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THE WATER RELATIONS OF RUBBER (*HEVEA BRASILIENSIS*): A REVIEW

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SUMMARY

The results of research done on water relations of rubber are collated and summarised in an attempt to link fundamental studies on crop physiology to crop management practices. Background information is given on the centres of origin (Amazon Basin) and production of rubber (humid tropics; south-east Asia), but the crop is now being grown in drier regions. The effects of water stress on the development processes of the crop are summarised, followed by reviews of its water relations, water requirements and water productivity. The majority of the recent research published in the international literature has been conducted in south-east Asia. The rubber tree has a single straight trunk, the growth of which is restricted by 'tapping' for latex. Increase in stem height is discontinuous, a period of elongation being followed by a 'rest' period during which emergence of leaves takes place. Leaves are produced in tiers separated by lengths of bare stem. Trees older than three to four years shed senescent leaves (a process known as 'wintering'). 'Wintering' is induced by dry, or less wet, weather; trees may remain (nearly) leafless for up to four weeks. The more pronounced the dry season the shorter the period of defoliation. Re-foliation begins before the rains start. The supply of latex is dependent on the pressure potential in the latex vessels, whereas the rate of flow is negatively correlated with the saturation deficit of the air. Radial growth of the stem declines in tapped trees relative to untapped trees within two weeks of the start of tapping. Roots can extend in depth to more than 4 m and laterally more than 9 m from the trunk. The majority of roots are found within 0.3 m of the soil surface. Root elongation is depressed during leaf growth, while root branching is enhanced. Stomata are only found on the lower surface of the leaf, at densities from 280 to 700 mm^{-2}. The xylem vessels of rubber trees under drought stress are vulnerable to cavitation, particularly in the leaf petiole. By closing, the stomata play an essential role in limiting cavitation. Clones differ in their susceptibility to cavitation, which occurs at xylem water potentials in the range of -1.8 to -2.0 MPa. Clone RRII 105 is capable of maintaining higher leaf water potentials than other clones because of stomatal closure, supporting its reputation for drought tolerance. Clones differ in their photosynthetic rates. Light inhibition of photosynthesis can occur, particularly in young plants, when shade can be beneficial. Girth measurements have been used to identify drought-tolerant clones. Very little research on the water requirements of rubber has been reported, and it is difficult to judge the validity of the assumptions made in some of the methodologies described. The actual evapotranspiration rates reported are generally lower than might be expected for a tree crop growing in the tropics (<3 mm d^{-1}). Virtually no research on the yield responses to water has been reported and, with the crop now being grown in drier regions, this is surprising. In these areas, irrigation can reduce the immaturity period from more than 10 years to six years. The important role that rubber plays in the livelihoods of smallholders, and in the integrated farming systems practised in south-east Asia, is summarized.

INTRODUCTION

The commercial rubber tree (*Hevea brasiliensis* Müell. Arg.) is indigenous to the Amazon rain forest, within 5°N and 5°S latitude of the equator. Its properties were well known

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to the Indians of South and Central America long before the arrival of the Europeans in the 16th century. It is cultivated for its latex, which is used in the production of natural rubber[1], 60% of which is utilised in the manufacture of tyres. Latex is a cellular fluid consisting of a suspension of rubber hydrocarbon particles, represented by the formula $(C_5H_8)_n$, in an aqueous medium. The 19th century saw the vulcanisation of rubber (heating with sulphur allows rubber to retain its physical properties unchanged over the temperature range of 0–100 °C), the development of specialist machinery and techniques for manufacturing rubber goods, the rise of commercial trade in rubber and the first efforts to cultivate rubber when the demand for raw rubber began to exceed the supply from wild trees in Brazil (Varghese and Abraham, 2005). In 1876, seeds were gathered from the rain forest and taken to Kew Gardens in London. Subsequently, seedlings were sent from London to Sri Lanka and later onward to Singapore, where they formed the basis of the rubber producing industry that developed throughout the 20th century, particularly in south-east Asia (Purseglove, 1968).

In 2008, the total annual production of natural rubber was about 10.6 million t from 8.9 million ha. The principal producers are Thailand (3.0 million t from 1.8 million ha), Indonesia (2.8 million t from 2.9 million ha), Malaysia (1.2 million t from 1.25 million ha), India (0.82 million t from 0.45 million ha) and Vietnam (0.61 million t from 0.63 million ha). The largest producer in West Africa is the Côte d'Ivoire (0.18 million t), and in South America it is Brazil (0.11 million t). In 2008, south-east Asia produced 94% of the world's crop (FAOSTAT, 2010; IRSG, 2010).

