Chapter 7

Physiology

☆ *K.B. Hebbar*

1. Introduction

The development of plant physiology in coconut is closely related to the general development of it as in other crops. However, plant physiology in coconut possesses some distinct features of its own; it is considered not only as the science concerned with the life of plants but also as a tool to identify solution to the frequently facing problems. The physiological data on the seedling characters and the equations developed for leaf area and dry matter production proved to be valuable tools for application in nursery selection. Physiological processes like leaf water potential, stomatal conductance, photosynthesis, chlorophyll fluorescence etc. are assisting in evaluating the performance of germplasm lines across target environments and thus essential for improving breeding programs. The experimental evidence provided by biochemical studies greatly helped in the identification of phenotyping traits, which assisted in the evolution of varieties suitable to specific regions, and the development of various management practices for the crop adaptation

Research on coconut physiology began in the 1970s. In India, the division of plant physiology and biochemistry came into existence with the inception of Central Plantation Crops Research Institute under Indian Council of Agricultural Research Institute in 1970. The importance of processes like water and nutrient absorption in coconut was felt as early as 1916 and accordingly classical studies on roots and its spread was conducted. In India, the then Deputy Director of Agriculture H.C. Samson realized the importance of water and nutrients to the coconut and accordingly a classical study was initiated to study the root system so as to understand the rate of water and nutrient uptake, zone of absorption and the depth and spread of root system. This understanding helped in deciding the place of manure application and effective root zone distance to be maintained between the trees and later became one of the important traits in the selection of drought tolerant genotypes. Now root architecture has become one of the important selection criteria, especially in the many environments characterized by low water and nutrient availability which influences productivity.

The 1970s and 1980s saw the emergence of a very active research group in plant physiology and biochemistry to find the etiology of root wilt disease at Kayankulam and to decipher the reasons for wide gap in productivity. Despite inadequate facilities, contributions were made initially in terms of understanding the morphology and growth studies. As seedling selection is of paramount importance in establishing a stand of superior yielders, criteria for selection of vigorous seedlings is done on the basis of a few easily measurable morphological characteristics. 1980s and 1990s saw a rapid change in terms of manpower recruitment and the procurement of sophisticated equipments. The division of plant physiology and biochemistry could purchase many modern and sophisticated equipments like photosynthetic system, porometer, water potential system, spectrophotometers, centrifuges etc. They not only helped in unraveling the basic processes contributing to the productivity but also in characterizing important abiotic stresses like drought. Further, it helped in dissecting biological and environmental constraints to adaptation, and for assessing the relative magnitude of the effects of individual genotype and or environmental factors. It helped to establish a robust screening method and set priorities and strategies for subsequent breeding and agronomic research. Here in this chapter the ways in which physiology has been exploited in improving the productivity of coconut is discussed.

2. Growth Analysis

2.1. Seedling Vigor

At the initial stages before the procurement of equipments contributions were made initially in terms of understanding the morphology and growth studies. As seedling selection is of paramount importance in establishing a stand of superior yielders, criteria for 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 (Ramadasan *et al.*, 1980a). Since growth is a function of leaf area development and dry matter (DM) production, the physiological approaches employed to identify superior seedlings area by correlating the phenotypic characteristics to the seedling vigour (Liyanage, 1953; Menon and Pandalai, 1958). Several regression equations have been developed for non destructive estimation of leaf area and dry matter production (Marar and Pappachan, 1964; Foale, 1968; Satheesan *et al.*, 1983). The LA of six month-old seedlings correlated (r^2=0.55) with SDM of 12 month old seedlings (Kasturi Bai and Ramadasan, 1996a). This implies that the efficiency/vigour of the seedlings can be determined before the attainment of complete autotrophy. Breeders and physiologists, undoubtedly, benefited from a method of leaf area estimation that is fast, inexpensive, and reliable, does not require destruction of the leaves, and is sufficiently manageable for use in field experiments.

2.2. Leaf Area and Dry Weight

A method to estimate the area and dry weight of the leaf non-destructively was developed (Ramadasan and Jacob Mathew, 1987). Regression equations for the estimation of leaf area (LA) and dry weights were developed taking into account all the absolute values derived from the base, middle and top three 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 six 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 LA of individual leaf ranges between 3.8 and 5.1 m^2 where as the dry weight ranges from 0.97 to 1.36 kg. Differences in area and dry weight between the leaves in a palm are low. Thus, the total canopy area as well as total dry weight produced per unit time can be estimated by multiplying the estimated leaf area or dry weight of single leaf by the number of leaves produced in a year. Variations exist in the leaf area and dry weights among the cultivars. Equations for non-destructive estimation of the total LA based on the LA of 12 leaflets and total number of leaf lets per leaf (Jayasekara and Mathes, 1992), and for the determination of the dry weight of the leaf by measuring the width and depth of the petiole (Friend and Corley, 1994) were developed.

