

## **THE WATER RELATIONS AND IRRIGATION REQUIREMENTS OF COCONUT (*Cocos nucifera*): A REVIEW**

By M. K. V. CARR†

*Emeritus Professor, School of Applied Sciences, Cranfield University, Cranfield, Bedfordshire,  
MK43 0AL, UK*

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### SUMMARY

The results of research on the water relations and irrigation needs of coconut are collated and summarized in an attempt to link fundamental studies on crop physiology to drought mitigation and irrigation practices. Background information on the centres of origin and production of coconut and on crop development processes is followed by reviews of plant water relations, crop water use and water productivity, including drought mitigation. The majority of the recent research published in the international literature has been conducted in Brazil, Kerala (South India) and Sri Lanka, and by CIRAD (France) in association with local research organizations in a number of countries, including the Ivory Coast. The unique vegetative structure of the palm (stem and leaves) together with the long interval between flower initiation and the harvesting of the mature fruit (44 months) mean that causal links between environmental factors (especially water) are difficult to establish. The stomata play an important role in controlling water loss, whilst the leaf water potential is a sensitive indicator of plant water status. Both stomatal conductance and leaf water potential are negatively correlated with the saturation deficit of the air. Although roots extend to depths >2 m and laterally >3 m, the density of roots is greatest in the top 0–1.0 m soil, and laterally within 1.0–1.5 m of the trunk. In general, dwarf cultivars are more susceptible to drought than tall ones. Methods of screening for drought tolerance based on physiological traits have been proposed. The best estimates of the actual water use (ET<sub>c</sub>) of mature palms indicate representative rates of about 3 mm d<sup>-1</sup>. Reported values for the crop coefficient (K<sub>c</sub>) are variable but suggest that 0.7 is a reasonable estimate. Although the sensitivity of coconut to drought is well recognized, there is a limited amount of reliable data on actual yield responses to irrigation although annual yield increases (50%) of 20–40 nuts palm<sup>-1</sup> (4–12 kg copra, cultivar dependent) have been reported. These are only realized in the third and subsequent years after the introduction of irrigation applied at a rate equivalent to about 2 mm d<sup>-1</sup> (or 100 l palm<sup>-1</sup> d<sup>-1</sup>) at intervals of up to one week. Irrigation increases female flower production and reduces premature nut fall. Basin irrigation, micro-sprinklers and drip irrigation are all suitable methods of applying water. Recommended methods of drought mitigation include the burial of husks in trenches adjacent to the plant, mulching and the application of common salt (chloride ions). An international approach to addressing the need for more information on water productivity is recommended.

### INTRODUCTION

The coconut (*Cocos nucifera*) contributes to the livelihoods of millions of people in the developing world, not only through its production but also through employment generated by the many associated industries. It is the most widespread, economically useful palm of the wet tropics, being found mainly in coastal areas between latitudes

†Address for correspondence: Pear Tree Cottage, Frog Lane, Ilmington, Shipston on Stour, Warwickshire, CV36 4LQ, UK. Email: mkekarr@cwms.org.uk

20°N and 20°S of the equator. A great deal of research has been reported on the ecophysiology and water relations of coconut and the adverse effects of water stress on yield are well established. This paper attempts to synthesize this research from an independent perspective and to do this in practically useful ways. It follows the format used in previous reviews in this series, notably those on coffee (Carr, 2001), banana (Carr, 2009), tea (Carr, 2010a; 2010b) and sugar cane (Carr and Knox, 2011). It begins with background information on the origin and centres of production of coconut. This is followed by descriptions of the stages of crop development, as influenced by water availability, and then by reviews of plant water relations, crop water use and water productivity, including drought mitigation. Various aspects of this topic have previously been reviewed (e.g. Murray, 1977), most recently in a paper by Gomes and Prado (2007), which focuses on the physiological responses of coconut to water stress. Emphasis is placed on those publications describing research of international relevance.

#### CENTRES OF PRODUCTION

##### *Origin*

Although there still remains some uncertainty about the coconut's centre of origin (it may be South America), it is generally accepted that the coconut originated in the south-west Pacific or the Indian Ocean and that it became domesticated in Malaysia and on the coasts and islands between Southeast Asia and the western Pacific. It has been present in the Pacific islands (a centre of genetic diversity), where it is an indigenous species, for millions of years, long before their settlement by Polynesians. It is believed that coconut was distributed widely by nuts floating in ocean currents and germinating after they were washed ashore in new locations. In this way it probably reached southern India and Sri Lanka, where the coconut has a recorded history of 2000–3000 years, and possibly Madagascar and eastern Africa. The nuts were probably also carried by humans as a source of food and drink on long sea voyages, reaching West Africa and the Americas about 500 years ago when the coconut became pan-tropical (Harries, 1978; 1995; Persley, 1992; Purseglove, 1972).

As already implied, coconut is a crop of the humid tropics. It grows best at altitudes below 1000 m and near the coast where the mean air temperature is in the range 25–29 °C (Persley, 1992). In their review paper, Gomes and Prado (2007) specify a slightly broader optimum temperature range of 23–34 °C, with the absence of temperatures below 15 °C, and a relative humidity between 60 and 90%. Annual rainfall should exceed 1500 mm, preferably evenly distributed throughout the year. Coconut palms can be grown on a wide range of soils, providing they are free draining (Murray, 1977; Purseglove, 1972). As Murray (1977) explains, deficiencies in rainfall can sometimes be compensated for by access to groundwater by roots especially, for example, where coastal beach plantations are backed by rain-fed freshwater swamps and lagoons that drain towards the sea.

In 2007, the total planted area was estimated by FAO (2010) to be about 11.2 million ha, spread across more than 90 countries, and producing 10 million t of copra

(the dried endosperm of the nut from which oil is extracted) equivalent and 6 million t of oil equivalent. The main producing countries are Indonesia, the Philippines (both with more than three million ha) and India (>one million ha). For many small island and coastal communities, the coconut is a major source of wealth. In such places, apart from fishing, there are often few other viable enterprises. Internationally it is a smallholder crop, with planted areas typically in the range 0.5 to 4.0 ha per household (Persley, 1992; Pursglove, 1972). Brazil, the fourth largest producer, has, for example, 220 000 small-scale producers occupying 300 000 ha mostly in the coastal zone. In addition, Brazil has about 80 000 ha of dwarf cultivars grown commercially in non-traditional areas (with irrigation) (Gomes and Prado, 2007).

### Uses

The coconut is often referred to as the 'tree of life' because of the diverse range of products, more than 100, which are derived from all parts of the plant (Persley, 1992). The oil is used for both edible and industrial purposes. The edible uses include the manufacture of margarine and cooking oil, and the industrial uses detergents, soap and fatty acids. The residue left after oil extraction from the copra is used as animal feed. The balance of production (about 50%) is consumed fresh in producing countries. Other components of the nut, as well as the rest of the palm, provide such diverse products as food, drinks, medicines, building materials, furniture, ornaments and household goods.

### Types

There are two naturally occurring types of coconut, the tall and the dwarf. In addition, hybrids (mainly tall × dwarf) have been bred in many countries. But, as Harries (1995) pointed out, although this is a convenient distinction it is misleading as even dwarf types can reach a considerable height given time. Dwarfness in coconut really means precocity as the first fruit is set close to the ground.

The coconut has a single, unbranched trunk, which in the tall type (var. *typica*) grows up to 30 m in height. The production of fruit begins five to seven years after planting and reaches a peak at 15–20 years. The economic life is considered to be 60 years but plants can live to 90 years. Under favourable conditions they produce 60–70 nuts a year. By contrast, the dwarf type (var. *nana*) starts bearing after three years and peaks after six years. Hybrids are early bearing, after four years, with peak production within 20 years when they can produce 160 nuts a year (30 kg copra) (Persley, 1992; Pursglove, 1972).

As tall palms are largely cross pollinated (by insects and wind), coconut populations are very variable. Dwarf palms in contrast are generally self fertilizing. A study of genetic diversity by Lebrun *et al.* (1998), using restriction fragment length polymorphism (RFLP) analysis, identified two major groups. One included ecotypes from the Far East and the South Pacific whilst the other comprised ecotypes from India, Sri Lanka and West Africa. All dwarf types belonged to the first group, even those collected in West Africa. Tall ecotypes were generally more polymorphic than dwarfs.

Where they are sufficiently distinctive local and regional populations receive names that reflect their location (e.g. Malayan Dwarf; West African Tall). Colour variants and local ecotypes within such populations have also been given names (Harries, 1995).

#### CROP DEVELOPMENT

##### *Stem and leaves*

As Tomlinson (2006) highlights, palms as a family are unique, possessing distinctive features of leaf development, vascular structure and anatomical properties of the stem. The coconut palm is conventionally propagated by seed. After germination, no visible trunk (stem) is formed in the tall ecotype for several years as there is no cambium (therefore no secondary thickening), and the trunk can only be formed when the apical meristem has attained its full diameter. The single stem develops entirely from cells derived from the apical meristem. Its structure means that it is not only a conductor of water to the leaves but also, because of its volume, acts also as an important water store or capacitor (Gomes and Prado, 2007). For example, Passos and Da Silva (1991) have described the diurnal variation in the circumference of the stem that can occur in response to changes in the water balance of the palm, a response that is enhanced when the fruits are removed. The carbohydrate reserves of coconut are mainly stored in the stem in soluble form (primarily sucrose). By contrast, the roots do not appear to have a storage function (Mialet-Serra *et al.*, 2008).

The terminal bud differentiates a single leaf at a time (it takes about 30 months from differentiation to the emergence of the leaf), an internode (the growth of which constitutes the incremental increase in height of the stem) and an inflorescence, in regular succession (Mialet-Serra *et al.*, 2008). The pinnate leaves are borne in a terminal radiating crown, which in an adult palm consists of 25–35 opened leaves and a central bud. In tall cultivars one leaf opens at intervals of about one month and in dwarfs about every three weeks. A fully mature leaf remains on the (tall) palm for 2.5–3 years before falling. There is a waxy cuticle on the upper epidermis beneath which are two layers of large hypodermal cells, which serve as water storage tissue. These and other leaf anatomical adaptations to drought tolerance have been described by Naresh Kumar *et al.* (2000) and cited by Gomes and Prado (2007).

