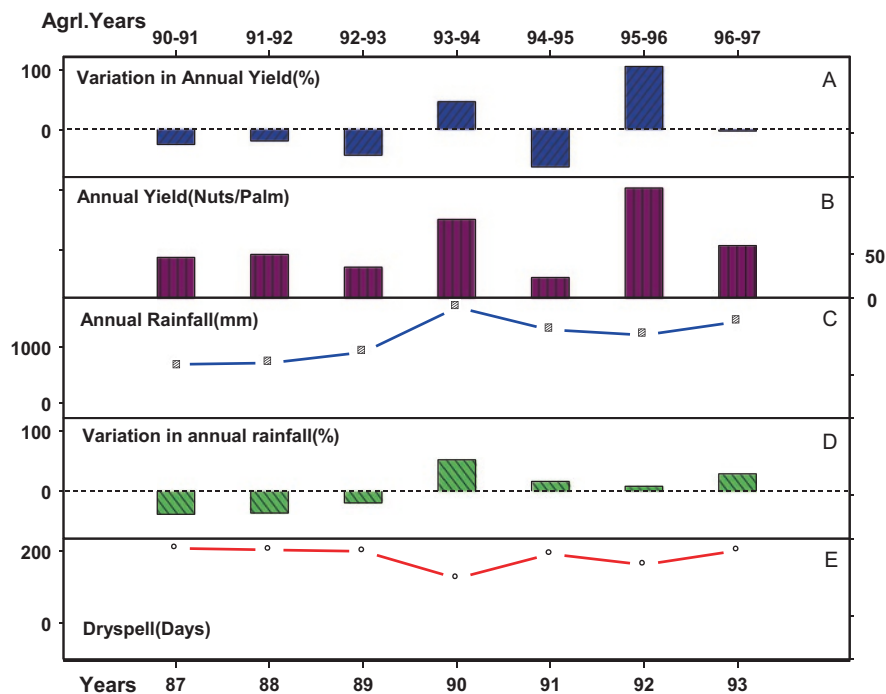


Fig. 9.4 Influence of dry spell and variation on annual rainfall on annual nut yield. Note the year lag (4 years) between lower and upper X axes. Dry spell, variation in annual rainfall and annual rainfall are represented by lower X1 axis. Annual yield and variation in annual yield are represented by upper X2 axis. Please note the difference in year in X1 and X2 axis

9.4.1 Selection Criteria for Drought Tolerance

Analysis of a range of cultivars over several years and with varying agronomic management showed drought as one of the major causes of yield loss in coconut (Rajagopal et al. 1996). The length of dry spell is positively correlated with nut yield reduction in different agroclimatic regions of India (Naresh Kumar et al. 2007b). Extensive research work carried out on coconut led to the delineation of drought tolerance mechanism (Fig. 9.5) and development of screening methods for identification of drought-tolerant genotypes (Fig. 9.6). Some of the essential anatomical, biochemical and physiological parameters such as cell size and number, sub-stomatal cavity size, stomatal frequency, epicuticular wax content, leaf thickness, stomatal resistance, water potential components, cell membrane stability and scavenging enzyme activities have been stipulated for assessing moisture stress in plants (Rajagopal et al. 1991, 2005; Kasturi Bai 1993; Champakam et al. 1993; Rajagopal and Kasturi Bai 2002; Naresh Kumar et al. 2000a, 2006a, 2016b). Some or all of these parameters were extensively used to screen coconut germplasm for drought tolerance (Pomier and de Taffin 1982; Rajagopal et al. 1990; Kasturi Bai