2.3. 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, 1980b). 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 C_3 species, as against high tissue density and low air space volume in C_4 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 size cells than lower epidermis. Cuticle on upper epidermis is two-fold thicker than the cuticle on lower epidermis (2.49 µm). Cuticle is even thicker at midrib and edges of leaflet. Coconut leaflets are hypostomatus. The guard cells have hook-like protuberances at both ends, a characteristic typical to Palme. Elongated epidermal cells surround the guard cells along their entire length. These cells are larger than guard cells on the lower epidermis multi -cellular, shortly stalked scales occur at regular intervals in short depressions. These scales contain tannins (Menon and Pandalai, 1958; 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 has very thin cuticle on both sides. Upper epidermal cell size, guard cell size, xylem tracheide lignification and sub-stomatal cavity size, hypodermal cell size also vary among the cultivars.

2.4. Flowering

Commencement of flowering in coconut is denoted 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 five years or at the 45th leaf stage of growth or beyond (Patel 1938). Both cultivar and environment influence spadix formation. Spadix initiation is high 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.

2.4.1. Factors Influencing the Onset of Flowering

In fruit trees, a high carbohydrate reserve in the stem is an essential pre-requisite for early initiation of flowering. In coconut differences exist in the carbohydrate fractions between the cultivars during different seasons in a year. Hybrids are superior to tall (WCT) in their efficiency in the 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, 1983). This shows that the period from August to October, when the sunshine hours as well as precipitation are adequate, is critical for the emergence of the first inflorescence since only during this period maximum mobilization of carbohydrate in the form of soluble fraction occurs (Kasturi Bai and Ramadasan, 1983).

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 that have not flowered (Ramadasan and Mathew, 1984). Not only the development of inflorescence but also 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, 1958), 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 the stem and leaf and a decrease in the soluble fraction. A positive correlation was observed between the insoluble fraction and the female flower production, whereas the sugar content showed a negative correlation (Kasturi Bai and Ramadasan, 1983).

Hastening the age of flower production is of particular interest in palms which do not flower for 5 to 10 years. Exogenous application of gibberellin and kinetin (500 ppm and 1000 ppm) enhanced only the elongation of the petiole of the youngest leaf emerging after the treatment, but the rate of leaf growth was slow. However, by injecting 1000 ppm gibberellin into the trunk of two year old seedlings, flowering could be induced in the 36th leaf axil instead of 45th leaf axil. Thinning of immature bunches at four months of maturity and extraction of the inflorescence sap, increased female flower production (Mathes, 1988).

2.5). 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.

Total nut production per palm per year shows great variation among the cutivars/hybrids, but bunch production or spikelet per bunch does not vary significantly among them. However, female flower production varies significantly among the cultivars/hybrids (range 100 to 400). Higher female flower production is observed in hybrids than in the cultivars. The genotypic differences in crop yields could be attributed to variations in the amount of assimilates synthesized (source capacity), in the capacity for storage of assimilates (sink size), and in efficiency of the transport system. Methodologies have been developed to quantify dry matter accumulation in different parts and growth functions were developed, which are helpful in explaining the partitioning of synthesized assimilates to different plant organs throughout the life cycle of the plant.

2.6. Total DM Production (TDM)

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 highest 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 the Ivory Coast (Corley, 1983). This indicates that there is a huge gap in the realization of yield and the production potential of the palms.

2.7. 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 Jacob Mathew (1987). coined the term 'Annual Productivity Index (API)'. They worked out HI in coconut by taking into account annual increment in DM production and expressed as the ratio of the dry weight of the economic product to total dry matter production. Being a crop of continuous productivity API is an appropriate criterion comparable to the harvest index 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 0.4-0.5 in a group of palms in which the annual yield of nuts 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.*, 1996). The hybrids gave higher harvest indices indicating better nut composition than talls and dwarfs. The HI based on the copra out turn ranged from 0.13- 0.23.

2.8. 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 (Patel, 1938). The relationship between height of the palm, number of leaves on the crown and the annual yield indicated that LA and DM production are important parameters regulating the production potential of coconut palm. Since the DM is the stored photosynthates, photosynthetic efficiency also is one of the important traits for high productivity.

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 (Chacko Mathew and Ramadasan, 1975). Cultivars with high rate of photosynthesis and lower respiration produce higher yields than the cultivars with high respiratory rates. Parent progeny relationship indicates that NAR, shoot dry weight and chlorophyll concentration have heritability values 0.64, 0.74 and 0.81, respectively (Ramadasan *et al.*, 1984).