As Huxley (1999) points out, the canopy of the young palm is dense and spreading, but as it grows older it becomes sparser and, as it is also well above ground, allows light penetration. So although young palms in a plantation cover the ground, well older palms do not. Using a mobile sampling method in Thailand, Moss (1992) measured the amount of photosynthetically active radiation intercepted by the leaf canopy at monthly intervals throughout one year. Seasonal reductions in the amount of light intercepted were related to water stress, its most immediate effect being to increase the rate of frond shedding and to slow the production of new fronds. As coconuts take about one month to produce a new frond, it can take many months for lost leaf area to be replaced, with long-term effects on yield. For crops well supplied with potassium, 60–70% of the incident light was intercepted by the canopy of an eight-year-old dwarf × tall hybrid (Malayan Yellow Dwarf × West African Tall) over the year (plant

density  $156 \text{ ha}^{-1}$ ). Increasing the plant density from  $142$  to  $205 \text{ ha}^{-1}$  (*cv.* Thai Tall; 13-years-old) increased light interception over the same year from 55 to 73%.

Based on these measurements, Moss (1992) was able to demonstrate a close linear relationship between yield of copra (and the whole fruit) and cumulative light interception ( $n = 6$ ;  $r^2 = 90\%$ ). As the line(s) did not pass through the origin, this suggested that there was a minimum level of light interception below which no yield is produced.

In the Solomon Islands, Friend and Corley (1994) showed how the maximum leaf area was reached about five years after planting in all three (tall, dwarf and hybrid) of the cultivars compared. The 'dwarf' had the smallest leaf area (*ca.*  $4 \text{ m}^2$ ) whilst the 'tall' and the 'hybrid' had similar values (*ca.*  $6\text{--}7 \text{ m}^2$ ). The leaf area indices were in the range 4–5 (modified by differences in plant density; average density =  $217 \text{ ha}^{-1}$ ).

In a comparison of five cultivars in Zanzibar, Juma and Fordham (1998) found that increases in the saturation deficit of the air had a negative effect on the rate of leaf expansion, while an increase in temperature within the range  $24\text{--}30 \text{ }^\circ\text{C}$  showed a positive effect.

### *Flowering*

When flowering commences (after about three years for dwarfs and five years for tall), a single inflorescence (botanically a spadix) is borne in the axil of each leaf with numerous male and a few (up to 30–40) female flowers (subject to seasonal variation). The fruit (botanically a drupe) develops its full size about six months after fertilization and matures within 12 months (Gomes and Prado, 2007; Purseglove, 1972; Murray, 1977). The inflorescence is in fact initiated up to 32 months before the spathe (a large bract enclosing the spadix) opens, or 44 months before the fruit is harvested (Wickramaratne, 1987).

### *Fruit*

Botanically the fruit consists of (1) the exocarp, or outer skin, (2) the mesocarp, or fibrous layer (source of coir), (3) the endocarp, or shell, and (4) a single seed. The 'nut' of commerce consists of the seed and endocarp (Purseglove, 1972). According to Murray (1977), variations in monthly and annual yields are determined largely by rainfall distribution. During the first few months after the inflorescence appears a considerable number of immature fruits are shed, and later-maturing nuts may be shed at the end of a long dry spell.

### *Roots*

Roots are adventitious, being formed on the lower part of the stem (the bole), which is usually beneath the soil surface. They are produced throughout the life of the plant; like the stem, they are also without cambium. The major roots (up to 4 mm in diameter) produce numerous secondary and tertiary roots; there are no root hairs (Murray, 1977). A marked ability to generate new roots allows palms to be transplanted

easily. Different measurement techniques have been used to study the root systems of the coconut in several countries, which makes direct comparisons difficult.

In a detailed study in the Philippines, Magnaye (1969) recorded roots extending laterally 5 m from the base of the trunk, and to a depth of 2 m. On a free draining, sandy loam soil, the greatest concentration of roots was within 0.3–1.0 m from the stem and at 0.6–1.2 m depth. In a similar study in Kerala, again on a sandy loam soil, roots of mature palms extended laterally about 3.5 m from the trunk (spacing 7.5 × 7.5 m), although the majority were within 2.0 m and reached depths of 1.5 m (Kushwah *et al.*, 1973).

In northern Venezuela, Avilan *et al.* (1984) compared the root systems of tall and dwarf cultivars of different ages (4 and 12 years, and 5 and 11 years, respectively). Root distribution was markedly influenced by the physical properties of the soil and by fertilizer application and irrigation. Roots of both cultivars reached depths of at least 0.8 m, regardless of age, with the majority (77–94%, by number) in the top 0.5 m.

In the Ivory Coast, Pomier and Bonneau (1987) completed a detailed study of factors influencing the depth and distribution of roots (dry mass per unit volume of soil). On free-draining sandy soils, roots of mature palms (hybrid PB-121) reached 3.5–4 m depths and extended laterally at least 4 m from the stem. The greatest density of roots was within 1 m depth and 1.2–1.5 m spread. Root growth beyond 1.5 m was restricted when the water table was within 3 m of the soil surface.

In northeast Brazil, on a sandy soil, Cintra *et al.* (1992) compared the root distribution (dry mass) of six dwarf cultivars (six-years-old) at the end of the rainy season and again at the end of the dry season. Roots reached a depth of 1.0 m (water table at 1.10 m), but with the highest root density in the 0.20–0.60 m layer. About 70% of the roots were within a 1.0 m radius of the trunk and 90% within 1.5 m. Cultivars Malayan and Gramame Yellow Dwarfs had better vertical and horizontal root distribution than, in particular, Jiqui Green Dwarf and Cameroon Red Dwarf. In a parallel study, Cintra *et al.* (1993) compared root distribution of six tall cultivars (also six-years-old). The maximum depth of rooting was 0.8 m, with 70% of the roots in the 0.1–0.5 m layer and within a 1.0 m radius from the trunk. Cultivars Polynesia Tall and Praia de Forte Brazil had 'better' root distributions (in terms of total root production and fine root density, and more roots at depth when subjected to water stress) than the others. It is not clear whether differences in the surface area of circles with different radii from the trunk were taken into account in the comparisons of total root mass at increasing distance from the trunk.

Also in northeast Brazil (10° 17'S; 37° 35'W; alt. 120 m asl), Azevedo *et al.* (2006) used digital image analysis to record root distribution of six-year-old dwarf green palms growing on a sandy soil (irrigated). All the roots were found in the top 1.0 m soil with the following distribution: 0–0.2 m 8%; 0.2–0.4 m 24%; 0.4–0.6 m 24%; 0.6–0.8 m 15%; 0.8–1.0 m 8%.

As part of a study to specify the design criteria for drip irrigation in Sri Lanka, Arachchi (1998) excavated roots of 15-year-old palms (*cv.* CRIC 60) to a depth of 1.5 m. In a Xanthic ferrasol soil, root distribution by mass declined exponentially

from 0.3 m downwards and spread laterally 2.0 m from the base of the palm (spaced 7.7 m square).

*Summary: crop development*

1. The single stem of the coconut palm is an important water store (or capacitor).
2. It takes about 30 months from differentiation of a leaf to its emergence. New leaves open at intervals of about four weeks (talls) or three weeks (dwarfs).
3. Water stress increases the rate of frond shedding and slows the emergence of new leaves.
4. There is a close linear relation between yield and cumulative light interception. Seasonal changes in light interception are related to water stress.
5. An inflorescence is initiated up to 44 months before the fruit is harvested.
6. Variations in monthly and annual yields are determined largely by rainfall distribution.
7. Roots are adventitious.
8. Root systems have been described in different ways, which makes direct comparisons difficult.
9. Roots can reach depths >2 m (down to 4 m), but the root density is usually greatest in the top 0.5–1.0 m.
10. Roots can extend laterally >3 m (up to 10 m), but the root density is usually greatest within 1.0–1.5 m of the trunk.
11. Tall and dwarf cultivars appear to have similar root distributions, but there are apparent differences in root distribution between cultivars within each ecotype.

#### PLANT WATER RELATIONS

Perhaps the first detailed review of the water relations of the coconut was that by Copeland (1906) who described in great detail the results of his experiences in the Philippines. Because of the simplicity of the apparatus available little of what he reported is of value today, although he did describe the structure and function of the root and the leaf, including the location (lower surface), size and density ( $144 \text{ mm}^{-2}$ ) of the stomata. He also attempted to measure transpiration by recording the loss in weight of individual severed leaves and by the cobalt-chloride colour test. By extrapolation, he derived daily water use figures for a single palm tree ranging from 25 to 45 l. He also recorded his observations of the effects of drought (including: the folding of the pinnae, ageing and loss of leaves, check to the growth of young leaves and flowering branches, and premature falling of nuts). He concluded that, as recovery after the onset of rain was a slow process, a 'dry season' occurring every other year would reduce the yield of nuts by half.

In more recent research, measurements of stomatal conductance, leaf water status, and gas exchange (photosynthesis and transpiration) have been used to monitor the effects of water stress on the coconut. As one output from this process, procedures for screening cultivars for drought tolerance have been proposed.

In Sri Lanka, Manthirirtna and Sambasivam (1974) compared stomatal densities of different cultivars and forms of the coconut palm. The results, expressed on an

unspecified unit area basis only, suggested that there may be varietal differences as all three colour forms of the self-pollinating *cv. nana* had higher densities than *cv. typica* (+12%). In Kerala, Mathew (1981) reported stomatal densities in the range 170–180  $\text{mm}^{-2}$  for healthy palms but more in root (wilt) diseased plants (220–230  $\text{mm}^{-2}$ ). Again in Kerala, Rajagopal *et al.* (1990), in a comparison of 23 cultivars, recorded stomatal densities averaging 208  $\text{mm}^{-2}$  for tall ( $n = 10$ ), 232  $\text{mm}^{-2}$  for dwarfs ( $n = 6$ ) and 216  $\text{mm}^{-2}$  for hybrids ( $n = 7$ ).

In healthy palms, partial stomatal closure was observed from mid-morning (*cv. West Coast Tall*) in Kerala. By contrast, stomata of palms suffering from root (wilt) disease remained open throughout the day regardless of the season (Rajagopal *et al.*, 1986). Leaf water potentials were also less in diseased plants (down to  $-1.99$  MPa) leading to flaccidity (Rajagopal *et al.*, 1987). Progressive stomatal closure (from 10:00 to 12:00 hours) was also observed by Kasturi Bai *et al.* (1988) alongside a decline in the leaf water potential (from  $-0.6$  to  $-1.55$  MPa). Stomatal conductances began to fall when the saturation deficit of the air exceeded about 2.4 kPa. During dry weather, conductances were always greater in a hybrid (dwarf  $\times$  tall) cultivar than in *cv. West Coast Tall*.

Using both a diffusion porometer and the infiltration technique, diurnal changes in stomatal opening were also monitored in Brazil (Passos and Da Silva, 1990). Both methods showed the stomata (leaf 14, mature palm, Géant de Brésil) to be wide open during the middle of the day (from 08:00 hours to 16:00 hours) before closing rapidly as solar radiation levels declined. In this example, the temperature (range 25 to 34 °C) and saturation deficit (up to 2.8 kPa) of the air, and leaf water potential (pressure bomb;  $-0.5$  to  $-2.5$  MPa) appeared to have little effect on stomatal opening.