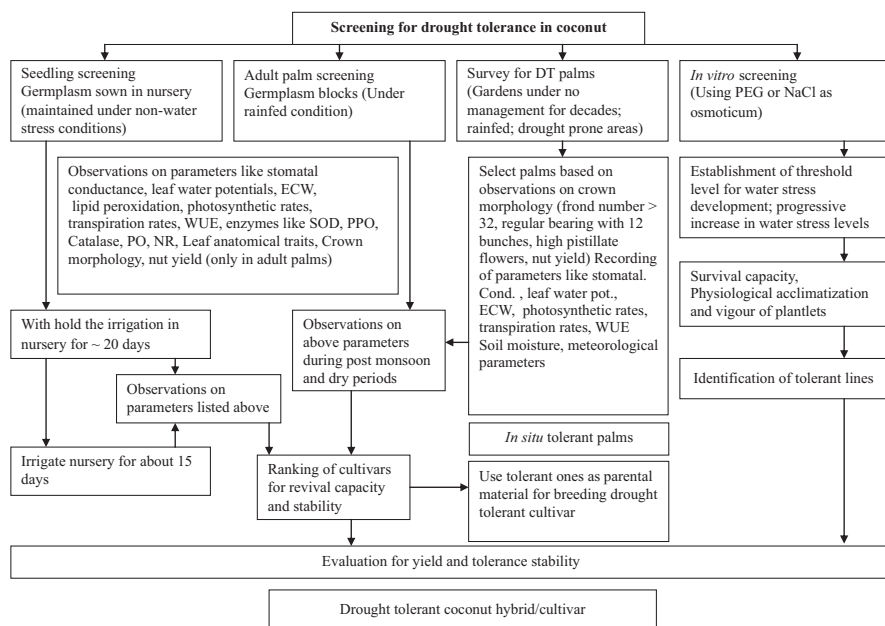
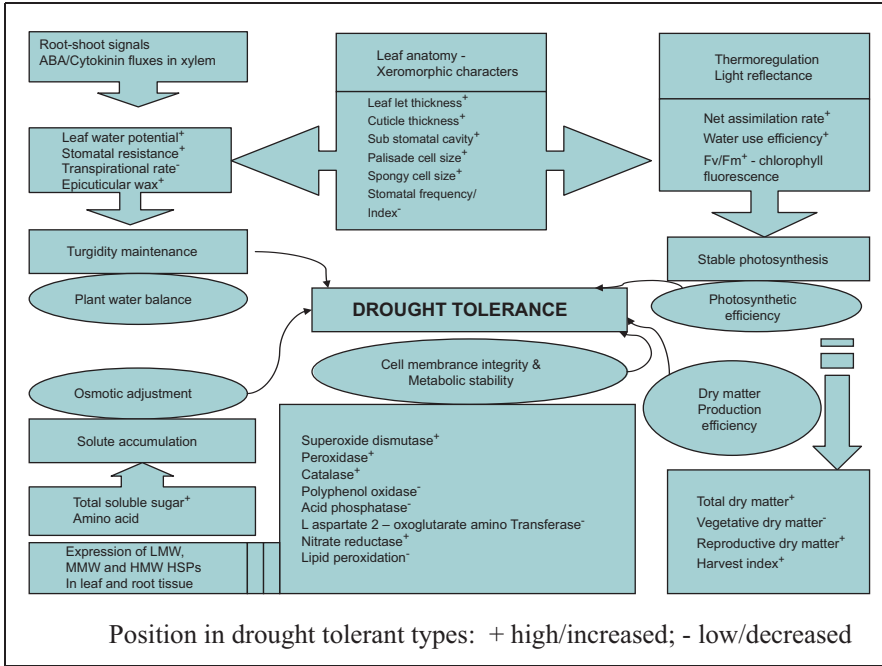


Fig. 9.5 Strategies for screening drought-tolerant germplasm/varieties in coconut. (Source: Naresh Kumar et al. 2016a, b)

1993; Repellin et al. 1994; Naresh Kumar et al. 2000a). Screening of parental lines and hybrids at the nursery stage indicated variations in tolerance to drought stress. The drought-tolerant cultivars/hybrids included were WCT, LCT, FMS, WCT x COD, LCT x GBGD and LCT x COD. Screening at the adult palm stage indicated WCT x WCT, FMST, LCT, WCT x COD, LCT x GBGD and LCT x COD as drought tolerant and MYD as drought susceptible (Rajagopal et al. 2000a, b).

9.4.2 Other Abiotic Stresses

Abiotic stresses that affect the growth, development and yield of coconut include flood, high light intensity and temperature apart from drought stress. Tropical cyclones uproot the palms, while flooding for long duration causes anoxia stress to roots affecting the water and nutrient uptake. The heat-stable protein fraction (HSPF) increased in leaf tissue of seedlings subjected to stresses like water scarcity, high temperature and flooding (Naresh Kumar et al. 2007a). The HSPF increased despite a decrease in total protein concentration. The HSPs that expressed during stress included ~66 KDa and ~76 KDa (water stress), ~66 KDa and ~76 KDa and LMW HSP of 14.4 KDa (high light intensity of ~1500 mmol/m²/s) ~30 KDa and ~17 KDa (temperature and flooding). The LMW protein (~20.1 KDa) disappeared during water stress, while a ~30 KDa protein in root tissue was observed under temperature stress (Naresh Kumar et al. 2007a). High light intensity, as mentioned