3. Physiological Processes

3.1. Leaf Photosynthesis

Under non-limiting conditions coconut develops a large and highly productive canopy, being capable of an estimated 51 ton ha^{-1} year^{-1} of total dry matter production (Foale, 1993). Short-term responses of coconut to water stress such as low g_s and water potential which often impair P_N and E have been extensively documented (Repellin *et al.*, 1994; 1997; Rajagopal and Kasturi Bai, 2002). Carbon assimilation rate is impaired in both tall (Reppellin *et al.*, 1997; Prado *et al.*, 2001) and dwarf genotypes (Gomes *et al.*, 2007) in response to atmospheric and soil water deficit. Reductions of P_N from 7 to 47 per cent and from 12 to 67 per cent have been reported for dwarf and tall genotypes, respectively. Drought-induced photosynthetic reductions are initially attributable to limited CO_2 diffusion from the atmosphere to the intercellular spaces as a result of stomatal closure (Reppellin *et al.*, 1994, 1997). Non-stomatal factors have been demonstrated to contribute to the reduction in P_N both during a period of severe water deficit and during the recovery phase after resuming irrigation (Gomes and Prado, 2007; Gomes *et al.*, 2007). In addition, fluorescence measurements recorded by Kasturi Bai *et al.* (2006). indicated reduction in FV/Fm (photochemical efficiency) with decreasing water potential suggesting damage to photosynthetic apparatus under stress.

3.2. Stomatal Resistance

Stomatal resistance (*rs*) differs during the period of adequate soil water availability *i.e.*, non-stress and during soil water deficit *i.e.*, stress among the cultivars and hybrids of coconut. During non-stress, *rs* shows the least variation among the cultivars, except in WCT x WCT, which exhibited relatively high *rs*. However, under stress conditions, where high evaporative demand in the atmosphere prevails, genotypes exhibit differential adaptability through stomatal regulation, which is high in the hybrids followed by talls, whereas in dwarfs it is almost 50 per cent less than that in hybrids. 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 *rs*. Rainfed palms had higher *LAVPD* (leaf to ambient vapor pressure deficit), leaf temperature (T_{leaf}) and leaf to ambient temperature difference (dineshddd*T*), whereas the irrigated palms had higher *Pn*, ψ_{leaf}, and transpiration rates (*E*). The *LAVPD* and dineshddd*T* influenced the *gs* and water relations of coconut (Rajagopal *et al.*, 2000).

3.3. Leaf Water Potential

Leaf water potential (ψ_{leaf}), an indicator of plant water status has a vertical gradation from middle leaf upwards, the magnitude being higher under rain fed condition. In the studies by Voleti *et. al.* (1993b), the spindle leaf showed significantly higher ψ_{leaf} throughout the day irrespective of rain fed or irrigated conditions. Under rain fed condition ψ_{leaf} showed a reduction from the spindle to the first leaf. Characteristic mid day depression in ψ_{leaf} was evident in both the spindle and the first leaf. Variation among the cultivars for ψ_{leaf} also was noted. Seasonal variations in the ψ_{leaf} occurs 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). 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). A rapid screening method was developed based on ψ_{leaf} in excised leaflets for easy handling of a large number of genotypes. The ψ_{leaf} declined with time to different degrees among the genotypes, indicating the degree of tolerance.

3.4. 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 with loss of chlorophyll content and loss of green leaf area (Hebbar *et al.*, 2014). 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.

Destructive methods of estimating leaf chlorophyll and leaf N are accurate but time-consuming and expensive. Portable, non-destructive meters are available and have been used successfully with many crop species to estimate foliar chlorophyll or N (Schaper and Chacko, 1991; Loh *et al.*, 2002; Abdelhamid *et al.*, 2003). These meters also measure chlorophyll or N on the same leaf over time (Yamamoto *et al.*, 2002), which allows tracking of senescence and determination of the duration of green leaf area. These meters calculate a chlorophyll index (CI) based on reflectance or absorbency at particular wavelengths and need to be calibrated for given species to estimate the actual chlorophyll or N content. In coconut at Leaf chlorophyll meter has been found to be suitable for determining foliar chlorophyll concentrations of coconut as a generic indicator of moisture or nutrient stress, but caution is required for it to be used directly to detect N deficiency of upper crowns. The wide range of foliage colors across the genotypes mismatches the relationship between CI and N in coconut, but detection was good for a given genotype with different management options. Thus, the Leaf meter has potential as a management tool for optimizing irrigation and fertilizer regimes in plantation crops (Hebbar *et al.*, 2016).

3.5. Chlorophyll Fluorescence

Chlorophyll florescence 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 (Laxman *et al.*, 2013; Djanaguriraman *et al.*, 2013). PS II plays an important role in photosynthesis under stress conditions.Chlorophyll florescence is widely used for quantifying the impact of drought and temperature stress. 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 (Naresh Kumar *et al.*, 2000b).

3.6. Osmotic Adjustment

Osmotic adjustments are really important physiological mechanism to combat with stress conditions, mainly under water deficit condition (Morgan, 2000). Plants can resist dehydration due to stress by reducing the cellular osmotic potential by accumulating certain organic compounds of low molecular mass, generally referred to as compatible osmolytes (O'Neill, 1983; Wahid *et al.*, 2007). Different crops responds in different ways to accumulate variety of osmolytes such as sugars and sugar alcohols (polyols), amino acids, tertiary and quaternary ammonium compounds, and tertiary sulphonium compounds (Sairam and Tyagi, 2004).

Coconut palms accumulate more 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. However, 6.2 per cent to 16.3 per cent increase in sugar accumulation was observed during stress period compared to non-stress period. Similarly free amino acid accumulation increased by 38 per cent 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 *et al.*, 2006).