Large estates initially dominated the rubber industry in Malaysia, but now smallholders prevail there (>500,000), as well as in Indonesia, Thailand and other Asian countries (Manivong, 2007). Large plantations have partly given up rubber because of its high labour requirements. In terms of world production, smallholders account for over 70% of the total area under rubber cultivation. The long immature phase can be a major constraint, particularly to smallholders, when costs accumulate without any returns (Gunasekara *et al.*, 2007b).

Although principally grown in the humid tropics (between latitudes 15°N and 10°S, with an annual total rainfall of 1500–4000 mm), rubber cultivation, in response to increasing demand, is being extended into drought prone areas. This is partly the result of land scarcity and competition from other crops (mainly oil palm) in traditional areas. New areas include the Central Highlands of Vietnam (12°N), north-central Vietnam, northern India (29°N), south-west China (22°N), the southern plateau of Brazil (23°S) and north-eastern Thailand (19°N), where there is a long dry season (Silpi *et al.*, 2006).

It is therefore timely to review the published research on the water relations and water productivity of rubber, and to try to do this in practically useful ways from an independent perspective. This review follows a similar format to that used in previous reviews in this series, notably on coffee (Carr, 2001), banana (Carr, 2009), tea (Carr 2010a, 2010b), sugar cane (Carr and Knox, 2011), coconut (Carr, 2011a), oil palm (Carr, 2011b) and cocoa (Carr and Lockwood, 2011). The paper begins by describing

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[1] c.f. 'synthetic rubber' derived from chemicals sourced from petroleum refining.

the influence of water on the development processes of the rubber tree (including its roots), followed by reviews of plant water relations, crop water requirements and water productivity. It ends by considering the important role that rubber plays in the livelihoods of farmers, and in the integrated farming systems practised in south-east Asia.

Priyadarshan (2003) has described key environmental constraints to rubber production in different regions of the world. These include low temperatures associated with high latitudes and altitude, extended dry seasons and wind damage. In addition, various aspects of the ecophysiology and productivity of rubber have been reviewed by Rodrigo (2007), who focused on genotype selection, planting density and intercropping.

CROP DEVELOPMENT

Hevea brasiliensis is an erect tree with a straight trunk. The latex is formed and stored in rings of latex vessels (laticifers). These occur between the inner cambium tissue and the outer hard bark layers. When the tree is five to seven years old the latex can be harvested (or ‘tapped’) at regular intervals by cutting a spiral groove in the bark and draining the latex into a collecting cup until it begins to coagulate and the flow ceases. In the wild, the tree can grow to a height of 40 m, but under cultivation it seldom exceeds 25 m, because ‘tapping’ restricts wood growth. Trees are usually replanted after 25–35 years when latex yields become uneconomic. At the end of their life rubber trees provide a valuable end product as a medium density tropical hardwood. In Malaysia timber characteristics are now among the selection criteria for clones.

Rubber trees are mainly grown as clones grafted on to seedling rootstocks, or as seedlings. The latter are derived from seeds produced by natural crossing between selected clones in isolated seed gardens. Clonal rootstocks as well as clonal scions are now being recommended, for example in Brazil (Cardinal *et al.*, 2007). The rootstock can have a positive effect on the scion, and the scion can also have a positive effect on the rootstock. The yield potential and adaptability of a selection of clones have been evaluated in north-east India, the highlands and coastal areas of Vietnam, southern China and the southern plateau of Brazil (Priyadarshan *et al.*, 2005). One clone (clone RRIM[2] 600) produced consistent moderate yields across all sub-optimal sites, while others were adapted to specific regions.

Increase in the stem height of rubber tree is discontinuous and is characterised by a period of elongation towards the end of which a cluster of leaves is formed. This is followed by a ‘rest period’ during which scale leaves develop around the terminal bud. By repetition of this sequence (four or five times annually), leaves are produced in tiers or whorls separated by lengths of bare stem. Although the elongation of stems is intermittent, stem girth increases continuously (Webster and Paardekooper, 1989). In Brazil, the base temperature for the initiation of a leaf flush has been estimated to be

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[2] RRIM represents the origin of a clone, namely the Rubber Research Institute of Malaya/Malaysia; similarly RRII corresponds to India, and RRIC/SL to Ceylon/Sri Lanka.