The pressure bomb was first used in Florida by Milburn and Zimmerman (1977) to record diurnal and seasonal changes in leaf water potential. The base of the 5 m tall tree (*cv. Malayan Dwarf*) was only 0.5–1.5 m above sea level at high tide. Using carefully prepared leaflet samples (rolled and stored *in situ* in a sealed plastic bag), leaf water potentials as low as  $-1.3$  MPa were reached during the day in the rainy season before increasing to  $-0.2$  MPa at night. Surprisingly, the minimum values were larger during the dry season ( $-0.9$  MPa) than during the rains. This was attributed to partial stomatal closure (measured with a viscous flow porometer) from mid-morning onwards. In Kerala, Voleti *et al.* (1993b) compared water potential measurements made on different leaves within the canopy. There was a vertical profile, with the spindle (unfolding) leaf having the highest (least negative) leaf water potential throughout the day in both irrigated and rain-fed plants.

Changes in leaf water potential (*cv. West Coast Tall*) were monitored over a six-month period in Kerala, South India (12°30'N; 70°00'E; alt. 11 m asl) by Shivashankar *et al.* (1991). Daytime values declined as the dry season progressed, from about  $-1.0$  MPa to  $-2.0$  MPa. By contrast, values for irrigated palms remained above  $-1.3$  MPa. These values were linked to the time when stress-induced changes in the activities of three enzymes were recorded.

In an irrigation trial in Kerala, there was a progressive reduction in stomatal conductance and leaf water potential (from  $-0.9$  to  $-1.4$  MPa), as the irrigation

interval was extended from 12 to 16 and 24 days. The epicuticular wax content increased over the same range. Irrigation treatments were applied from December to May over two consecutive years. At this time of the year, there was both soil and atmospheric (saturation deficits  $>3$  kPa, as recorded from 10:00 to 12:00 hours) induced stress (Rajagopal *et al.*, 1989).

The leaf gas exchange processes and water relations of six tall genotypes were compared by Prado *et al.* (2001) in Sergipe State, northeast Brazil ( $10^{\circ}26'S$ ;  $36^{\circ}32'W$ ; alt. 26 m asl). During the wet season, the controlling factor for photosynthesis and transpiration was solar radiation, whereas in the dry season it was stomatal conductance. One cultivar (Brazilian Tall) maintained gas exchange at a higher level than the other five during the dry season, despite low daytime leaf water potentials ( $-1.9$  MPa).

Similarly, Gomes *et al.* (2002b) compared gas exchange processes of two dwarf coconut genotypes (Malayan Yellow Dwarf and Brazilian Green Dwarf) over four days in Bahia State, Brazil ( $15^{\circ}16'S$ ;  $39^{\circ}06'W$ ; alt. 105 m asl). The two cultivars differed in rates of photosynthesis and transpiration, and in stomatal conductance, with values for BGD exceeding those of MYD in all three processes. For both genotypes, stomatal conductance (and photosynthesis) was negatively correlated with the leaf-to-air saturation deficit (within the chamber): BGD was more sensitive than MYD (but the evidence presented is not very convincing due to large variability). In a parallel study, Gomes *et al.* (2002a) confirmed (based on a comparison of two contrasting sites; see below for details) that the dryness of the air (between 0.7 and 3.5 kPa) influenced stomatal control of gas exchange in BGD.

More recently, Passos *et al.* (2009) compared the responses of *cv.* Jiqui Green Dwarf to atmospheric water stress at the same two sites in northeast Brazil. One, described as wet tropical, was near the coast ( $10^{\circ}17'S$ ,  $36^{\circ}30'W$ ; alt. 75 m asl) the other was at an inland site in a semi-arid area ( $09^{\circ}09'S$ ;  $42^{\circ}22'W$ ; alt. 387 m asl). Both crops were irrigated ( $150$  l palm $^{-1}$  d $^{-1}$ ). A portable infra red gas analyser was used to measure the diurnal and seasonal changes in stomatal conductance, photosynthesis and transpiration. Leaf water potentials were measured with a pressure chamber. Measurements were made on leaf 14 counting from the top. Although several correlations between these variables are presented, they are not all statistically convincing. Leaf water potentials declined linearly with increases in the saturation deficit of the air at both sites. In general, stomatal conductance was less at the semi-arid site where the saturation deficit was larger (monthly mean values reaching 1.6 kPa; daytime summer maximum *ca.* 2.8 kPa) than at the coastal site (1.0 kPa; 1.8 kPa). Instantaneous water use efficiencies *increased* linearly with increases in the saturation deficit, but only at the coastal site. The authors concluded that, as global warming would lead to increased saturation deficits, coconut plantations could not be justified in semi-arid areas even with irrigation. They did not however consider the effects of increased carbon dioxide levels on photosynthesis and water use efficiency.

In Brazil, Gomes *et al.* (2009) monitored abscisic acid (ABA) accumulation in the leaves of droughted coconut palms (Brazilian Green Dwarf ecotypes) grown in a

greenhouse. ABA is produced in the root tips in response to dry soil conditions and is carried to the leaves in the transpiration stream. Its accumulation in the leaflets occurred before there were significant changes in predawn leaf water potentials and remained high even after eight days of rewatering. Under mild stress stomatal conductance was 'controlled' by ABA accumulated in the leaflets, and at greater stress levels by the leaf water status (pre-dawn leaf water potential down to  $-1.2$  MPa, when photosynthesis ceased). Stomatal conductances (and photosynthetic rates) were slow to recover on rewatering but sufficient to sustain photosynthesis and to allow rapid recovery of transpiration. Intrinsic water use efficiency was improved at mild stress levels without impairment of the photosynthetic rate. This suggested that 'regulated deficit irrigation' may have a role in increasing the water productivity of irrigated palms.

In a related paper on the same experiment, Gomes *et al.* (2008) described in more detail the photosynthetic limitations encountered during the recovery phase after the relief of water stress. Non-stomatal factors were identified as contributing to the delayed and incomplete recovery of photosynthesis following rewatering. The two ecotypes tested differed in their responses. The one normally cultivated in a hot dry environment (Una Green Dwarf) recovered more quickly than the one cultivated under hot humid conditions (Jiqui Green Dwarf).

The influence of canopy shape on gas exchange processes of mature coconut palms (*cv.* West Coast Tall) has recently been described by Naresh Kumar and Kasturi Bai (2009). An oval shaped canopy was considered to be superior to X- or semi-circle shaped canopies in terms of photosynthetic and water-use efficiencies under both irrigated and rain-fed conditions (in Kerala). Nut productivity was however only influenced by canopy shape in rain-fed palms. Gas exchange properties varied with the position of the leaf within the canopy, and with the stage of development of the subtended fruit.

In most species, chloride ions ( $\text{Cl}^-$ ), and potassium ions ( $\text{K}^+$ ), increase in concentration in the guard cells during stomatal opening with a corresponding reduction in their concentration in the adjacent subsidiary cells. In coconut the important role of  $\text{Cl}^-$  in regulating stomatal opening has been demonstrated by Braconnier and d'Auzac (1990) in a greenhouse study in which plantlets were exposed to osmotic stress in a hydroponic medium. Chloride deficiency resulted in delayed stomatal opening at the start of the day, and a reduction in the capacity for osmoregulation when plants were stressed. Subsequently, Braconnier and Bonneau (1998) showed clearly in a field study in Sumatra (*cv.* PB-121) how stomatal conductance was reduced in chloride deficient palms, but only in the dry season *not* in the rains. This observation has implications in terms of gas exchange (net assimilation and transpiration were also reduced) and drought mitigation (see below). The role of the chloride ion (and other biochemical mechanisms) in water regulation at the cell level, including osmotic adjustment to maintain leaf turgor when plants are under water stress, has been reviewed in detail by Gomes and Prado (2007).

*Screening for drought tolerance*

Being able to identify drought resistant cultivars early in the selection process using physiological traits would be a great asset to breeders of coconuts. Many attempts have been made using a range of techniques. Some of these are summarized below.

In Kerala, Rajagopal *et al.* (1988) described how the relative rate of decline in leaf water potential in dehydrating excised leaflets could act as an index of drought tolerance. Despite a lack of statistical analysis, three cultivars were identified as being drought tolerant in this way.

In a comparison of the response to drought of 23 cultivars, again in Kerala, Rajagopal *et al.* (1990) recorded stomatal conductance (steady state porometer), leaf water potential (pressure bomb) and epicuticular wax content of physiologically mature leaves (the 11<sup>th</sup> counting from the top) on 22-year-old palms. Measurements were made between 10:00 hours and 12:00 hours on successive days before there was water stress (November) and when the plants were experiencing stress (March). Stomatal conductances declined over this period in all cases but the dwarf types showed the least change (that is the stomata remained open longer), together with one hybrid (Chowghat Orange Dwarf × West Coast Tall). In general, leaf water potentials of all types fell to similar mean values in March,  $-1.27$  MPa tall,  $-1.36$  MPa dwarfs;  $-1.24$  MPa hybrids. The epicuticular wax content was consistently least in the dwarf types. Ranking drought tolerance on the basis of all four indicators (including stomatal frequency) suggested that a 'hybrid' (West Coast Tall × West Coast Tall) was the most drought tolerant cultivar, followed by six of the tall genotypes. The dwarf types were, with one exception, the most drought susceptible because of limited stomatal and epicuticular control of water loss by transpiration. Some of the hybrids had desirable drought resistance characteristics, including Laccadive Ordinary × Gangabondam, LO × Chowghat Orange Dwarf and West Coast Tall × Chowghat Orange Dwarf. Based on a selection of these indices, a rapid screening method was developed (Rajagopal *et al.*, 1993).

In a similar follow-up study, Voleti *et al.* (1993a) compared the responses of three genotypes (WCT, WCT × COD and COD × WCT) to drought stress on two contrasting soils (laterite and sandy loam). Cultivar West Coast Tall again showed effective stomatal regulation of water loss, whilst there was some evidence (not very clear) that the three cultivars differed in their responses (in terms of stomatal conductance and the components of leaf water potential) depending on the soil type.

In Sri Lanka, Jayasekara *et al.* (1993) used similar physiological criteria to screen for drought tolerance amongst a selection of 32–35 year old individual tall × tall hybrid palms. Their criteria were based on the relative sensitivity of stomatal conductance, transpiration rates and leaf water potentials of individual palms thought to be drought tolerant compared with the environmental mean for each variable measured over a four-year period. It is not easy to follow the details of the methodology as described in the paper, but genotypes demonstrating stability in two out of the three variables (after screening twice) were considered to be drought tolerant.