4. Biochemical Traits

Information concerning the protoplasmic tolerance to drought stress has led to the conclusion that coconut leaves have highly efficient 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). Coconut cultivars considered drought tolerant 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, WCT x COD and the talls *viz.*, JVGT, FMST, PHOT and CCNT show higher ECW (epicuticular wax) content than the other cultivars including dwarfs. The transpiration (E) is inversely proportional to the content of ECW on the leaf surface (Rajgopal *et al.*, 1990).

5. Refining Selection Criteria

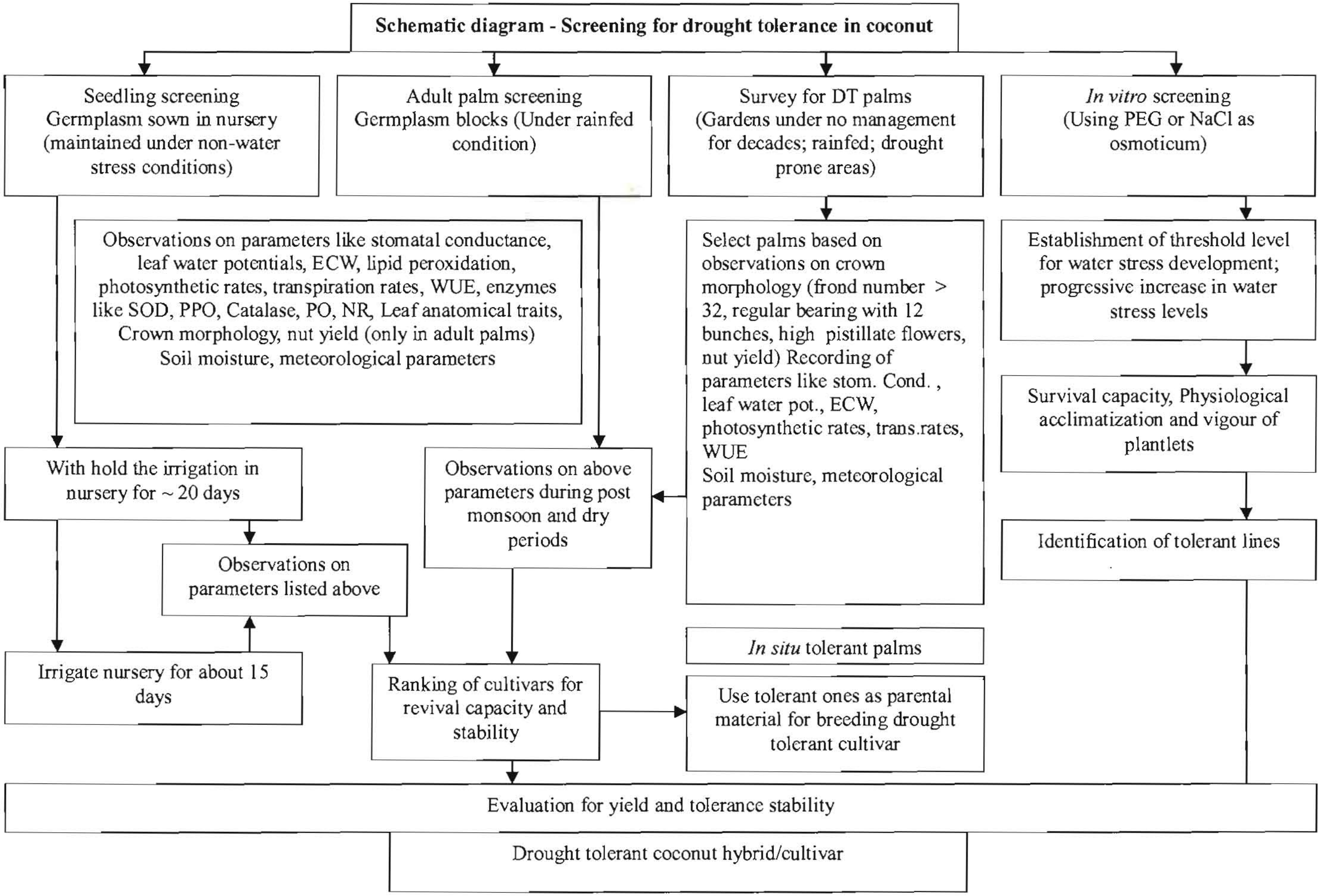
Analysis of a range of genotypes over several years and with varying agronomic management showed that the immediate cause of low nut yield in warmer years was due to the occurrence of drought. Drought is one of the main environmental factors that limit coconut productivity. Extensive research work carried out on coconut led to the development of screening methods for identification of drought tolerant genotypes.

Physiological characters, nut yield, biochemical characters and their integration with physiological responses to drought tolerance led to the identification of drought tolerant coconut cultivars. Screening of seedlings of parental lines and hybrids at the nursery stage indicated variations in stress responsive physiological characters like leaf water potential, lipid peroxidation, net photosynthetic and transpiration. High membrane stability, osmoprotection, osmoregulation and enhanced activity of antioxidant enzymes are characteristics often found in leaves of drought-stressed coconut trees. Diffrences in leaf gas exchange, leaf water potential, water-use efficiency and stomatal behavior among cultivars and hybrids under water stress largely explain the agronomic performance of field-grown coconut trees under drought conditions.