Functional relationship in mechanism of drought tolerance in coconut

Fig. 9.6 Adaptive strategies of coconut palm under stressful conditions. (Source: Naresh Kumar et al. 2016a, b)

earlier, causes oxidative stress with cascading effects such as membrane lipid peroxidation, reduced photochemical quenching, reduced water potential and chlorophyll bleaching leading to leaf scorching and seedling death (Naresh Kumar and Kasturi Bai 2009a). More details on the effect of abiotic stresses on coconut are presented in several publications (Naresh Kumar et al. 2016b).

Coconut is capable of using Na effectively, and application of NaCl is recommended. Coconuts grown on beaches and near brackish waters indicated salt tolerance. For instance, dwarf coconut seedlings are tolerant to a salinity level of 5.2 dS m⁻¹ and moderately tolerant to salinity of 10.1 dS m⁻¹. This indicates the possibility of using saline water for raising quality seedlings. Moreover, studies on organic solute retention revealed that root system of dwarf coconut plays a role in tolerance of seedlings to salinity (Lima et al. 2017).

9.4.3 Biotic Stresses

The physiological responses of palms to pathological diseases like root (wilt), lethal yellowing and basal stem rot were used to develop diagnostic techniques for early detection of diseases.

9.4.3.1 Root (Wilt) Disease (RWD)

It is the most serious malady affecting the coconut palms in India causing impairment in the physiology and biochemistry, viz. derangement in the root functioning, mineral nutrition, water relations, respiration, photosynthesis and phenol metabolism of palms.

In diseased palms, the number of functional roots reduces due to poor regeneration capacity. Membrane integrity of leaf and root tissues is affected in diseased palms. Root sap of apparently healthy palms is acidic, odourless, clear and rich in potassium and magnesium content, whereas the root sap of diseased palms is neutral to alkaline and poor in potassium and magnesium content. Solid content is more in the root sap of diseased palms than that of healthy palms (Ramadasan 1964). Application of hormones, phenols and amino acids in the debarked region of the stem just above the bole could induce new roots. Palms which received IBA 500 ppm and phenols 400 ppm produced maximum number of roots followed by NAA 500 ppm and glutamic acid 500 ppm (Sumathy Kutty Amma and Patil 1982).

Abnormal stomatal opening in the diseased palms with impaired regulation leads to excessive transpiration and low leaf water potential, irrespective of the time of the day, season or growing condition (Table 9.2). With the advancement of disease, increased disturbance in stomatal regulation resulted in excessive water loss. Root (wilt) affected palms had consistently lower ψ_{leaf} than the healthy palms at any given time (Rajagopal et al. 1986, 1987).

The flow rate of phloem sap from the inflorescence of coconut depends on the age and disease severity (Rajagopal et al. 1989a). In general, in a palm, 4 to 5 inflorescences yield the phloem sap. However, rate of sap flow decreases when the successive inflorescences are tapped (Fig. 9.7).

The rate of sap flow is higher during the day than at night, and the sap quality also varies in pH, osmotic concentration and total and reducing sugars which are generally higher during the day (Rajagopal et al. 1989a). The concentration of biochemical constituents was low in the phloem sap collected from inflorescences of diseased palms. Concentrations of arginine, aspartic acid and tyrosine as well as

Table 9.2 Changes ψ_{leaf} (Mpa) with age of leaf and leaflet condition in root (wilt) affected palms

Leaf position in canopy	Apparently healthy palm	ψ_{leaf} (Mpa)	Diseased palm	ψ_{leaf} (Mpa)
Spindle	Yellow to light green thick, stiff	-0.37	White to dull cream, thin papery, brown spots	0.72
First whorl	Green, normal, erect	-0.68	Light green, slight flattening and bending at the tip	-1.24
Middle	Dark green normal, erect	-0.79	Flaccidity, yellowing, necrosis	-1.28
Outer whorl	Dull green, senescent, but normal	-0.89	Ribbing, necrosis, abnormal, senescence	-1.26