In the Ivory Coast, Repellin *et al.* (1993; 1997) compared several physiological tests for characterizing the response to drought (by withholding water for 29 days)

of young (two years old) coconut palms grown in plastic containers. The dwarf varieties tested (Malayan Yellow Dwarf and Cameroon Red Dwarf, both known to be susceptible to drought) dehydrated (as measured by the rate of decline in leaf water potential and relative water content) more quickly than West African Tall (moderately drought resistant), whilst the hybrid PB-121 was intermediate between its two parents (WAT × MYD). These differences between cultivars were only observed under severe stress when stomatal closure was complete. The reduction in gas exchange (transpiration and carbon assimilation) with drought, primarily due to stomatal closure, was similar in all the cultivars tested. (This is in contrast to the findings of Rajagopal *et al.* (1990) who reported that stomatal conductance discriminated between adult palms.) As this response was virtually independent of the plant water status, it suggested that a chemical signal (possibly abscisic acid) from the root may be the cause of stomatal closure. The activity of two hydrolytic enzymes (lipase and protease) increased in response to drought and the research suggested that their micro-sequencing could provide molecular tools for selecting drought-tolerant coconut parents.

Based on the research done in Kerala, Rajagopal and Kasturi Bai (2002) summarized the many possible drought tolerance mechanisms in coconut. These included the maintenance of high leaf water status through effective stomatal regulation, deposition of wax on the leaf surface and the accumulation of organic solutes aided by anatomical adaptations. They believed that genotypes with these characteristics could be used in breeding programmes. Rajagopal *et al.* (2007) have since reported on their attempt, with some success, to understand the genetics of drought resistance, whilst Kasturi Bai *et al.* (2008) have suggested that the chlorophyll fluorescence technique (in combination with measurements of leaf water potential) may have a role in screening coconut seedlings for adaptation to water stress.

*Summary: plant water relations*

1. Stomata are confined mainly to the abaxial surface of the leaf at a density of about  $200 \text{ mm}^{-2}$ . Dwarf ecotypes may have a higher density than tall (+12%).
2. Depending on the weather conditions, partial closure of the stomata usually occurs from mid-morning onwards.
3. Stomata are slow to reopen fully after the relief of water stress.
4. Stomatal conductances decline as the saturation deficit of the air increases (atmospheric drought).
5. As water stress levels increase, the stomata of adult dwarf ecotypes remain open for longer than those of tall ones.
6. Abscisic acid may be involved in controlling stomatal closure, at least under mild stress conditions.
7. Leaf water potential is a sensitive indicator of plant water status, declining to values as low as  $-1.3 \text{ MPa}$  in the middle of the day even when the soil is wet, or  $-2.0 \text{ MPa}$  if the soil is dry (unless stomatal conductance is reduced by dry air).
8. Leaf water potentials decline linearly with increases in the saturation deficit of the air (at least until the stomata begin to close).

9. Pre-dawn leaf water potentials of  $-1.2$  MPa correspond to complete stomatal closure during the day.
10. Instantaneous water use efficiencies appear to increase in plants experiencing moderate water stress.
11. Chloride ions play an important role in the stomatal opening process, in osmoregulation and in drought tolerance.
12. Epicuticular wax content increases as the soil water deficit increases. It is normally higher in dwarf ecotypes than tall.
13. The activities of certain hydrolytic enzymes increase in response to drought.
14. Various physiological traits have been identified that can assist in the screening for drought tolerance.
15. In general, tall are considered to be more resistant to drought than dwarfs, and than most dwarf  $\times$  tall hybrids. West Coast Tall in particular is recognized for its drought resistance.

#### CROP WATER USE

Several techniques have been used in different regions of the world to quantify (or predict) the water use of the coconut palm. They include lysimeters, the soil water balance, sap flow and the eddy-flux methods. Results are reported in terms of litres palm<sup>-1</sup> d<sup>-1</sup> and/or as mm d<sup>-1</sup>, depending on whether the plant population is specified.

In Kerala, Jayakumar *et al.* (1988) used a pair of drainage lysimeters to measure the actual water use of two six-year-old irrigated palms (*cv.* West Coast Tall; leaf area index 2.4) over a six-month period (May to November, the dry season). Actual water use (ET<sub>c</sub>), averaged over five-day intervals, ranged from 2.7 to 4.1 mm d<sup>-1</sup> (mean 3.3). By comparison, reference crop evapotranspiration (ET<sub>o</sub>) averaged 6.2 mm d<sup>-1</sup> (Penman equation), 4.6 mm d<sup>-1</sup> (Blaney Criddle) and 5.3 mm d<sup>-1</sup> (USWB Class A pan) (Doorenbos and Pruitt, 1977). The corresponding crop coefficients (K<sub>c</sub>) were 0.54, 0.73 and 0.65 respectively.

A similar study was reported by Rao (1989), also in Kerala (11°13'N 75°52'E; alt. 70m). A five-year-old palm (*cv.* West Coast Tall; 3 m tall with six or seven functional leaves) was transplanted into each of a pair of drainage lysimeters (3.5  $\times$  3.5 m square). Monthly evapotranspiration rates (ET<sub>c</sub>) were recorded over a year. For irrigated palms, ET<sub>c</sub> varied from 3.3 mm d<sup>-1</sup> in June to 7.8 mm d<sup>-1</sup> in April, with an annual mean of 5.1 mm d<sup>-1</sup>. By comparison, evaporation from a USWB Class A pan averaged 4.4 mm d<sup>-1</sup> over the year. Depending on the season, K<sub>c</sub> varied from 0.60 to 0.68 in the rains to 0.87 to 0.96 in the summer, with an annual mean value of 0.82. An attempt was made to allow for the wider spacing (7.0  $\times$  7.0 m) of palms in a plantation on crop water use, based on changes in soil water content, but it is not easy to evaluate how well this was done.

In Sri Lanka (08°02'N; 79°E; alt. 35 m asl), on a gravelly soil, water use of 15-year-old palms (CRIC 60, spaced 7.7  $\times$  7.7 m, 170 plants ha<sup>-1</sup>) was monitored with a neutron probe over four consecutive dry periods. Water use (ET<sub>c</sub>) averaged about

3.8 mm d<sup>-1</sup> for the first eight days before declining as the soil dried. This equates to about 220 l palm<sup>-1</sup> d<sup>-1</sup>. The average ETc over the whole 45-day dry period was 2.5 mm d<sup>-1</sup>, or 150 l palm<sup>-1</sup> d<sup>-1</sup> (Arachchi, 1998).

Using a soil water balance approach, Azevedo *et al.* (2006) estimated actual evapotranspiration (ETc) for six-year-old dwarf green palms in northeast Brazil. Depending on the irrigation treatment, mean values were 2.5, 2.9 and 3.2 mm d<sup>-1</sup>, with cumulative annual totals of 900–1100 mm. At a planting density of 205 ha<sup>-1</sup> (triangular arrangement, 7.5 × 7.5 × 7.5 m) these equate to 120–160 l palm<sup>-1</sup> d<sup>-1</sup>. By comparison, the Penman-Monteith estimate of reference crop evapotranspiration (ETo, Allen *et al.* 1998) over the year averaged 4.6 mm d<sup>-1</sup>, giving a peak crop coefficient (Kc) of 0.7. For comparison, in Brazil, Miranda *et al.* (2007) derived Kc values for an irrigated (micro-sprinklers) dwarf green cultivar (Jiqui) over a 32-month period, beginning 11 months from planting (spacing 7.5 m triangular; 205 palms ha<sup>-1</sup>). Using the water balance approach (based on tensiometers), ETc increased from a minimum 0.5 mm d<sup>-1</sup> (25 l palm<sup>-1</sup> d<sup>-1</sup>) up to a maximum of 5 mm d<sup>-1</sup> (244 l palm<sup>-1</sup> d<sup>-1</sup>) at a coastal site in Ceará State (3°17'S; 39°15'W; alt. 30 m asl). Over the same period, ETo (Penman–Monteith) varied between 3 and 6 mm d<sup>-1</sup>. During the canopy development phase, Kc increased linearly from 0.63 (11 months after planting) to 1.0 (23 months, when the palms were flowering). Thereafter it remained constant, with an average value of 1.02.

In a detailed experiment in Vanuatu (15° 26.6'S 167° 11.5'E; alt. 80 m asl), Rounsard *et al.* (2006) monitored water use of a coconut plantation (Vanuatu Red Dwarf × Vanuatu Tall Hybrid) over a three year period. The eddy-flux method was used to estimate actual evapotranspiration (ET) from the palms and grass under-storey, and the sap flow method to measure transpiration (T) from the palms alone. Water was freely available in the soil throughout the experimental period. The leaf area index was constant (L = 3), and the crop cover averaged 75% (both values for palms only). Transpiration (annual total 640 mm) represented 68% of ET (950 mm). ET rates varied seasonally between 1.8 and 3.4 mm d<sup>-1</sup>, T from 1.3 to 2.3 mm d<sup>-1</sup> and ETo (Penman-Monteith) from 2.4 to 5.8 mm d<sup>-1</sup>. At a density of 144 palms ha<sup>-1</sup>, these ET values equate to 93–160 l palm<sup>-1</sup> d<sup>-1</sup>. The crop coefficient Kc (= ET/ETo) values averaged 0.79 and 0.59 in the cool and warm seasons respectively. Canopy transpiration during the warm season was apparently limited by partial stomatal closure linked to the saturation deficit of the air, although the maximum daytime value did not exceed 1.2 kPa.

Recently, Madurapperuma *et al.* (2009b) used the 'compensation heat pulse method' to measure actual water use of two cultivars of mature palms (20 years old) grown on two contrasting soils in Sri Lanka (7°35'N; 80°57'E; alt. 100 m asl; square spacing 8.3 × 8.3 m, 145 palms ha<sup>-1</sup>). Diurnal patterns of sap flow were clearly discernable on successive days, averaging about 3 l h<sup>-1</sup> at night before, on the water retentive soil, typically rising rapidly from about 06:00 hours until 10:00 hours. Sap flow then remained high until about 16:00 hours before declining in the late afternoon. Peak rates of water use differed between the two cultivars, reaching 13–14 l palm<sup>-1</sup> h<sup>-1</sup> for CRIC 60 (a tall × tall hybrid) but only 9–10 l palm<sup>-1</sup> h<sup>-1</sup> for CRIC 65

Table 1. Summary of measured crop water use (ET<sub>c</sub>, mature coconut palms) and corresponding estimates of the crop coefficient (K<sub>c</sub> = ET<sub>c</sub>/ET<sub>o</sub>, mean and seasonal range in brackets).