16 °C (for clones RRIM 600 and GTI) with 420 day °C (summed above a mean air temperature of 16 °C on a daily basis) needed to be accumulated between successive leaf flushes. The corresponding base temperature for stem extension is 19 °C (Filho *et al.*, 1993).

Canopy

Trees older than three to four years shed all their leaves annually, a process known as 'wintering'. This renders the tree leafless for a short while (up to four weeks) before new leaves emerge from the terminal bud. 'Wintering' is believed to be induced by dry, or less wet, weather. In regions having a marked dry season, the period of defoliation is short and re-foliation occurs before the commencement of the rainy season, and triggered by an increase in day length, following the equinox (Guardiola-Claramonte *et al.*, 2008). By contrast if the dry season is less pronounced, leaf fall occurs gradually, new leaves develop slowly and, although the trees are never completely leafless, latex yields are reduced more than in situations where complete defoliation occurs. Leaf disease can be a problem if the old and new leaves are present simultaneously (Rao, 1971). Clones differ considerably in their 'wintering' behaviour.

The optimum plant density for rubber is in the range 500–700 trees per hectare, based on comparisons mainly done under wet conditions (Rodrigo, 2007). Competition for light between trees begins in about the fourth year after planting, which leaves opportunities for short-term intercropping in the early years. For convenience in crop management, rubber trees are usually grown in alleys or clusters. A leaf area index of five or six is reached within five or six years from planting with a recorded peak of 14 in 10 years. Trees grown from seed reach the end of the juvenile phase of growth when branches begin to form on the main stem. The scion (provided it is taken from mature wood) on budded rootstocks does not pass through a juvenile phase (Webster and Paardekooper, 1989).

The architecture of the rubber tree can be considerably modified by irrigation. For example, in the Konkan region of western India (20°04′N 72°04′E; alt. 48 m), where there is an extended dry season, eight years of irrigation increased all aspects of growth by 20–30% compared with rain-fed trees (*cv.* clone RRIM 600; 10-year old), namely, girth and height, width and depth of the canopy and number and diameter of primary branches. In addition, the angle of the branches to the main stem was greater in the irrigated trees (58°) than in the rain-fed ones (44°). The amount of water applied was not specified (Devakumar *et al.*, 1999).

Roots

The results of studies of root systems of rubber trees grown as seedlings or as clones grafted on to seedling rootstocks in Malaysia were summarised by Webster and Paardekooper (1989). Within three years of planting, taproots had reached depths of 1.5 m, and by seven or eight years, they reached depths of 2.4 m. In the same time intervals, roots had spread laterally 6–9 m from the trunk and more than 9 m, respectively, well beyond the spread of the branches. The majority of these laterals were within 0.3 m of the soil surface. Feeder roots (*ca.* 1-mm diameter) with hairs grew from the lateral roots. In a detailed study done in Malaysia, Soong (1976) found that feeder root development varied considerably between different scion clones (e.g. clone RRIM 605 had 80% more roots by dry mass than clone RRIM 513 in the 0–0.45-m soil depth), while soil texture also had a marked effect (sandy soils contained two and a half times more roots than clayey soils). Feeder root growth in the surface layers also varied seasonally, being at its maximum when the trees were re-foliating after leaf shedding in the winter (February/March), and at a minimum prior to leaf fall (August–December). At greater depths, root growth was at its peak three months later than in the upper soil layers. Root density declined with soil depth such that the dry mass of roots in the 0.30–0.45-m layer represented only 10% of the total in the top 0.45 m.

The growth pattern of the root system of young seedling rubber trees was described by Thaler and Pagès (1996) in relation to shoot development. Based on detailed measurements of roots in root observation boxes over a three-month period, they found that whereas shoot growth was typically rhythmic, root development was periodic. Thus, root elongation was depressed during leaf growth, while branching was enhanced. During leaf expansion, the taproot continued to grow but at a reduced rate, and the emergence and elongation rate of secondary roots also declined. Tertiary root elongation ceased all together at this time. Root types were considered to differ in their capacity to compete for assimilates, while root branching was promoted by leaf development. This study followed detailed observations of the architecture of the root system of rubber plants (Pagès *et al.*, 1995). The positions where root axes develop and their morphogenic characteristics were described under different conditions as a prelude to the construction of a mathematical model (Thaler and Pagès, 1998). This model successfully simulated periodicity in root development as related to shoot growth, and reproduced differences in sensitivity to assimilate availability in relation to root type. The apical diameter of a root was considered to be a good indicator of root growth potential (i.e. the larger the diameter the greater the potential for growth).