Rajagopal et al. 1986

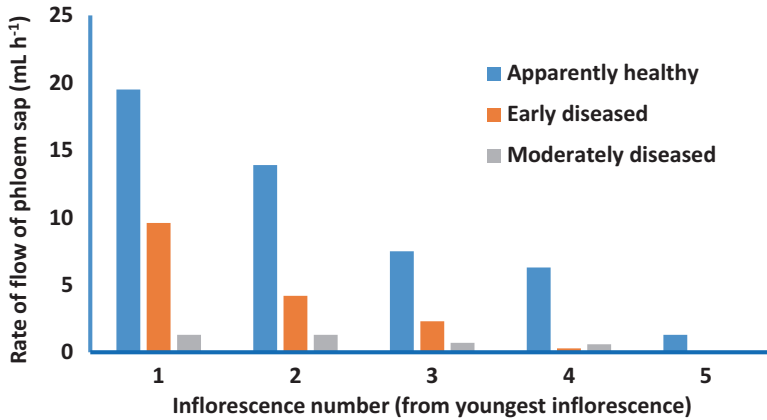


Fig. 9.7 Rate of flow of phloem sap (mL h⁻¹) from successive inflorescences

glucose and galactose were higher in sap from the diseased palms than from apparently healthy palms (Chempakam et al. 1991).

The root (wilt) diseased palms show higher respiratory rates in leaf and roots compared to apparently healthy palms (Michael 1978). On the other hand, chlorophyll concentration and photosynthetic rates are high in apparently healthy palms compared to those in root (wilt) affected palms. An impairment of sugar metabolism, translocation and distribution and a reduction in the C/N ratio were noticed in the roots and leaves of diseased palms (Varkey et al. 1969). Derangement in the nitrogen metabolism resulted in increase in the nonprotein nitrogen content, concomitant with a sharp decrease in the water-soluble nitrogen and protein nitrogen fractions in the diseased tissue (Padmaja et al. 1981). Free amino acids in the leaves, particularly arginine, increases with the incidence and intensity of the disease. The activity of carbonic anhydrase (CA), the enzyme-limiting carbon metabolism, is low in leaves of diseased palms as compared to that in healthy palms. On the other hand, higher activity of cellulase and pectin lyase activity was noticed in roots of diseased palms as compared to the healthy ones (Padmaja and Sumathykutty Amma 1979). Isotopic (³²P) studies revealed delayed uptake of phosphorus in diseased palms compared to healthy palms (Dwivedi et al. 1979). This indicates less utilization of absorbed phosphorus in the synthesis of phosphorus constituted organic substances in diseased palms.

Physiological Trait-Based Diagnosis for Early Detection Based on the abnormal stomatal opening phenomena in diseased palms, an early diagnostic tool for root wilt has been developed. In this method, stomatal resistance is used as a criterion for the pre-visual detection of root (wilt) disease in coconut (Rajagopal et al. 1988). This is comparable to the serological test, using the cross-absorption technique, to detect the disease before the manifestation of visual symptoms. Both the tests could detect disease-affected palms 6–20 months earlier than the actual manifestation of flaccidity symptom. Stomatal resistance determinations are also employed for diag-

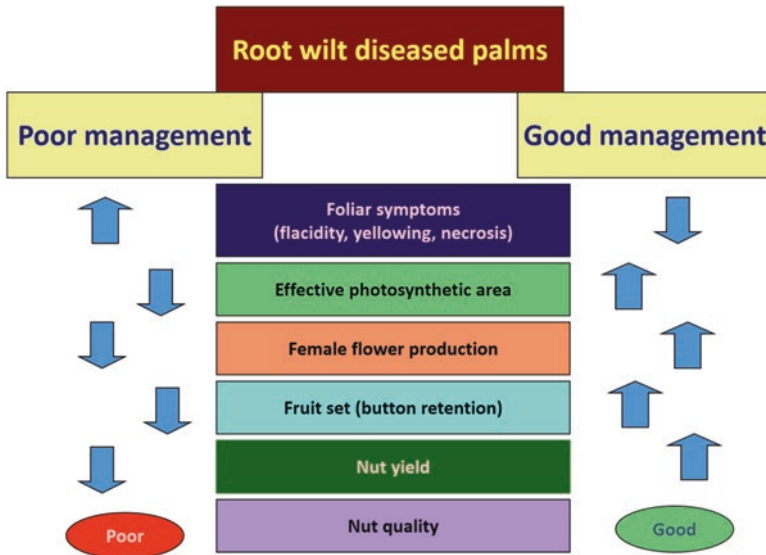


Fig. 9.8 Influence of good management on source and sink parameters and yield of root (wilt)-affected coconut gardens

nosing the lethal yellowing affected coconut palms (Eskafi et al. 1986). The leaf water potential measurements are also effective for the early diagnosis of palms affected by phytoplasmas as shown both in LYD (Eskafi et al. 1986) and RWD (Rajagopal et al. 1986).