Site	Method	Type	ET <sub>o</sub> method	ET <sub>c</sub> (mm d <sup>-1</sup> )	K <sub>c</sub>	Reference
Kerala 1	Lysimeter	Tall	Class A pan	2.7–4.1	0.65	Jayakumar <i>et al.</i> (1988)
Kerala 2	Lysimeter	Tall	Class A pan	3.3–7.8	0.82(0.65–0.91)	Rao (1989)
Sri Lanka 1	Water balance	Tall		3.8		Arachchi, 1998
Brazil 1	Water balance	Dwarf	Penman-Monteith	3.2	0.7	Azevedo <i>et al.</i> (2006)
Brazil 2	Water balance	Dwarf	Penman-Monteith	5.0	1.02	Miranda <i>et al.</i> (2007)
Vanuatu	Eddy-flux + sap flow	Dwarf	Penman-Monteith	1.8–3.4	0.69(0.59–0.79)	Roupsard <i>et al.</i> (2006)
Sri Lanka 2	Sap flow	Tall	Not specified	1.7	0.5	Madurapperuma <i>et al.</i> (2009a)
		Dwarf		1.3	0.37	

(a dwarf × tall hybrid). Total daily water use averaged 120 l palm<sup>-1</sup> d<sup>-1</sup> (range 105–135 l palm<sup>-1</sup> d<sup>-1</sup>) or 1.74 mm d<sup>-1</sup> for CRIC 60, and 25% less at 90 l palm<sup>-1</sup> d<sup>-1</sup> (range 75–97 l palm<sup>-1</sup> d<sup>-1</sup>) or 1.31 mm d<sup>-1</sup> for CRIC 65. By comparison, daily water use on the second, less water retentive soil was less, averaging 92 and 79 l palm<sup>-1</sup> d<sup>-1</sup> (1.33 and 1.15 mm d<sup>-1</sup>) for each of the two cultivars respectively. The mean daily ET rate (method not specified) over the period of measurement was stated as 3.5 mm giving a K<sub>c</sub> value of 0.37–0.50. Concurrent measurements over the study period indicated that stomatal conductance was substantially greater in CRIC 60 (tall) than in CRIC 65 (dwarf). Palms growing on the water retentive soil had larger leaf areas and trunk diameters (and hence more stem water storage) than the corresponding palms grown on the second soil. In Sri Lanka, CRIC 65 is known for its sensitivity to water stress, whilst CRIC 60 is recognized as being drought tolerant. The ‘compensation heat pulse method’ had previously been successfully evaluated (except at very low flow rates) on palms in Australia by Madurapperuma *et al.* (2009a).

#### Summary: crop water use

1. A diverse selection of methods has been used to measure the water use of coconut palm so that direct comparisons of the results are not easy (Table 1).
2. Across all the sites, ET<sub>c</sub> for mature palms ranged from 1.2 to 7.8 mm d<sup>-1</sup>. A ‘typical’ rate of water use is probably 3.0–3.5 mm d<sup>-1</sup>.
3. Corresponding values of K<sub>c</sub> for mature palms range from 0.5 to 1.02, with some evidence of seasonal variability. A ‘working’ value for irrigation planning purposes is probably 0.7, but this needs to be confirmed. For immature palms the value is proportionally less.

#### WATER PRODUCTIVITY

This section covers first the attempts made to forecast yields based on statistical correlation techniques and, more recently the development of a process-based

simulation model. Second, the results of irrigation experiments in which yield responses to water are quantified are reviewed. Third, some of the recommended drought mitigation practices are summarized.

### *Yield forecasting*

In an analysis of the effects of the 1931 drought (80 mm rain in five months) on the commercial yield of coconuts in Sri Lanka, Park (1934) observed that the minimum nut yield occurred 13 months after the drought ended. The spathes that opened when the drought was most severe were more affected by drought than the flowering and fruiting branches at other stages of development. Yields of nuts did not recover fully until two years after the conclusion of the drought, but the yield of copra per nut had recovered within 12 months. This analysis was followed up by Abeywardena (1968) who attempted to develop a yield forecasting model using long-term rainfall and yield data (1935–1966) in Sri Lanka. But, because of the great time lapse between the initiation of leaf and flower primordia and flowering, and with many other inflorescences at various stages of development present at the same time, it is difficult to relate yield responses to any particular climatic condition. It is not surprising therefore that Abeywardena (1968), using multiple regression techniques, was unable to establish a causal link between rainfall over the 12 months prior to harvest and yield. However, by breaking the year into different periods, when other external factors were similar, he developed an equation (with 12 variables) that explained 86% of the yield variation. Because of the complexity, it is doubtful if this analysis has generic value. Later, Peiris *et al.* (1995) reviewed the many attempts to develop statistical relationships between climatic factors and nut yield (including button shedding and premature nut fall). This highlighted the difficulties (and weaknesses) in this approach to the development of yield forecasting models. Notwithstanding, Peiris and Thattil (1998) subsequently used multivariate analysis in an attempt to explain within and between year variation in nut yield in Sri Lanka. They believed that their ‘parsimonious’ approach (three key variables were identified as important determinants: maximum air temperature, afternoon relative humidity and pan evaporation) could be used to develop meaningful models in other locations. It has not been reported whether or not this is the case.

Of greater potential generic value is the simulation model (InfoCrop-coconut) developed, calibrated and validated in India by Naresh Kumar *et al.* (2008). The model simulates development stages of growth (based on thermal time), dry matter production (solar radiation interception  $\times$  radiation conversion efficiency) and dry matter partitioning. There were good linear relationships between simulated dry matter production and measured values ( $r^2 = 0.95$ ) and between the corresponding nut yields ( $r^2 = 0.86$ ) across a range of sites and experimental treatments. Nut productivity under rain-fed and irrigated conditions at four sites within India was simulated. In north Kerala, for example, irrigation (200 l palm<sup>-1</sup> every four days plus fertilizer) was predicted to increase the (simulated) average annual nut yield from about 4000 to 15500 kg ha<sup>-1</sup>. Further evaluation of this model is justified.

The long-term effect (up to four years) of an extended dry period on nut yields was confirmed by Naresh Kumar *et al.* (2007) in an analysis of the impact of rainfall amount and distribution on yields from commercial plantations in the different agro-ecological zones in India. Whether the simulation model takes this into account is not clear.

#### *Yield responses to irrigation*

Actual yield responses to irrigation have been recorded in field experiments in India (Kerala), Sri Lanka and Brazil.

The irrigation requirement of immature palms (from 5–7 years in the field; *cv.* West Coast Tall) was reported by Nelliath and Padmaja (1978) in Kerala. The ‘best’ combination of treatments in terms of yield of nuts and water use efficiency was the application of 40 mm of irrigation water (I) when the cumulative potential evaporation (CPE) total reached 53 mm (I/CPE ratio 0.75, which is equivalent to a Kc value of 0.75). In this way, an average total of 680 mm of water was applied in the summer months, yielding a total of 157 nuts palm<sup>-1</sup> over the three years after the palms started to come into bearing. By comparison, when the I/CPE ratio was 0.5 the total yield was significantly less, at 126 nuts palm<sup>-1</sup>. There was no unirrigated/rain-fed control treatment.

In Kerala, Nair (1989) reported the results of an irrigation trial in which water was applied at 500 l palm<sup>-1</sup> (at a plant density of 178 ha<sup>-1</sup> this is equivalent to 9 mm) at different intervals (*cv.* WCT) during the summer months (December to May) over a five-year period. Water was applied in 1.8 m radius basins to a sandy clay loam soil. Compared to the control rain-fed treatment (average yield *ca.* 90 nuts palm<sup>-1</sup>) significant increases (range +15–39 nuts palm<sup>-1</sup>) in yield were obtained in the third and subsequent years from irrigation applied when the ‘cumulative potential evaporation’ totalled 50 or 25 mm. No indication is given on how much water in total was applied in each year.

Previously, Bhaskaran and Leela (1978) had described a similar trial in Kerala lasting 12 years with the same cultivar (WCT). Water was applied at a rate of 800 l palm<sup>-1</sup> every seven days (equivalent to 2 mm d<sup>-1</sup> only) in 2 m radius basins during the summer months. The soil was a red sandy loam. It took three years before the full yield benefits (averaging +30 nuts palm<sup>-1</sup> year<sup>-1</sup> compared with pre-irrigation yields of a variable 40) were realized. Before that, in the ‘transition period’, the yield increase was about half this. The largest increase (+39 nuts palm<sup>-1</sup>) came from palms initially classified as ‘low’ yielding (20–40 nuts palm<sup>-1</sup>). Yield increases followed an increase in female flower production and setting percentage. This and other work on water management of coconut undertaken in India is summarized in Yusuf and Varadan (1993).

In Sri Lanka, Nainanayake *et al.* (2008) evaluated the responses of mature palms (20 years old; cultivar not named), growing on a shallow (0.6 m) sandy clay loam soil, to drip irrigation over a two-year period, two to four years after irrigation began. During this period there were three dry spells lasting 48, 78 and 83 days. Irrigation during these dry periods (80 l palm<sup>-1</sup> d<sup>-1</sup>, or 1.3 mm d<sup>-1</sup>) reduced the afternoon soil temperature

(from 31 to 27 °C), nut surface (seventh bunch from the top, by up to 2.5 °C) and air (by up to 2.0 °C) compared with the control (unirrigated) treatment. Irrigation therefore ameliorated the temperature regime and created conditions close to the optimum (27 °C) for coconut. Even with irrigation, stomatal conductance declined during the dry periods but applications of 80 l palm<sup>-1</sup> d<sup>-1</sup> (1.3 mm d<sup>-1</sup>) maintained transpiration at rates similar to those recorded in the rainy season. Irrigation also increased female flower production and reduced premature nut fall. Over the two year period, applications of 80 l palm<sup>-1</sup> d<sup>-1</sup> resulted in a 45% yield increase over the control. Halving the amount of water applied (to 40 l palm<sup>-1</sup>; 0.65 mm d<sup>-1</sup>) halved the yield benefit (to 20%). The absolute yields were not clearly specified.