In south-east Brazil, Mendes *et al.* (1992) traced roots of five-year old trees to depths in excess of 2.5 m and laterally up to 3.4 m from the trunk (trees spaced 7 × 3 m). By far the most roots (50%) were within 0–0.30 m from the soil surface.

In Kerala, George *et al.* (2009) used the ^{32}P soil injection technique to determine active root distribution of mature (18-year-old) rubber trees (clone RRII 105). They based their observations on a radio assay of the latex serum after 45 days. Of the four depths of application compared, 55% of ^{32}P uptake was from a depth of 0.10 m, 25% from 0.30-m, 13% from 0.60-m and 6% from 0.90-m depth. These values were assumed to represent similar differences in relative root activity. Uptake was comparatively uniform with distance from the trunk (up to 2.5 m).

After eight years of differential irrigation in the Konkan region of western India, where there is an extended dry season, the total root biomass was similar in both irrigated and rain-fed treatments within the volume of soil sampled (to a depth of 0.45 m and up to 1.5 m from the trunk). The rain-fed trees had a greater concentration of roots in the top 0–0.15-m layer than the irrigated trees. Most roots were also within 0.5 m from the trunk (Devakumar *et al.*, 1999).

In north-east Thailand, Gonkhamdee *et al.* (2009) traced fine roots of rubber trees (*cv.* clone RRIM 600) in a sandy loam soil to 4.5-m depths. Using a permanent root observation access-well, active root growth was monitored at the onset of the dry season in November at depths of 1.0 to 4.0 m. This was followed by a period of 'rest' before roots resumed growth at 3.0–4.0-m depth at the time the leaves were flushing in March. With the onset of the rainy season in May, active root growth occurred in the top soil above 1.0 m. The greatest root length density was in the top 0.5 m. Fine roots growing at all depths had a life expectancy measured in months rather than weeks, while the decay rate of dead roots was slow, particularly at depth (also cited by Isarangkool Na Ayutthaya *et al.*, 2011b).

Yield

The annual yield of rubber per tree (dry mass, Y) is the product of the yield of rubber per tree per tapping (y) and the number of tappings per year (N):

$$Y = y \times N,$$

where y is the product of the volume of latex per tapping (L) and its dry rubber content (r %), i.e.

$$y = L \times r,$$

where L is a function (f) of the initial flow rate (F), the length of the cut (C) and the plugging index (P), which is an indirect measure of the duration of latex flow:

$$L = f\,(F \times C \times P).$$

The supply of latex is dependent on the pressure potential (turgor pressure) within the latex vessels, and this varies with the time of day and the rate of transpiration. Tapping is best started very early in the morning (subject to interference by rain) when the pressure potential is high. Then the flow of latex declines as transpiration increases and the pressure potential falls. On a diurnal basis, there is a close negative relationship between the rate of latex flow and the saturation deficit of air (Paardekooper, 1989; Paardekooper and Sookmaark, 1969). By contrast, the dry rubber content of the latex follows a reverse trend, being higher at mid-day than at night. The plugging index is not affected.

In Sri Lanka (6°32′N 80°09′E), Gunasekara *et al.* (2007b) highlighted the complexity of the interactions between the commencement of tapping, the frequency of tapping and genotype on dry rubber yield and its components. For example, commencing tapping early, at a stem girth of 400 mm (1.20 m above the bud union) instead of the normal 500 mm, increased yields (over three and a half years total; density 500 trees per hectare) of one clone (RRIC 121, from 6.90 to 10.44 kg per tree, averaged across all other treatments), had no effect on the second one (RRISL 211) and reduced yields on the third clone (RRIC 102, from 8.16 to 6.39 kg per tree). Clones also differed in their responses in terms of tapping treatment effects on tree girth increment. The yield benefits reported for clone RRIC 121 resulted from increases in the dry rubber content that exceeded the reductions in latex volume.