Physiological Basis for Management of Root (Wilt) Disease The CGD (Kalpasree) is identified as a relatively tolerant variety to root (wilt) disease. Kalpa Sankara (CGD x WCT) has been released for cultivation in the RWD affected tracts, considering its low disease incidence and high yield potential (Shareefa and Regi Thomas 2016). Management of coconut root (wilt)-affected gardens and managing leaf rot are viable options to maintain nut yield in affected gardens (Fig. 9.8). Increase in photosynthetically active LA resulted in improved TDM production resulting in higher nut yield.

9.4.3.2 Lethal Yellowing Disease (LYD)

Physiological and biochemical disorders in LYD-affected palms have been reported by Eskafi et al. (1986). Extensive root necrosis observed in diseased palms (Eskafi et al. 1986) has been correlated with foliar yellowing (Eden Green and Waters 1982). Lower stomatal conductance during noon, concomitant with greater stomatal closure, has been observed in LYD-affected coconut palms than in healthy palms (Eskafi et al. 1986). A permanent stomatal closure was observed with the

development of LY symptoms. Ψ leaf was in the range of -0.1 to -1.0 MPa between night and midday in healthy palms, whereas diseased palms rarely exhibited Ψ leaf lower than -0.4 Mpa. This implies that stomatal closure is exhibited in the diseased palms (Mc Donough and Zimmermann 1979). Decrease in turgor, osmotic and water potentials with disease intensity were also observed (Leon et al. 1995). Due to the permanent closure of stomata, water transport through xylem was affected in LYD-affected palms. When ^{32}P was applied at the base of the petiole of diseased palms, xylem transport was reduced by 75%, while the reduction was 100% when applied through either stem or roots (Eskafi et al. 1986). The photosynthetic rate and protein content were maintained at higher level during the early stages of the disease, whereas during the advanced stage, a sharp decline in these traits was noticed. Free amino acids and disease susceptibility are related (McCoy et al. 1983). Arginine content in the leaf is an important diagnostic tool for the early detection of LY disease. Sharp decline in respiration, total sugars and reducing sugars has been observed in both the primary and secondary roots of LYD-affected palms (Oropeza et al. 1995).

A comparison made between the LY disease of Jamaica and RWD of India (Rajagopal 1991) showed certain similarities and distinct differences in some of the characteristics (Table 9.3). Although both are caused by phytoplasmas, LYD-affected palms differ from the RWD not only in the primary foliar symptoms but also in the water relations. The water transport is affected to different degrees in both the diseases, but it is the stomatal regulation which seems to play a key role in the ultimate expression of foliar symptoms. Rapid closure of stomata due to infection led to a

Table 9.3 Comparison between the lethal yellowing disease and root (wilt) disease

Description	LYD	RWD
Earliest record/location	1904, Cayman Islands	1874–1884, Kottayam, Kerala, India
Symptoms, primary associated	Yellowing, inflorescence necrosis, immature fruit drop	Flaccidity, yellowing, necrosis
Nature of disease	Lethal	Debilitating
Causal organism	Phytoplasma-like organisms	Phytoplasma-like organisms
Insects associated with transmission	Plant hopper (<i>Haplaxius crudus</i> (van Duzee))	Lace bug (<i>Stephanitis typica</i>) and <i>Proutista moesta</i> (Westwood)
Transmission through	Not done	<i>Cassytha filiformis</i>
Water absorption/transport	Decreased	Decreased
Stomata	Closed	Abnormal opening
Transpiration rate	Normal	Excessive
Leaf water potential	Low	Low
Early diagnosis	Stomatal resistance and water potential	Serological reaction, Stomatal resistance, water potential
Flow of phloem sap	Nil or very low	Low
Arginine content	High in leaves	High in leaves and phloem sap
Antibiotic therapy	Tetracycline	Tetracycline

Modified from Rajagopal (1991)

typical symptom expression, viz. yellowing in LY diseased palms, whereas impaired stomatal regulation (abnormal opening) led to excessive transpirational loss of water and resulted in wilt (flaccidity) symptom in RWD palms. Interestingly, although both the water absorption and transpiration rates are affected, the RWD remained as a debilitating disease in contrast to the lethal nature of LY disease. This shows that the metabolic status of these palms differed in some respects. The insects involved in the transmission of phytoplasmas are also different for the two diseases.