In northeast Brazil, Azevedo *et al.* (2006) applied 50, 100 or 150 l palm<sup>-1</sup> d<sup>-1</sup> (equivalent to 1.0, 2.0 and 3.0 mm d<sup>-1</sup> respectively) to six-year-old dwarf green palms on a sandy soil over a two-year period. It appears that these daily applications were made regardless of rainfall. There was no rainfall-only control treatment. The whole experimental area had previously been irrigated. Using a water balance approach actual evapotranspiration was estimated from which water use efficiencies were calculated (i.e. apparently based on total ETc not on the depth of irrigation water applied). There were no yield differences between treatments in terms of the number of bunches per palm or the number of fruits per bunch but extra irrigation water increased the volume of water per fruit by about 16%. When yield was expressed as the number of fruits per hectare there was a significant 12% yield loss from applying 1.0 mm d<sup>-1</sup> compared with 2 mm d<sup>-1</sup> (equivalent to a reduction in the number of nuts per palm from 93 to 82). Water use efficiencies (as inadequately defined) were essentially the same for all three irrigation treatments.

In Kerala, irrigation was recently reported to have increased annual yields from mature coconut palms (*cv.* West Coast Tall) over a six-year period by, on average, an estimated 30–40 nuts palm<sup>-1</sup> (from 50–60 to 90 nuts palm<sup>-1</sup>; Naresh Kumar and Kasturi Bai, 2009).

In Sri Lanka, Arachchi (1998) developed criteria for the design of a drip irrigation system for coconuts grown on a gravelly soil. The maximum flow rate he recommended was 30 l h<sup>-1</sup> for 2.5 h from each of four drippers spaced equidistant around, and 1.0 m from, the base of the trunk. This regime wetted a large volume of soil within the effective root zone of 15-year-old palms (*cv.* CRIC 60; 170 plants ha<sup>-1</sup>) and equates to 5.1 mm d<sup>-1</sup> (300 l palm<sup>-1</sup> d<sup>-1</sup>). By comparison, actual crop water use during the first eight days of the dry period averaged about 3.8 mm d<sup>-1</sup> (220 l palm<sup>-1</sup> d<sup>-1</sup>) before declining (see *Crop water use* above). Eight days became the recommended irrigation interval. Such an analysis does not allow for the fact that drip irrigation enables small quantities of water to be applied frequently, rather than requiring the whole root zone to be wetted at extended intervals. The productive and economic advantages of designing drip systems for deficit (under) irrigation as compared to standard drip systems designed for full irrigation to meet potential evapotranspiration have been described by Keller *et al.* (1992) in Kerala.

However, the limited size of the wetted soil volume under drip irrigation was identified as a cause for concern during an on-farm evaluation of drip irrigation in

South India, although that view may have been influenced by the fact that only very small quantities of water ( $32 \text{ l palm}^{-1} \text{ d}^{-1}$ ;  $0.6 \text{ mm d}^{-1}$ ) were being applied (Thambam *et al.*, 2006). What also appear to be very small amounts of water ( $30\text{--}40 \text{ l palm}^{-1} \text{ d}^{-1}$ ) are recommended for drip (and basin) irrigation on sandy soils in the Konkan region of Maharashtra (India) (Nagwekar *et al.*, 2006). This advice is inconsistent with the recommendation of the Coconut Development Board of India, which states 'generally' an adult palm requires 600–800 litres of water once in four to seven days' (CDB, 2010).

### *Drought mitigation*

In view of the sensitivity of palms to water stress, water conservation is strongly recommended (Mahindapala and Pinto, 1991). In Sri Lanka, this means: *mulching* (to restrict evaporation from the soil surface) by placing a layer of vegetation (such as coconut husks) in a 1.75 m radius circle around the trunk. *Husk* or *coir dust pits* or *trenches* increase the retention and availability of water especially in sandy soils. They should be at least 0.6 m deep and 1.2–1.5 m wide and situated within reach of the roots of each palm. They are filled with alternating layers of husk (or coir dust) and soil. The results of original studies undertaken in India by Marar and Kunhiraman (1957) and by Balasubramanian *et al.* (1985) on husk burial as a drought mitigation measure have been summarized by Yusuf and Varadan (1993). For young palms in South India, Shanmugam (1973) describes other drought mitigation practices including deep planting (with the bole 0.6–1.2 m below ground level), the placement of porous earthen pots regularly filled with water (pitcher irrigation) adjacent to the stem, in addition to husk burial (500–1000 husks per palm) and husk mulch. Xavier Bonneau (personal communication) confirms the benefits that can result from these interventions.

In Indonesia (Gunung Patan, Sumatra), hybrid palms, four to six-years-old, were observed to be more susceptible to drought than younger or older palms because of an imbalance between the relative sizes of the foliage and the root systems (Bonneau and Subagio, 1999). Other things being equal, dwarfs (e.g. Malayan Yellow Dwarf and Cameroon Red Dwarf) were more susceptible to drought than tall or hybrids. They also found that the mortality of commercially grown palms during the long dry season was negatively correlated with the chloride status of the palm (as measured in leaf 14 at the beginning of the dry season). Applying common salt (sodium chloride) at annual rates of up to  $4.5 \text{ kg palm}^{-1}$  reduced mortality, reduced defoliation, advanced recovery after the start of the rains and increased the yield of copra from 10 to 15  $\text{kg palm}^{-1}$  (averaged over eight seasons). Previously, Braconnier and Bonneau (1998) had confirmed the important role that the chloride ion plays in maintaining gas exchange (net assimilation and transpiration) in dry weather through stomatal regulation. Indeed, sodium chloride is recommended as a cheaper alternative to potassium chloride as a fertilizer in Indonesia, particularly in dry areas, where it contributes to drought mitigation (Bonneau *et al.*, 1997).

For example, in a field experiment in Indonesia, in which different levels of common salt (from 0 to 4.5 kg palm<sup>-1</sup> y<sup>-1</sup>) were compared, mature hybrid palms (*cv.* PB-121) responded as follows to these two extreme treatments, averaged over the period 1989–1996: an increase from 55 to 76 nuts palm<sup>-1</sup> y<sup>-1</sup>; from 184 to 201 g copra nut<sup>-1</sup>; from 10.7 to 15.8 kg copra palm<sup>-1</sup> y<sup>-1</sup>; from 6.4 to 14.9 green leaves palm<sup>-1</sup> (at the end of the 1991 drought); from 78 to 148 palms ha<sup>-1</sup> (at the end of the 1996 drought, the original plant population was 152 ha<sup>-1</sup>); and from 1.47 to 2.38 t copra ha<sup>-1</sup> y<sup>-1</sup>. The critical chloride concentration in the leaf (14<sup>th</sup>) of mature palms is considered to be 0.5% (Bonneau *et al.*, 1997).

The role of chloride in the nutrition of palms and its contribution to drought resistance in coconut has been well reported. Only in plantations close to the sea, where salt spray occurs naturally, is there apparently no benefit from its application (Bonneau *et al.*, 1993; Ollagnier *et al.*, 1983; Von Uexhull, 1985).

In this context, Yusuf and Varadan (1993) cited a study by Shanmugam (1973) which demonstrated that coconut can withstand irrigation with sea water (salt content 0.6–1.0%; 90 l palm<sup>-1</sup> twice a week; sandy or sandy loam soils; 1.5 m radius basins). The monsoon rains leached out any residual salt. In Brazil (5°46'S; 35°12'W; alt. 18 m asl), Marinho *et al.* (2006) evaluated the viability of using saline water for irrigation. In a two year study with (initially) three and a half-year-old green dwarf coconut (*cv.* Anão Verde), the number of female flowers was increased when salt was added to the irrigation water, but at an electrical conductivity (EC<sub>w</sub>) greater or equal to 5 dS m<sup>-1</sup> the mean weight of a fruit (beginning at the 11<sup>th</sup> harvest) and the number of fruits (14<sup>th</sup> harvest) were both reduced compared with the control treatment (EC<sub>w</sub> = 0.1 dS m<sup>-1</sup>). However, even when the EC<sub>w</sub> was 10 dS m<sup>-1</sup> acceptable yields were still achieved.

*Summary: water productivity*

1. Partly because of the long time interval (44 months) between flower initiation and harvest of the mature nut, it has not been possible to establish a direct causal link between yield and rainfall for coconut.
2. Full responses to irrigation are only obtained in the third and subsequent years after irrigation is introduced.
3. There is a limited amount of reliable and complete field data on actual yield responses to irrigation/drought. In general, it appears that relatively small quantities of water have been applied in the irrigation trials compared with ET<sub>c</sub>.
4. In Kerala, yield increases of 20–40 nuts palm<sup>-1</sup> (mature *cv.* West Coast Tall) have been recorded after the application of the equivalent of about 2 mm d<sup>-1</sup> during the summer months. This represents a 50% yield increase on base yields averaging about 60 nuts palm<sup>-1</sup>.
5. In Sri Lanka, applications of 1.3 mm d<sup>-1</sup> during the dry season ameliorated the microclimate, maintained transpiration and increased yields by 45%.
6. In northeast Brazil, yields were reduced by 12% if only 1.0 mm d<sup>-1</sup>, rather than 2.0 mm d<sup>-1</sup>, was applied during the dry season to dwarf green cultivars
7. Irrigation increases female flower production and reduces premature nut fall.

8. It has not been possible to derive yield/water-use (water productivity) response functions here because of incomplete data.
9. Drought mitigation practices include husk burial and mulching, and the application of common salt.
10. Mature palms can withstand irrigation with sea water.

#### CONCLUSIONS

Until relatively recently much of the research reported was empirical, so that the results were only of value in the immediate location of the experiments. They were time and space limited. This is understandable and is due, in part, to the difficulty of undertaking research on this fascinating crop. It is also due in part to limited funding at the relatively small research institutes with the mandate to undertake this research. There has also been, with some exceptions, a notable lack of international collaboration in research (coconuts are outside the CGIAR system) for a crop on which millions of people depend for their livelihoods (Carr and Punchihewa, 2002).

Potential and actual yields are determined mainly by climate, and its day to day variability which is known as weather. In the case of coconuts, this simple statement is complicated by the long time interval between the initiation of the inflorescence and the harvesting of the mature nut (44 months). Changing weather conditions during this period will influence yield development in different ways.

In 1992, following a visit to Sri Lanka, I wrote 'to the best of my knowledge only a limited amount of research on the physiological basis of yield development in coconuts has been reported. For example, how do environmental (and agronomic) factors influence such variables as fractional light interception by the canopy; dry matter production and partitioning and the harvest index; conversion efficiency for solar radiation; crop water use and water-use efficiency? What are the potential yields of copra (and other commercially valuable products) in given locations with existing cultivars? Why do actual yields differ from potential yields? How important is water stress as a limiting factor? Is irrigation justified economically? What are the other principal limiting factors? If we can begin to quantify some of these variables and the relationships between them in systematic ways, it should be possible to develop procedures for yield forecasting (with and without water stress as a limiting factor) and even perhaps to identify selection criteria for new cultivars. To do this successfully though will require a co-ordinated team approach within an agreed framework for analysis. Experiments must be designed so that key measurements are taken to provide basic data that can be used to develop and validate a yield forecasting model' (Carr, 1992).