By employing screening techniques (as shown in flow chart) for desirable traits for drought tolerance, varieties have been selected and released for planting in drought prone areas. Some of the drought tolerant varieties/hybrids are: WCT, LCT, FMST, WCT x COD, LCT x GBGD, LCT x COD.

6. Characterization of the Growing Environment

The coconut palm is a tropical plant growing mostly between 20° N and 20° S latitudes. A well distributed rainfall (annual rainfall between 130 and 230 cm), mean annual temperature of 27°C with diurnal variation of 5°C, abundant sunlight ranging from 250 to 350 Wm^{-2} with annual sunshine of 2000 hours (at least 120 h per month) are optimum conditions for good growth and nut yield in coconut. A rainfall of about 200 cm per year, distributed throughout is the best for proper growth and high yield. In areas of inadequate rainfall with uneven distribution, coconut palms experience moisture stress of different magnitude. The summer dry



Schematic diagram - Screening for drought tolerance in coconut

spells and restricted rainfall duration causes the rainfed plantations to face water stress situation.

6.1. Identification of Physiological and Environmental Constraints to Productivity

Weather variables like rainfall, day/night temperature regimes, relative humidity, sun shine duration, vapour pressure deficits play pivotal role in crop growth, development and yield. Earlier studies indicated relationship between rainfall, other weather variables and nut yield in coconut. The influence of weather on nut yield in coconut in fact starts from inflorescence initiation and lasts till nut maturity. The time lag between inflorescence initiations to nut maturity is 44 months. Coincidence of critical sensitive period with unfavorable weather results in drastic reduction in yield. A close relationship exists between dry spell and nut yield and identified three critical stages during the ontogeny of nut development, namely initiation of inflorescence primordium, ovary development and button size nut.

Short-term responses of coconut to water stress such as low stomatal conductance to water vapour (*gs*) and leaf water potential (ψW) with negative consequences for the net photosynthesis rate (*A*) and transpiration rate (*E*) have been demonstrated. Stomatal closure is often considered as an early physiological response to water deficit, which results in decreased *A*, through limited CO_2 availability in the mesophyll. However, there is strong evidence that photosynthetic processes in the mesophyll such as Rubisco activity, RuBP regeneration, ATP supply, electron transport rate (*J*) and light capture efficiency in the photosystems are impaired as water stress increases. Identification of above physiological, biochemical and environmental constraints to adaptation and nut productivity assisted in assessing the relative magnitude of the effects of individual genotype and or environmental factors. It served to establish priorities and strategies for subsequent breeding and agronomic research. Thus for *e.g.* irrigated coconut varieties of coastal tract WCT or ECT might not be ideal in the dry season of the Tamil Nadu and concluded that the limitations of the existing cultivars could not be readily overcome by agronomic management and that better adapted cultivars were required.

6.2. Defined Target Environments in Terms of the Key Agroclimatic Factors that are Limiting in those Environments

India is divided into various agroclimatic zones based on the climate of the region. Accordingly 15 agroclimatic zones are identified. The coconut growing areas lie mostly in zones 9, 10, 11, 12 and to some extent in 2 and 3. The amount and distribution of rainfall, temperature regimes, sunshine durations, etc. vary among these zones and soil types vary even within a zone. Variation in annual rainfall was from a maximum of 3337.7 mm (Kasaragod) to a minimum of 718.23 mm (Arsikere). Dry spell was longer in Ratnagiri (216 days) and Arsikere (202 days), and shorter at Kidu (146 days). The annual nut yield under rainfed conditions varied from 68 (Ambajipeta) and 66 (Kasaragod) to 41 (Arsikere) and 30 (Kidu). Impact of variations in dry spell on nut yield was discernible from the study. It can be inferred that the longer dry spell affects the nut yield for next four years to follow with stronger impact on fourth year, irrespective of the total rainfall. The above analysis helped in identification of putatively superior traits like better stomatal regulation and root traits for improving adaptation, nut yield and nut quality depending on the rainfall pattern.

6.3. Optimise the Growth and Development to the Resources and Constraints

In physiological terms two complimentary strategies are employed to improve genotypic adaptation to the variable and frequently stressful weather conditions. The first is to understand and match the growth and development of the crop to the resources and constraints of the environment and second is to select for tolerance or resistance to the impact of stressful extremes.

6.3.1. Drought Management

Studies revealed that drought occurs once in three to four years with different intensities in major plantation areas. Depending on the length of dry spell and its coincidence with the critical stages of crop growth the yield will be affected. In order to have sustained yields it is important to have strategies to manage drought, which includes the soil, as well as atmospheric droughts. Drought management strategies mainly include the conservation of available soil moisture and efficient use of available water resources for high production. Different agronomic practices can be used for soil management for conservation of water during drought periods such as adoption of organic farming technologies and tillage practices like summer ploughing, soil mulching and addition of soil stabilizers.