In order to determine seasonal changes in both latex and wood production, displacement sensors (dendrometers) were successfully used by Silpi *et al.* (2006) to monitor the effects of water shortage on radial growth of rubber trees (clone RRIM 600) in an area of Thailand with a marked dry season (13.4°N 101.4°E). In untapped trees, radial growth began with the onset of the rains and ceased completely during the dry season. When re-foliation began in the middle of the dry season, there was a net shrinkage of the trunk. In tapped trees, radial growth slowed considerably within two weeks of the start of tapping so that by the end of the season cumulative growth was about half that of untapped trees. In the second year, the yield of latex increased but wood production was reduced.

In a paper comparing the productivity of several tropical perennial crops, Corley (1983) considered the annual dry matter production of rubber (above ground) for a well-managed crop to be 26 t ha^{-1} with a rubber yield of 2 t ha^{-1} (harvest index = 0.08). The corresponding best yields recorded were 36 t ha^{-1} and 5 t ha^{-1}, respectively (harvest index = 0.14), whereas the highest harvest index reported was 0.37 for dry latex or 0.34 for rubber (rubber represents 90% of the dry matter in latex). The potential yield was estimated to be 46 t ha^{-1} (total dry matter) and 15 t ha^{-1} (rubber). When assessing the potential productivity, Corley (1983) assumed that (1) leaves remain on the tree for nearly 12 months, and are shed; (2) trees may remain leafless for as long as one month and (3) newly emerged leaves may not be active photosynthetically for at least one week after emergence (Samsuddin and Impens, 1979a, 1979b).

Quoting Templeton (1969), Corley (1983) noted that clones with the highest harvest indices were all susceptible to wind damage (trunk breakage) because insufficient proportions of assimilates were allocated to trunk growth. A realistic target yield for breeders was considered to be 15 t rubber per hectare (from clones selected with short fat trunks). As the lactifers delivering the latex become blocked in response to being severed, the yield from a rubber tree is considered to be 'sink' limited rather than 'source' limited (an inadequate supply of assimilate) (Squire, 1990).

Summary: crop development

1. The rubber tree has a single straight trunk, the growth of which is restricted by 'tapping' for latex.
2. Increases in stem height are discontinuous, a period of elongation being followed by a 'rest' period during which emergence of leaves takes place.
3. Leaves are produced in tiers separated by lengths of bare stem.
4. Trees older than three or four years shed all their leaves annually (a process known as 'wintering').

5. ‘Wintering’ is induced by dry or less wet weather; trees may remain (nearly) leafless for up to four weeks. The more pronounced the dry season the shorter the period of defoliation.
6. Re-foliation begins before the rainy season starts, perhaps triggered by an increase in day length.
7. Roots can extend in depth to more than 4 m and laterally more than 9 m from the trunk.
8. The majority of roots are found within 0.3 m of the soil surface.
9. Root elongation is depressed during leaf growth, while root branching is enhanced.
10. The supply of latex is dependent on the pressure potential in the latex vessels: the rate of flow is negatively correlated with the saturation deficit of the air.
11. In tapped trees, radial growth of the stem declines relative to untapped trees within two weeks of the start of tapping.

PLANT WATER RELATIONS

Stomata

Stomata are only present on the lower epidermis of leaves at densities ranging, in a sample of 12 clones, from 278 mm^{-2} (clone RRIM 605) to 369 mm^{-2} (clone IRCI 10) (Gomez and Hamzah, 1980). Expressed in another way, these densities are equivalent to 2.2 million and 3.5 million stomata per leaflet, respectively. Senanayake and Samaranayake (1970) also reported large (+70%) differences between clones (25) in the density of the stomata, but unfortunately recorded their data on a per unit leaf area (unspecified) basis. In neither piece of research were any obvious links found between yield, or other attributes of growth, of an individual clone (or group of clones) and stomatal density.