9.4.3.3 Basal Stem Rot

Basal stem rot (BSR) disease of coconut is caused by two species of *Ganoderma*, viz. *Ganoderma applanatum* and *Ganoderma lucidum*. The disease is referred to as Ganoderma Wilt or Thanjavur Wilt or Anabe roga in different parts of India. In Sri Lanka, the disease is caused by *G. boninense*. The diseased palms are characterized by low stomatal resistance and high transpiration rate, as compared to healthy palms. The transpiration rate increases with the severity of the disease, and higher transpiration rates are observed at least 6 months before the expression of disease symptoms. In diseased palms, the contents of mineral nutrients, viz. N, P, K, Ca and Mg in the leaf, stem, bole and root tissue, decreased (Anbalagan et al. 1987). An increase in total phenols (20–35%) and orthodihydroxy phenols (40–48%) and a reduction in total and reducing sugar levels have been noted in the diseased palms. Impairment in membrane stability has also been observed in the diseased palms as expressed by high electrolyte leakage in root and leaf tissues of diseased palms than in healthy palms. Similarly, the leaves of diseased palms show a reduction in the relative water content as compared with healthy leaves. For the early detection of disease, EDTA colour test was employed (Natarajan et al. 1986).

9.5 Conditions for Optimum Growth and Yield

The coconut palm (*Cocos nucifera* L.), mainly a crop of humid tropics, grows mostly between 26°N and 27°S and up to the altitudes of 600 m above mean sea level. A well-distributed rainfall (annual rainfall between 130 and 230 cm), mean annual temperature of 27 °C with diurnal variation of 5 °C and abundant sunlight ranging from 250 to 350 W m⁻² with annual sunshine of 2000 h (at least 120 h per month) are optimum conditions for good growth and nut yield in coconut.

9.5.1 Characterization of the Growing Environment

Inadequate or uneven distribution of rainfall and summer dry spells cause water stress situation in rainfed plantations. Minimum temperature of above 10 °C is required for flowering, whereas a temperature below 10 °C for a month causes nut

fall, and similarly, temperature above 40 °C during April–July leads to decline in effective functional leaf area index, dry matter production and consequently nut yield (Naresh Kumar et al. 2008b). Prevalence of high ambient leaf temperatures and high VPD (Escbach et al. 1982; Rajagopal et al. 2000a), low water potentials (Repellin et al. 1997; Rajagopal et al. 2000a) and stomatal and non-stomatal limitations (Gomes et al. 2008; SijuThomas et al. 2008) lead to impaired photosynthetic rates and lesser dry matter accumulation resulting in low yield. Coconut being a perennial crop, previous years' rainfall influence total annual yield (Peiris et al. 1995; Peiris and Thattil 1998). The inflorescence and nut development stages are more sensitive to the coinciding dry spell (Rajagopal et al. 1996). Coconut adapts to different weather conditions through accumulation of biochemicals (SijuThomas et al. 2006). Besides, the quantum of rainfall and length of dry spells experienced over the preceding 4 years heavily hamper the productivity of coconut in different agroclimatic zones of India (Naresh Kumar et al. 2007b). Weather change in the past has been influencing the coconut yields in India (Naresh Kumar et al. 2009b). In coastal Andhra Pradesh, 1995 cyclone severely affected coconut palms and it took seven years (2003–04) to recover to pre-cyclone period yield levels (Naresh Kumar 2011b).