6.3.2. Improving Genotypic Adaptation

In addition to the traits identified as described above, the gene action with respect to drought responsive physiological traits was studied in a 2 x 4 line x tester mating design involving coconut cultivars (two Dwarfs - CGD and MYD; four Talls - ECT, PHOT, LCT and FMST) with desirable characters (Rajgopal *et al.*, 2002). Analysis of variance for seedling transpiration rates and leaf water potentials showed higher specific combining ability (SCA) effects than general combining ability (GCA) effects due to predominance of non-additive gene action indicating heterosis for this character. The Pn under stress was additive with good combining ability, while the Pn during non-stress and recovery were governed by non-additive gene action that can be exploited for heterosis. In case of lipid peroxidation, gene action was unpredictable in non-stress with additive gene action being nil with low dominance. Whereas, during stress and recovery, non-additive gene action was observed. These results indicate the possibility of exploiting the nature of gene action governing drought sensitive traits in breeding for tolerant coconuts.

7. New Tools for Complex Tasks

In early 2000 plant physiology research in plantation crops has been integrated with information processing and molecular biology which is enhancing the potential for exploiting physiological understanding in crop improvement. Simulation models enhanced our ability to handle large amounts of data and to explore the dynamics of physiological processes and their complex interactions with the environment on the other, though the application of molecular genetics is limited in plantation crops still it assisted in better understanding the basics of stress responses.

7.1. Simulation Modeling of Growth and Development

The data on soil, plant and weather collected over the years has been utilized to calibrate and validate a generic coconut simulation model Infocrop. Naresh Kumar *et al.* (2013). validated the model using the soil, plant and weather data from different agroclimatic regions and showed a reasonably good fit with r^2 value of 0.86. The same model was later used to predict the coconut production under future climate.

7.2. Crop Monitoring through Spectral Reflectance Signature

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. Limited effort has been made to obtain biomass, vigour and canopy cover on a temporal and spatial scale using Remote Sensing and GIS (Bharathkumar and Aslam, 2015). It has huge potential in determining the cropping pattern which is a basic element of cropping system.

References

Abeywardena, V. (1968). Forecasting coconut crops using rainfall data: A preliminary study. *Ceylon Cocon. Q.*, **19**: 161-76.

Ahdelhamid, M., Horiuchi, T. and Oba, S. (2003). Evaluation of the SPAD value in faba bean (*Vicia faba* L.) leaves in relation to different fertilizer applications. *Plant Production Science*, **6**: 185-189.

Bharathkumar, L., M.A. and Aslam, M. (2015). Crop Pattern Mapping of Tumkur Taluk using NDVI Technique: A Remote Sensing and GIS Approach. *Aquatic Procedia*, 1397 – 1404.

Castelli, F., R. Contillo, and Miceli. F. (1996). Non-destructive determination of leaf chlorophyll content in four crop species. *Journal of Agronomy and Crop Science*, **177**: 275-283.

Cattivelli L, Rizza F, Badeck F-W, Mazzucotelli E, Mastrangelo AM, Francia E, Mare C, Tondelli A, and Stanca A. M. (2008). Drought tolerance improvement in crop plants: An integrated view from breeding to genomics. *Field Crops Res.*, **105**: 1-14.

Chempakam, B., Kasturi Bai, K.V and Rajagopal V. (1993). Lipid peroxidation and associated enzyme activities in relation to screening for drought tolerance in coconut (*Cocos nucifera* L.). *Plant Physiol Biochem.*, **20**: 5-10.

Chacko Mathew and Ramadasan, A. (1975). Photosynthetic efficiency in relation to annual yield and chlorophyll content in the coconut palm. *Journal of Plantation Crops*, **3**(1): 26-28.

Corley, R.H.V. (1983). Potential productivity of tropical perennial crops. *Expl. Agric.*, **19**: 217-237.

Datt, B. (1999). A new reflectance index for remote sensing of chlorophyll content in higher plants: tests using *Eucalyptus* leaves. *Journal of Plant Physiology*, **154**: 30-36.

Djanaguiraman, M., Prasad, P. V. V. and Schapaugh, W. T. (2013). High day- or nighttime temperature alters leaf assimilation, reproductive success, and phosphatidic acid of pollen grain in soybean [*Glycine max* (L.) Merr.]. *Crop Science*, **51**: 2125–2131.

Foale M. A. (1993). Physiological basis for yield in coconut. In: Nair MK, Khan HH, Gopalasundaran P, Bhaskara Rao EVV (Eds.), *Advances in Coconut Research and Development*, Oxford and IBH Publishing Co. Pvt., New Delhi.

Foale, M.A. (1968). The growth of the young coconut palm (*Cocos nucifera* L.). 1. The role of the seed and photosynthesis in seedling growth up to 17 months of age. *J. Agri. Res.*, **19**: 781-789.

Friend, D. and Corley, R. H. V., (1994). Measuring coconut palm dry matter production. *Exp. Agric.*, **30**: 223-235.