In a detailed comparison of the leaf anatomy of two clones on the same rootstock, Martins and Zieri (2003) recorded 296 mm^{-2}stomata (clone RRIM 600) and 364 mm^{-2} (clone GT1). For the same two clones, Samsuddin (1980) reported densities of 465 mm^{-2} and 372 mm^{-2}, respectively. Stomatal size and frequency, as well as the structure and distribution of leaf waxes, of three seedling *Hevea* families were described by Gomes and Kozlowski (1988). In their greenhouse study in Wisconsin, United States, the average density of stomata was about 700 mm^{-2}. Both leaf surfaces were covered with heavy deposits of amorphous wax, except near the stomatal pores. In Côte d’Ivoire, Monteny and Barigah (1985) recorded stomatal densities of three clones (clones RRIM 600, GT1 and Pb 235) in the range 389–568 mm^{-2} (units assumed). There is a clear variability in density with a range from 280 mm^{-2} to 700 mm^{-2} depending on such factors as leaf age, size and exposure to the sun.

Leaf water status

In Kerala, South India (9°22′N 76°50′E), Gururaja Rao *et al.* (1990) compared the responses of two 10-year-old clones to water stress in terms of (amongst others) leaf water status, stomatal conductance and yield. Clone RRII 105 maintained higher mid-afternoon (and also pre-dawn) leaf water potentials (measured with a psychrometer) during the dry season (*ca* −1.3 Mpa) than clone RRII 118 (−2.4 Mpa) as a result of reduction in stomatal conductance, confirming its relative drought tolerance (the ability to conserve water) compared with clone RRII 118. Clone RRII 105 was also able to maintain a faster latex flow in the dry weather than clone RRII 118 as a result of a higher pressure potential in the latex vessels, while the osmotic potentials were less.

Xylem cavitation

In a container-based study in Thailand, Sangsing *et al.* (2004a) found that the xylem vessels in immature rubber trees under drought stress were relatively vulnerable to cavitation (particularly in the leaf petiole), clones differed in their degree of vulnerability and stomata, by closing, played an essential role in the control of cavitation. On the basis of these observations (based on two clones only), the authors predicted that cavitation-resistant clones would exhibit less xylem dysfunction after a drought than susceptible clones, and that this could be an important attribute for drought survival in dry areas of northern Thailand. In a related paper, Sangsing *et al.* (2004b), on the basis of a comparison of the same two clones (clones RRIM 600 and RRIT 251), postulated that variations in xylem hydraulic efficiency between clones may explain differences in stomatal conductance and xylem water potential and, hypothetically, growth performance. In a similar study done in China, Chen *et al.* (2010) also found that stomatal closure reduced the risk of cavitation induced by water stress, and that the leaf petiole acts as a safety valve to protect the hydraulic pathway in the stem. Previously, Ranasinghe and Milburn (1995) had shown in a glasshouse-based study in Australia how cavitation occurred in *Hevea* clones when the relative leaf water content fell to 85% (corresponding to a xylem water potential of −1.8 to −2.0 MPa). This resulted in a reduction in the hydraulic conductivity of the petiole to about 40% of the original value, since gas bubbles blocked the flow of water inside many of the conduits. When specimens were rehydrated, the conductivity again increased. They concluded that xylem transport in *Hevea* is disrupted relatively easily under water stress.

Gas exchange

Samsuddin and Impens (1978), on the basis of single-leaf net photosynthesis light intensity response curves, first showed that it was possible to differentiate between rubber genotypes in photosynthetic rates.

In Côte d'Ivoire, Monteny and Barigah (1985) monitored the changes in rates of photosynthesis over the lifespan of individual leaves of three clones. Clone GT1 maintained a steady rate for longer (up to 180 days) than the others (clones RRIM 600 and PB225). When water stress was imposed on the container-grown plants, photosynthesis rates dropped sharply and did not return to their original values after re-watering.

In Kerala, *Hevea* clones were shown to differ in single leaf net photosynthetic rates, particularly at low light intensities. Of the 12 immature container-grown clones compared, two in particular stood out (clones RRII 203 and RRIC 100) as having higher instantaneous water use efficiencies than the others, and as being less dependent on stomatal conductance than on the capacity of the mesophyl to regulate photosynthesis (Nataraja and Jacob, 1999).

Rodrigo (2007) has summarised the attempts made by Nugawela *et al.* (1995) to develop a method for screening genotypes at an early stage in the selection process on the basis of photosynthetic parameters. A complication in this approach is that the canopy architecture of juvenile plants is very different from that of a mature rubber tree because of high level of light attenuation within the mature tree. This makes it difficult to predict the yield potential of mature trees. Similar problems arise in attempts to select trees for water-use efficiency on the basis of instantaneous measurements of photosynthesis and transpiration.