9.5.2 Physiological Optimization for Growth and Development in Resource Constraint Environments

Physiological-Based Agronomic Management Options Coconut palms exposed to moisture stress for 16–24 days show a reduction of 15–18% in vegetative dry matter (VDM) and 20–22% reduction of reproductive dry matter (RDM) production compared to control palms kept under well-watered conditions. Similarly, palms grown under rainfed conditions showed a reduction of 29% in RDM and 19% in VDM (Rajagopal et al. 1989b). Drought management strategies mainly include the conservation of available soil moisture and efficient use of available water resources for high production. Improvement of soil moisture status through conservation measures such as burial of husks or coir pith in basins, mulching of dried leaves including gliricidia, farm waste and compost application in the basins resulted in increased nut yield (Rajagopal and Naresh Kumar 2001; Naresh Kumar et al. 2006b). Application of water greatly increased photosynthetic rates and improved stomatal conductance. Moreover, irrigation significantly increased the Pn rates and stomatal conductance. Among the various methods of irrigation, drip irrigation resulted in conducive physiological efficiency of source and sink for high yield and water use efficiency (Table 9.4) Naresh Kumar et al. 2002a). Palms grown under drip irrigation have been demonstrated to have high leaf water potential that could be attributed to better regulation of stomatal conductance leading to improved water use efficiency. Efficient irrigation conditions such as drip irrigation improved production of female flowers and nut set. Other agronomic practices for soil management

Table 9.4 Source-sink response of coconut to different water availability conditions

Source	Sink	Condition	Yield and WUE
Low ψ_{leaflets} , E , g_s and P_n	<i>Less FFP and nut retention</i>	Rainfed	Low/low
Low ψ_{leaflets} , high E , g_s and P_n	<i>More FFP and nut retention</i>	Basin irrigated	High/low
High ψ_{leaflets} , medium E , g_s and high P_n	<i>More FFP and nut retention</i>	Drip	High/high

to conserve soil water include organic farming and tillage practices like summer ploughing, soil mulching and addition of soil stabilizers.

Among the nutrients, potassium chloride or sodium chloride nutrition imparts drought tolerance to coconut through stomatal regulation (Braconnier and Bonneau 1998). Absence of chloroplasts in the coconut leaf guard cells causes non-availability of malate. The Cl ion possibly replaces malate as an osmoticum to maintain water potential. Hence Cl ion (from KCl or NaCl) is essential for coconut growth in dry conditions. By maintaining cell osmoregulation, the Cl ion increased water absorption and reduced transpiration from leaf (Escbach et al. 1982; Ollagnier et al. 1983). The critical level of Cl in 14th leaf is about 0.7%. Application of KCl increased the drought tolerance of palms under dry conditions as potassium nutrition also plays an important role in drought tolerance in coconut (Ollagnier et al. 1983; Rajagopal et al. 2000b; Rajagopal and Naresh Kumar 2001). Deficiency of K and Cl results in yellowing and drying of leaves due to impaired water potential. Palms fertilized with higher levels K_2O have shown higher stomatal regulation under rainfed condition. For water logging situations, planting on raised bunds is a good practice. The seedlings are to be provided with shade to protect from high light intensity stress.

Improving Genotypic Adaptation Genetic analysis of drought-responsive physiological traits such as water potential, P_n and transpiration indicated that transpiration rate and leaf water potential showed higher specific combining ability effects due to predominant nonadditive gene action (Rajagopal et al. 2007). Using morphological criteria (number of leaves, nut yield), physiological parameters (P_n , g_s , WUE), stable isotope discrimination (C^{13}) and biochemical constituents, some in situ drought-tolerant palms were identified for use in population improvement programme (Naresh Kumar et al. 2002b). Strategies for improving drought tolerance in coconut (Fig. 9.5) need to be implemented for improving coconut yield especially in rainfed conditions and water-limited conditions (Naresh Kumar et al. 2016a).

9.6 New Tools for Complex Tasks

From early 2000, plant physiology research in plantation crops has been integrated with information processing and molecular biology to enhance the potential for exploiting physiological understanding in crop improvement. Spectral reflectance signature based on the chlorophyll character can be used to identify the vegetation or material, if the sensing system has sufficient spectral resolution to distinguish particular spectrum of the targeted vegetation or material. Though as early as 1968 the first application of remote sensing technology in agriculture was on mapping coconut root (wilt) affected area, it was not taken forward. Limited effort has been made to obtain biomass, vigour and canopy cover on a temporal and spatial scale using Remote Sensing and GIS. It has huge potential in determining the coconut area and crop condition. In combination with simulation model, the technology can be used as decision support system for improved management for higher productivity. Simulation models enhance the ability to handle large amount of data and to explore the dynamics of physiological processes and their complex interactions with the environment. Development of simulation model (InfoCrop-COCONUT) opened up several possibilities for spatiotemporal studies (Naresh Kumar et al. 2008b). Model-based assessment of coconut productivity under the current scenario and changing climatic scenarios in the future has been worked out. This study also warned that where productivity levels are expected to be gaining, current poor management practices would be limiting factors to reap the benefits of elevated CO₂ levels in future climatic scenario.