Substantial progress has been made since 1992 in many of these areas, including the development of a yield forecasting model, although this needs to be developed and validated further. In the immediate context of this review, there is still a lack of knowledge on the actual water use of coconut and of yield responses to water. Indicators of drought tolerance have been identified but it is not clear whether these have resulted in new genotypes. The challenge that remains is to quantify how little

rather than how much water is needed to produce an economically viable crop. A co-ordinated international approach to addressing this issue is recommended.

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#### REFERENCES

- Abeywardena, V. (1968). Forecasting coconut crops using rainfall data – a preliminary study. *Ceylon Coconut Quarterly* 19:161–176.
- Allen, R. G., Pereira, L. S., Raes, D. and Smith, M. (1998). Crop evapotranspiration: guidelines for computing crop water requirements. *Irrigation and Drainage, Food and Agriculture Organization of the United Nations, Paper 56*, Rome, Italy.
- Arachchi, L. P. V. (1998). Preliminary requirements to design a suitable drip irrigation system for coconut (*Cocos nucifera* L.) in gravelly soils. *Agricultural Water Management* 38:169–180.
- Avilan, L. A., Rivas, N. and Sucre, R. (1984). Estudio del sistema radical del cocotero (*Cocos nucifera* L.). *Oléagineux* 39:13–23.
- Azevedo, P. V., Sausa, I.F. and Silva, B. B. (2006). Water-use-efficiency of dwarf-green coconut (*Cocos nucifera* L.) orchards in northeast Brazil. *Agricultural Water Management* 84:259–264.
- Balasubramanian, R., Ramanathan, T. and Vijayaraghavan, H. (1985). Certain aspects of moisture conservation in coconut gardens. *Indian Coconut Journal* 16:13–15.
- Bhaskaran, U. P. and Leela, K. (1978). Response of coconut to irrigation in relation to production status of palms and soil type. In *Proceedings of First Annual Symposium on Plantation Crops (PLACROSYM 1)*, 200–206 (Ed. E. V. Nelliath) Kasaragod, India.
- Bonneau, X., Boulon, D., Bourgoing, G. and Sugariato, J. (1997). Le chlorure de sodium, fertilisant idéal du cocotier en Indonésie. *Plantations, Recherche, Développement* 4:336–346.
- Bonneau, X., Ochs, R., Kitu, W. T. and Yuswohadi. (1993). Chlorine: an essential element in the mineral nutrition of hybrid coconuts in Lampung (Indonesia). *Oléagineux* 48:179–189.
- Bonneau, X. and Subagio, K. (1999). Culture du cocotier en zone exposée au risque de sécheresse. *Plantations, recherche, développement* 6:432–439.
- Braconnier, S. and d’Auzac, J. (1990). Chloride and stomatal conductance in coconut. *Oléagineux* 45:259–264.
- Braconnier, S. and Bonneau, X. (1998). Effects of chlorine deficiency in the field on leaf gas exchanges in the PB121 coconut hybrid. *Agronomie* 18:563–572.
- Carr, M. K. V. (1992). *Plantation Crop Research in Sri Lanka*. Unpublished report, Silsoe College, Cranfield University, 12–20.
- Carr, M. K. V. (2001). The water relations and irrigation requirements of coffee. *Experimental Agriculture* 37:1–36.
- Carr, M. K. V. (2009). The water relations and irrigation requirements of banana (*Musa* spp.). *Experimental Agriculture* 45:333–371.
- Carr, M. K. V. (2010a). The role of water in the growth of the tea (*Camellia sinensis*) crop: a synthesis of research in eastern Africa. 1. Plant water relations. *Experimental Agriculture* 46:329–349.
- Carr, M. K. V. (2010b). The role of water in the growth of the tea (*Camellia sinensis*) crop: a synthesis of research in eastern Africa. 2. Water productivity. *Experimental Agriculture* 46:351–379.
- Carr, M. K. V. and Knox, J. W. (2011). The water relations and irrigation requirements of sugar cane (*Saccharum officinarum*): a review. *Experimental Agriculture* (in press).
- Carr, M. K. V. and Punchihewa, P. G. (2002). External Review Report. BUROTROP, Montpellier, France, 13–46.
- CDB (2010). Coconut Development Board of India. Available from: [www.coconutboard.nic.in/package.htm](http://www.coconutboard.nic.in/package.htm) [Accessed 13 December 2010].
- Cintra, F. L. D., Leal, M. de L. da S.L. and Passos, E. E. de M. (1992). Evaluation of root system of dwarf coconut cultivars. *Oléagineux* 47:225–234.
- Cintra, F. L. D., Passos, E. E. de M. and Leal, M. de L. da S.L. (1993). Evaluation de la distribution du système racinaire de cultivars de cocotier Grands. *Oléagineux* 48:453–461.
- Copeland, E. H. (1906). On the water relations of the coconut palm (*Cocos nucifera*). *Journal of Science*, Manila 1:6–57.

- Doorenbos, J. and Pruitt, W. O. (1977). Crop water requirements. *Irrigation and Drainage, Food and Agriculture Organization of the United Nations, Paper 24*, Rome, Italy.
- FAO (2010). UN Food and Agriculture Organization <http://faostat.fao.org/site/339/default.aspx>
- Friend, D. and Corley, R. H. V. (1994). Measuring coconut palm dry matter production. *Experimental Agriculture* 30:223–235.
- Gomes, F. P., Mielke, M. S. and Almeida, A-AF. (2002a). Leaf gas exchange of green dwarf coconut (*Cocos nucifera* L. var. *nana*) in two contrasting environments of the Brazilian north-east region. *Journal of Horticultural Science and Biotechnology* 77:766–772.
- Gomes, F. P., Mielke, M. S., Almeida, A-AF and Muniz, W. S. (2002b). Leaf gas exchange in two dwarf coconut genotypes in the southeast of Bahia State, Brazil. *Coconut Research and Development* 18:37–55.
- Gomes, F. P., Oliva, M. A., Mielke, M. S., De Almeida, A-A.F., Lette, H. G. and Aquino, L. A. (2008). Photosynthetic limitations in leaves of young Brazilian Green Dwarf coconut (*Cocos nucifera* L. 'nana') palm under well-watered conditions or recovering from drought stress. *Environmental and Experimental Botany* 62:195–204.
- Gomes, F. P., Oliva, M. A., Mielke, M. S., De Almeida, A-A.F., Lette, H. G. and Aquino, L. A. (2009). Is abscisic acid involved in the drought responses of Brazilian Green Dwarf coconut? *Experimental Agriculture* 45:189–198.
- Gomes, F. P. and Prado, C. H. B. A. (2007). Ecophysiology of coconut palm under water stress. *Brazil Journal of Plant Physiology* 19:377–391.
- Harries, H. C. (1978). The evolution, dissemination and classification of *Cocos nucifera* L. *Botanical Review* 44:265–320.
- Harries, H. C. (1995). Coconut *Cocos nucifera* L. In *Evolution of Crop Plants* 2nd Edn, 389–394 (Eds J. Smart and N. W. Simmonds). Harlow: Longmans.
- Huxley, P. (1999). *Tropical Agroforestry*. Oxford: Blackwell Science.
- Jayakumar, M., Saseendran, S. A. and Hemapraba, M. (1988). Crop coefficient for coconut (*Cocos nucifera* L.): a lysimetric study. *Agricultural and Forest Meteorology* 43:235–240.
- Jayasekara, C., Ranasinghe, C. S. and Mathes, D. T. (1993). Screening for high yield and drought tolerance in coconut. In *Advances in Coconut Research and Development*, 209–218. (Eds. M.K. Nair, H.H. Khan, P. Gopalasundaram & E.V.V. Bhaskara Rao). New Delhi, Oxford and IBH Publishing.
- Juma, M. and Fordham, R. (1998). The effect of environmental stress on coconut (*Cocos nucifera* L.) growth in Zanzibar. In *Proceedings of the International Cashew and Coconut Conference: Trees for Life – the Key to Development*, 342–347 (Eds C.P. Topper *et al.*). BioHybrids International Ltd, Reading, UK.
- Kasturi Bai, K. V., Naresh Kumar, S., Rajagopal, V. and Vijayakumar, K. (2008). Principal component analysis of chlorophyll fluorescent transients for tolerance to drought stress in coconut seedlings. *Indian Journal of Horticulture* 65:471–476.
- Kasturi Bai, K. V., Voleti, S. R. and Rajagopal, V. (1988). Water relations of coconut palms as influenced by environmental variables. *Agricultural and Forest Meteorology* 43:193–199.
- Keller, J., Sivanappan, R. K. and Varadan, K. M. (1992). Design logic for deficit drip irrigation of coconut trees. *Irrigation and Drainage Systems* 6:1–7.
- Kushwah, B. L., Nelliath, E. V., Markose, V.T. and Sunny, A. F. (1973). Rooting pattern of coconut (*Cocos nucifera* L.). *Indian Journal of Agronomy* 18:71–74.
- Lebrun, P., N'cho, Y. P., Seguin, M., Grivet, L. and Baudouin, L. (1998). Genetic diversity in coconut (*Cocos nucifera* L.) revealed by restriction fragment length polymorphism (RFLP) markers. *Euphytica* 101:103–108.
- Madurapperuma, W. S., Bleby, T. M. and Burgess, S. S. O. (2009a). Evaluation of sap flow methods to determine water use by cultivated palms. *Environmental and Experimental Botany* 66:372–390.
- Madurapperuma, W. S., de Costa, W. A. J. M., Sangakkara, U. R. and Jayescara, C. (2009b). Estimation of water use of mature coconut (*Cocos nucifera* L.) cultivars (CRIC 60 and CRIC 65) grown in the low country intermediate zone using the compensation heat pulse method (CHPM). *Journal of the National Science Foundation of Sri Lanka* 37:175–186.
- Magnaye, A. B. (1969). Studies on the root system of healthy and cadang-cadang affected coconut trees. *Philippine Journal of Plant Industry* 34:143–154.
- Mahindapala, R. and Pinto, J. L. J. G. (1991). *Coconut Cultivation*. Coconut Research Institute of Sri Lanka, Lunuwila, Sri Lanka.
- Manthirratna, M. A. P. P. and Sambasivam, S. (1974). Stomatal density in varieties and forms of the coconut. *Ceylon Coconut Journal* 25:105–108.
- Mathew, C. (1981). Water relations of coconut palm affected by root (wilt) disease. *Journal of Plantation Crops* 9:51–55.
- Marar, M. M. K. and Kunhiraman, C. A. (1957). Husk burial for the improvement of coconut gardens. *Indian Coconut Journal* 10:3–11.