Gomes, F.P, Oliva, M.A, Mielke, M.S, Almeida, A-AF, Leite, H.G, Aquino, L. A. (2007). Photosynthetic limitations in leaves of young Brazilian Green Dwarf coconut (*Cocos nucifera* L. '*nana*') palm under well-watered conditions or recovering from drought stress. *Environ Exp Bot.*, in press: oi: 10.1016/j. envexpbot.2007.08.006.

Gomes, F.P., Prado, CHBA. (2007). Ecophysiology of coconut palm under water stress. *Brazilian J Plant Physiol*, **19**: 377-391.

Hebbar K.B., Rane, J., Ramana, S., Panwar,N.R., Ajay, S., Subba Rao, A. and Prasad, P.V.V. (2014). Natural variation in the regulation of leaf senescence and relation to N and root traits in wheat. *Plant and Soil*, **378**: DOI 10.1007/s11104-013-2012–6.

Hebbar K.B., Subramanian, P., Sheena, T.L., Shweta, K., Sugatha, P., Arivalagan, M. and Prasad, P.V.V. (2016). Chlorophyll and nitrogen determination in coconut using a non-destructive method. *Journal of Plant Nutrition*, **39**; doi10.1080/019 04167.2016.1161781.

Jayasekara, K. S., Wahala, M. P. B., Jayasekara, C. and Peries, R. R. A. (1993) Water use of coconut (*Cocos nucifera* L.). *Proc. 49th Annual Sessions SLAAS* 1993.

Kasturi Bai, K.V, Rajagopal, V., Prabha, C.D., Ratnambal, M.J. and George, M.V. (1996). Evaluation of coconut cultivars and hybrids for dry matter production. *J. Plantn. Crops*, **24**: 23-28.

Kasturi Bai, K.V. (1993). Evaluation of coconut germplasm for drought tolerance. Ph.D. Thesis, Mangalore University, Mangalore. India.

Kasturi Bai, K.V. and Ramadasan, A. (1983). Changes in the levels of carbohydrate as a function of environmental variables in hybrids and tall coconut palms. In: N.M. Nayar (Ed), *Coconut Research and Development*, Wiley Eastern Limited. pp. 203-209.

Kasturi Bai, K.V. and Rajagopal, V. (2000). Osmotic adjustment as a mechanism for drought tolerance in coconut (*Cocos nucifera* L). *Indian J. Plant Physiol.,*: 320-323.

Kasturi Bai, K.V.,Rajagopal,V., Chempakam, B. and Prabha, C.D. (1996b). Assay of enzymes in coconut cultivars and hybrids under non-stress and stress conditions. *J. Plantn Crops*, **24** (Suppl): 548-554.

Katuri Bai, K.V., Rajagopal, V and Naresh Kumar, S. (2006). Chlorophyll fluorescence transients with response to leaf water status in coconut. *Indian J Plant Physiol.*, **11**: 410-414.

Laxman, R. H., Srinivasa Rao. N. K., Bhatt, R. M., Sadashiva, A. T., Sunoj, J. V. S., Geeta, B., Pavithra, C. B., Manasa, K. M and Dhanyalakshmi, K. H. (2013). Response of tomato (*Lycopersicon esculentum* Mill.) genotypes to elevated temperature. *Journal of Agrometerology*, **15**: 38–44.

Liyanage, D.V. and Abeywardena, V. (1957) Correlations between seed nuts, seedling and adult palm characters in coconut. Trop. Agric., **113**: 1-16.

Loh, F.C.W., Grabosky, J.C. and Bassuk, N.L. (2002). Using the SPAD-502 meter to assess chlorophyll and nitrogen content of Benjamin fig and cottonwood leaves. *Hort Technology*, **12**: 682-686.

Marar, M.M.K. and Pappachan, G. (1964). A note on the estimation of leaf area in coconut seedlings. *Indian Coconut J.*, **17**: 137-141.

Mathes, D.T. (1988). Influence of weather and climate on coconut yield. Coconut Bulletin, **5**: 8-10.

Menon, K.P. and Pandalai, K.M. (1958) The coconut palm, a monograph. Kerala, South India: Indian Central Coconut Committee. 384

Morgan, J.M., (2000) Increases in grain yield of wheat by breeding for an osmoregulation gene: relationship to water supply and evaporative demand. *Australian Journal of Agricultural Research*, **51**: 971–978.

Naresh Kumar, S., Rajagopal, V, and Karun A. (2000a). Leaflet anatomical adaptations in coconut cultivars for drought tolerance, Recent Advances in Plantation Crops Research, CPCRI contribution, pp. 225-229.

Naresh Kumar, S. and Aggarwal, P.K. (2013). Climate change and coconut plantations in India: Impacts and potential adaptation gains. *Agricultural Systems*, **117**: 45–54.

Naresh Kumar, S., Rajagopal, V., Laxman, R.H., Dhanapal, R. and Maheswarappa, H. P. (2000b). Photosynthetic characteristics and water relations in coconut palms under drip irrigation levels on sandy and laterite soils. *Proceedings of PLACROSYM XIV* (In press).