Though application of genetic engineering and genome editing is limited in plantation crops, the molecular biology studies are improving the understanding on stress responses of coconut. Expression of low, medium and high molecular weight stress proteins in seedlings exposed to drought stress is reported (Naresh Kumar et al. 2007a). The RAPD and ISSR markers which correlated with leaf water potential in coconut cultivars are identified (Manimekalai et al. 2004, 2005). Water stress-related MAPK genes were sequenced in coconut (Bobby et al. 2012). Though a viable regeneration technique is yet to be achieved, efforts are going on to develop molecular markers for drought tolerance for marker-assisted selection (MAS). From the RFLP analysis (Lebrun et al. 1998, 1999) to SCoT analysis (Rajesh et al. 2017), several studies have quantified the genetic relationship and diversity among coconut accessions. A cDNA clone (467 bp) encoding MAPK, significantly homologous to that of maize, rice and wheat, was isolated from leaves of water-stressed coconut plantlets. Coconut MAPK belongs to the serine/threonine kinases plant TEY MAPK subfamily group A (Bobby et al. 2012). The water stress-responsive candidate genes such as AP2, CBF, MAPK, NAC and 14-3-3 were upregulated during stress. These, as well as new molecular markers and techniques, will be extremely useful to identify the lines with desirable traits for crop improvement.

9.6.1 Simulation Modelling of Growth and Development

Simulation models are being increasingly used as decision support systems in agricultural management. Crop simulation models are effective tools for the assessment of growth and yield of crops in diverse environmental and management conditions. These are being used for identifying optimal resource management options, desired cultivar characteristics, performance evaluation of weather forecasters, regional yield prediction, yield gap analysis, crop zonation, research need identification and climate change studies. They become even more important for perennial crop management and for research and development decisions. A model for simulating growth, development and yield of coconut, InfoCrop-COCONUT, was developed, calibrated and validated using data on palm, soil and weather over the years (Naresh Kumar et al. 2008b). The InfoCrop model developed not only could simulate dry matter production of coconut, DM partitioning and nut yield but also was useful for ascertaining potential coconut yields in various agroclimatic zones of the country (Naresh Kumar et al. 2008b). Furthermore, the model obviates the need for agronomic or plant breeding experiments as it can help simulate multilocation trials and forecasts yield levels of coconut. Using the model, climate change impacts on coconut plantations in India, adaptation options and adaptation gains were quantified at spatial scale (Naresh Kumar and Aggarwal 2013). The assessment indicated positive impacts of climate change on coconut in the western coastal region, Kerala, parts of Tamil Nadu, Karnataka and Maharashtra and also in North-Eastern states, islands of Andaman and Nicobar and Lakshadweep, while negative impacts are projected for Andhra Pradesh, Odisha, West Bengal, Gujarat and parts of Karnataka and Tamil Nadu in India. On all India basis, even with current management, climate change is projected to increase coconut productivity by about 1.9–6.8% towards the end of the century. A study indicated the current productivity can be improved by 20% to almost double if all plantations in India are under improved management.

9.7 Future Strategy

Classic plant physiological techniques have been effectively employed to study the physiology of coconut which helped identification of cultivars or forms suitable for drought tolerance, improved water use efficiency, photosynthetic efficiency and with good root characteristics. Further, suitable climatic parameters have been worked out to identify target environment, and operating future environment has also been identified using simulation model and growth gains under elevated CO₂ and temperature. Future thrust may involve identification of natural sources of resistance to biotic and abiotic stresses using advanced phenomics, metabolomics, proteomics and genomic analysis approaches complementary to physiological and biochemical studies. Evaluating identified drought-tolerant genotypes in different agroclimatic zones, and using identified in situ drought-tolerant palms in population

improvement programmes should be strengthened. Detailed physiological studies are required on developing physiological thresholds for sensor-based precision management practices. There is also a need to develop DSS for coconut management using simulation model and remote sensing technology. The simulation model can be used to optimize the plantation management, identify research and development priorities and optimize the multilocation experimentation, among many other potential applications such as precision management of plantations.

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