- Marinho, F. J. L., Gheyi, H. R., Fernandes, P. D., de Holanda, J. S. and Neto, M. F. (2006). Cultivo de coco 'Anão Verde' irrigado com águas salinas. *Pesquisa Agropecuária Brasileira, Brasília* 41:1277–1284.
- Mialet-Serra, I., Clement-Vidal, A., Rouspard, O., Jourdan, C. and Dingkuhn, M. (2008). Whole plant adjustments in coconut (*Cocos nucifera*) in response to sink-source relationships. *Tree Physiology* 28:1199–1209.
- Milburn, J. A. and Zimmermann, M. H. (1977). Preliminary studies on sapflow in *Cocos nucifera* L. 1. Water relations and xylem transport. *New Phytologist* 79:535–541.
- Miranda, F. R., de, Gomes, A. R. M., Oliveira, C. H. C., de, Montenegro, A. A. T. and Bezerra, F. M. L. (2007). Evapotranspiration and crop coefficients for green-dwarf coconut in the coastal area of Ceara State, Brazil. *Revista Ciência Agronômica* 38:129–135.
- Moss, J. R. J. (1992). Measuring light interception and the efficiency of light utilization by the coconut palm (*Cocos nucifera* L.). *Experimental Agriculture* 28:273–285.
- Murray, D. B. (1977). Coconut palm. In *Ecophysiology of Tropical Crops*, 383–407 (Eds. P. de T. Alvim and T.T. Kozłowski), London: Academic Press.
- Nagwekar, D. D., Desai, V. S., Sawant, V. S., Haldankar, P. M., Joshi, G. D. and More, T. A. (2006). Effect of drip irrigation on yield of coconut (*Cocos nucifera* L.) in sandy soil of Konkan region of Maharashtra (India). *Journal of Plantation Crops*. 34:344–346.
- Nainanayake, A., Ranasinghe, C. S. and Tennakoon, N.A. (2008). Effects of drip irrigation on canopy and soil temperature, leaf gas exchange, flowering and nut setting of mature coconut (*Cocos nucifera* L.). *Journal of the National Science Foundation, Sri Lanka* 38:43–50.
- Nair, R. R. (1989). Summer irrigation requirements of the coconut palm. *Indian Coconut Journal* 19:3–7.
- Naresh, Kumar, S. and Kasturi Bai, K. V. (2009). Photosynthetic characters in different shapes of coconut canopy under irrigated and rainfed conditions. *Indian Journal of Plant Physiology* 14:215–223.
- Naresh Kumar, S., Kasturi Bai, K. V., Rajagopal, V. and Aggarwal, P.K. (2008). Simulating coconut growth, development and yield with the InfoCrop-coconut model. *Tree Physiology* 28:1049–1058.
- Naresh Kumar, S., Rajagopal, V. and Karun, A. (2000). Leaflet anatomical adaptations in coconut cultivars for drought tolerance. In *Recent Advances in Plantations Crops Research*, 225–229 (Eds. N. Muraleedharan and R. Rajkumari). New Delhi: Allied Publishers Ltd.
- Naresh Kumar, S., Rajagopal, V., Siju Thomas, T., Cherian, V.K., Ratheesh Narayanan, M. K., Ananda, K. S., Nagawekar, D. D., Hanumanthappa, M., Vincent, S. and Srinivasulu, B. (2007). Variations in nut yield of coconut and dry spell in different agro-climatic zones of India. *Indian Journal of Horticulture* 64:309–313.
- Nelliath, E. V. and Padmaja, P. K. (1978). Irrigation requirement of coconut and response to levels of fertilizer under irrigated condition during the early bearing stage. In *Proceedings of First Annual Symposium on Plantation Crops (PLACROSYM 1)* 186–199 (Ed. E.V. Nelliath). Kasaragod, India.
- Ollagnier, M., Ochs, R., Pomier, M. and de Taffin, G. (1983). Action du chlore sur le cocotier hybride PB 121 en Côte d'Ivoire et en Indonésie. *Oléagineux* 38:309–321.
- Park, M. (1934). Some notes on the effects of drought on the yield of coconut palms. *Tropical Agriculturalist* 33:141–150.
- Passos, E. E. M. and Da Silva, J. V. (1990). Fonctionnement des stomates de cocotier (*Cocos nucifera*) au champ. *Canadian Journal of Botany* 68:458–460.
- Passos, E. E. M. and Da Silva, J. V. (1991). Détermination de l'état hydrique du cocotier par le méthode dendrométrique. *Oléagineux* 46:233–238.
- Passos, E. E. M., Prado, C. H. B. A. and Aragão, W. M. (2009). The influence of vapour pressure deficit on leaf water relations of *Cocos nucifera* in northeast Brazil. *Experimental Agriculture* 45:93–106.
- Peiris, T. S. G. and Thattil, R. O. (1998). The study of climate effects on the nut yield of coconut using parsimonious models. *Experimental Agriculture* 34:189–206.
- Peiris, T. S. G., Thattil, R. O. and Mahindapala, R. (1995). An analysis of the effect of climate and weather on coconut (*Cocos nucifera*). *Experimental Agriculture* 31:451–460.
- Persley, G. J. (1992). *Replanting the Tree of Life: Towards an International Agenda for Coconut Palm Research*. Oxford: CAB International.
- Pomier, M. and Bonneau, X. (1987). Développement du système racinaire du cocotier en fonction de milieu en Côte d'Ivoire. *Oléagineux* 42:409–421.
- Prado, C.H.B.A., Passos, E. E. M. and de Moraes, J. A. P. V. (2001). Photosynthesis and water relations of six tall genotypes of *Cocos nucifera* in wet and dry seasons. *South African Journal of Botany* 67:169–176.
- Purseglove, J. W. (1972). *Tropical Crops: Monocotyledons*. London: Longman.

- Rao, A. S. (1989). Water requirements of young coconut palms in a humid tropical climate. *Irrigation Science* 10:245–249.
- Rajagopal, V. and Kasturi Bai, K.V. (2002). Drought tolerance mechanism in coconut. *Burotrop Bulletin* 17:21–22.
- Rajagopal, V., Kasturi Bai, K. V., Kumar, S. N. and Niral, V. (2007). Genetic analysis of drought responsive physiological characters in coconut. *Indian Journal of Horticulture* 64:181–189.
- Rajagopal, V., Kasturi Bai, K. V. and Voleti, S. R. (1990). Screening of coconut genotypes for drought tolerance. *Oléagineux* 45:215–223.
- Rajagopal, V., Patil, K. D. and Sumathykuttyamma, B. (1986). Abnormal stomatal opening in coconut palms affected with root (wilt) disease. *Journal of Experimental Botany* 37:1398–1405.
- Rajagopal, V., Ramadasan, A., Kasturi Bai, K. V. and Balasimha, D. (1989). Influence of irrigation on leaf water relations and dry matter production in coconut palms. *Irrigation Science* 10:73–81.
- Rajagopal, V., Shivishankar, S. and Kasturi Bai, K. V. (1993). Characterisation of drought tolerance in coconut. In *Advances in Coconut Research and Development* 191–199 (Eds. M. K. Nair, H. H. Khan, P. Gopaldasundaram and E. V. V. Bhaskara Rao). Oxford and IBH Publishing Co., New Delhi.
- Rajagopal, V., Shivishankar, S., Kasturi Bai, K. V. and Voleti, S.R. (1988). Leaf water potential as an index of drought tolerance in coconut (*Cocos nucifera* L.). *Plant Physiology and Biochemistry* (India) 15:80–86.
- Rajagopal, V., Sumathykuttyamma and Patil, K. D. (1987). Water relations of coconut palms affected with root (wilt) disease. *New Phytologist* 105:289–293.
- Repellin, A., Laffray, D., Daniel, C., Braconnier, S. and Zuily-Fodil, Y. (1997). Water relations and gas exchange in young coconut palm (*Cocos nucifera* L.) as influenced by water deficit. *Canadian Journal of Botany* 75:18–27.
- Repellin, A., Zuily-Fodil, Y. and Daniel, C. (1993). Merits of physiological tests for characterizing the performance of different coconut varieties subjected to drought. In *European Research Working for Coconut*, 71–89, Seminar Proceedings September 1993, CIRAD-CP, Montpellier, France. Also published as Repellin, A., Daniel, C and Zuily-Fodil, Y. (1994). *Oléagineux* 49:155–168.
- Roupsard, O., Bonnefond, J-M., Irvine, M., Berbigier, P., Nouvellon, Y., Dauzat, J., Taga, S., Hemel, O., Jourdan, C., Saint-André, L., Mialet-Serra, I., Labouisse, J-P, Epron, D., Joffre, R., Braconnier, S., Rouzière, A., Navarro, M. and Bouillet, J-P. (2006). Partitioning energy and evapo-transpiration above and below a tropical palm canopy. *Agricultural and Forest Meteorology* 139:252–268.
- Shanmugan, K. S. (1973). Moisture management for coconut. *Coconut Bulletin* 4:2–10.
- Shivashankar, S., Kusturi Bai, K. V. and Rajagopal, V. (1991). Leaf water potential, stomatal resistance and activities of enzymes during the development of moisture stress in the coconut palm. *Tropical Agriculture*, Trinidad 68:106–110.
- Thamban, C., Mathew, A.C. and Arulraj, S. (2006). Field performance of drip irrigation system in coconut gardens. *Journal of Plantation Crops* 34:98–102.
- Tomlinson, P. B. (2006). The uniqueness of palms. *Botanical Journal of the Linnean Society* 151:5–14.
- Voleti, S. R., Kasturi Bai, K. V., Nambiar, C. K. B. and Rajagopal, V. (1993a). Influence of soil type on the development of moisture stress in coconut (*Cocos nucifera* L.). *Oléagineux* 48:505–509.
- 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 *Advances in Coconut Research and Development* 243–245 (Eds. M. K. Nair, H. H. Khan, P. Gopaldasundaram and E. V. V. Bhaskara Rao). Oxford and IBH Publishing Co., New Delhi.
- Von Uexhull, H. R. (1985). Chlorine in the nutrition of palm trees. *Oléagineux* 40: 67–72.
- Wickramaratne, R. T. (1987). Breeding coconuts for adaptation to drought. *Coconut Bulletin* 4:16–23.
- Yusuf, M. and Varadan, K.M. (1993). Water management studies on coconut in India. In *Advances in Coconut Research and Development* 337–346 (Eds. M. K. Nair, H. H. Khan, P. Gopaldasundaram and E. V. V. Bhaskara Rao). Oxford and IBH Publishing Co., New Delhi.