O'Neill, S. D. (1983). Role of Osmotic Potential Gradients during Water Stress and Leaf Senescence in Fragariavirginiana. *Plant Physiology*, **72**: 931-937.

Patel, J.S. (1938). The coconut: a monograph. Madras, Government Press.

Prado, C.H.B.A., Passos, E.E.M., Moraes, J.A.P.V. (2001). Photosynthesis and water relations of six tall genotypes of Cocos nucifera in wet and dry seasons. *South Afr. J. Bot.* **67**: 169-176

Rajagopal, V and Kasturi Bai K.V. (2002). Drought tolerance mechanism in coconut. *Burot Bull.*, **17**: 21-22.

Rajagopal, V, Kasturi Bai K.V. and Naresh Kumar, S. (2000). Adaptive mechanism of coconut palms in the changing environment conditions for higher production. In: Extended summaries Vol 2. Natural Resources- Agrobiodiversity, International conference on managing natural resources for sustainable agricultural production in the 21st century, New Delhi.

Rajagopal, V., Kasturi Bai, K.V and Voleti, S.R. (1990). Screening of coconut genotypes for drought tolerance. *Oleagineux*, **45**: 215-223.

Rajagopal V. and Naresh Kumar, S. (2001). Avenues to improve productivity potential under drought condition-A case study on coconut. In: Abstracts National Seminar on role of plant physiology for sustaining quality and quanity of food production in relation to environment, 5-7 Dec. 2001, UAS, Dharwad. pp. 31-36.

Ramadasan, A and Mathew, J. (1987). Leaf area and dry matter production in adult coconut palms. *J. Plantn. Crops*, **15**: 59-63.

Ramadasan, A., Satheesan, K.V. and Balakrishnan, R. (1980). Leaf area and shoot dry weight in coconut seedling selection. *Indian J. Agric.Sci.*, **50**: 553-554.

Ramadasan, A. and Satheesan, K.V. (1980). Certain leaf anatomical characteristics of two coconut cultivars and hybrids. *J. Plantn. Crops*, **8**: 55-57.

Ramadasan, A., Mathew, C., Mathew, J. and Satheesan, K.V. (1984). Relative assimilation rate (RAR) in coconut palms. *J. Plantn. Crops*, **12**: 186-188.

Repellin, A., Daniel, C and Zuily-Fodil, Y. (1994). Merits of physiological tests for characterizing the performance of different coconut varieties subjected to drought. *Oleagineux*, **49**: 155-168.

Repellin, A., Pham, Thi A.T., Tashakorie, A., Sahsah, Y., Daniel, C and Zuily-Fodil, Y. (1997). Leaf membrane lipids and drought tolerance in young coconut palms (*Cocos nucifera* L.). Eur. *J. Agron.*, **6**: 25-33.

Sairam, R. K. and Tyagi, A. (2004). Physiology and molecular biology of salinity stress tolerance in plants. *Curr. Sci.*, **86**: 407-421.

Satheesan, K.V., Narasimhayya, G. Ramadasan, A. (1983). A rapid method for estimation of leaf area of one year old seedlings of Tall variety of Coconut palms. *Journal of Plan. Crops*, **11**(1): 47-49.

Schaper, H. and Chacko, E.K. (1991). Relation between extractable chlorophyll and portable chlorophyll meter readings in leaves of eight tropical and sub-tropical fruit tree species. *Journal of Plant Physiology*, **138**: 674-677.

Shivashankar, S., Kasturi Bai, K. V. and Ramadasan, A. (1982). A comparative study of coconut genotypes for components of photosynthesis and respiration. *Proceedings of Placrosym V*, p. 231-234.

Shivashankar, S., Kasturi Bai, K. V. and Rajagopal, V. (1991). Leaf water potential, stomatal resistance and activity of enzymes during the development of moisture stress in coconut palm. *Trop Agric.*, **68**: 106-110.

Voleti, S.R., Kasturi, Bai K. V. and Rajagopal, V. (1993b). Water potential in the leaves of coconut (*Cocos nucifera* L.) under rainfed and irrigated conditions. In: Nair, M.K., Khan, H.H., Gopalasundaran, P and Bhaskara Rao, E.V.V (eds) Advances in Coconut Research and Development, Oxford and IBH Publishing, New Delhi.

Wahid, A., Gelani, S., Ashraf, M and Foolad, M.R. (2007). Heat tolerance in plants: An overview. *Environmental and Experimental Botany*, **61**: 199–223.

Wikrama Suriya, C.A. (1968). Some observations on the effect of photoperiod on the flowering behaviour of the coconut palm, *Cocos nucifera* Linn. *Ceylon Coconut*, pp. 152-160

Yamamoto, A., Nakamura, T., Adu-Gyamfi, J.J and Saigusa, M. (2002). Relationship between chlorophyll content in leaves of sorghum and pigeon pea determined by extraction method and by chlorophyll meter (SPAD-502). *Journal of Plant Nutrition*, **25**: 2295-2301.