During the early stages of growth the leaves of young rubber plants are often fully exposed to incident light at levels above the light saturation for photosynthesis (>1000 μmolPAR m^{-2} s^{-1}; PAR levels can reach 2000–2500 μmol m^{-2} s^{-1} in the tropics). This results in light-induced inhibition of photosynthesis and, taken together with shade adaptation by the exposed leaves, explains why early growth of rubber is enhanced by shade/intercropping (Rodrigo, 2007; Senevirathna *et al.*, 2003).

In a comparison of two mature eight-year-old clones in Sri Lanka, canopy photosynthesis of one (RRISL 211) was 20% greater than the other (RRIC 121). This was primarily due to greater light saturated photosynthetic rates and a larger leaf area index in the top layer of the canopy of clone RRISL 211 (18–22 m above ground level). Tapping increased canopy photosynthesis in one clone (RRISL 211), but this was not reflected in the yields of dry rubber obtained, as these were similar for both clones. Clone RRISL 211 partitioned more of its assimilates to the *volume of latex* produced, whereas clone RRIC 121 partitioned more to the *rubber content*. There was a gradual increase in stomatal conductance (and transpiration) with increasing light intensity (0 to 1200 μmolPAR m^{-2} s^{-1}), particularly with clone RRISL 211 when tapped (Gunasekara *et al.*, 2007a).

Drought tolerance

In the Konkan region of western India (20°04′N 72°04′E; alt. 48 m) where there is an extended dry season, Chandrashekar *et al.* (1998) monitored the monthly, seasonal and annual changes in girth of 15 immature clones over a six-year period. They identified five clones that they considered to be more drought-tolerant than the remainder, namely RRII 208 (an Indian hybrid), RRIC 52 (a primary clone from Sri Lanka), RRII 6 (a primary clone from India), RRIC 100 and RRIC 102 (both hybrids from Sri Lanka). Clone PR 261 (a hybrid from Indonesia) was particularly drought-susceptible. In this location, only clone RRII 208 was considered to have reached maturity (defined as 50–70% of the trees having reached a girth of 500 mm at a height of 1.25 m) within nine years from planting. A primary clone is the one chosen from a polycross population, while a hybrid clone is chosen from a single cross of known parentage.

Summary: plant water relations

1. Stomata are only found on the lower surface of the leaf, at densities from 280 mm^{-2} to 700 mm^{-2}.
2. The xylem vessels of rubber trees under drought stress are vulnerable to cavitation, particularly in the leaf petiole.
3. By closing, the stomata play an essential role in limiting cavitation.
4. Clones differ in their susceptibility to cavitation.
5. Cavitation occurs in the xylem of the leaf petiole at water potentials in the range -1.8 to -2.0 MPa.
6. As a result of stomatal closure, Clone RRII 105 has the capacity to maintain higher leaf water potentials than other clones, supporting its reputation for drought tolerance (through water conservation).
7. Clones differ in their photosynthetic rates. Light inhibition of photosynthesis can occur particularly in young plants, which can therefore benefit from shade.
8. Girth measurements can be used to identify drought-tolerant clones.

CROP WATER REQUIREMENTS

In a catchment level study, Guardiola-Claramonte *et al.* (2010) proposed a modified method for estimating actual water use by rubber trees during the dry season when there is leaf shedding followed by a leaf flush. Measurements were made at two sites in south-east Asia (northern Thailand, 19°03′N 98°39′E, and China, 22°N 101′E), where there is concern about the impact that any expansion of rubber planting will have on the water balance of the catchments. In order to allow for the changes in the phenology of the rubber tree during dry season, the energy-based Penman–Monteith estimate of reference crop evapotranspiration (ETo; Allen *et al.*, 1998) was combined with a new empirical crop coefficient (K_{rubber}). These changes in phenology were believed to be influenced by three variables, namely the saturation deficit of the air, temperature and photoperiod. After incorporating this revised estimate of crop evapotranspiration for rubber ($\text{ETc} = K_{\text{rubber}} \times \text{ETo}$) into a hydrological model, the belief that water use during the dry season, after rubber trees were planted, was greater than that from indigenous vegetation was upheld. This was believed to be a result of (day length induced) re-foliation by rubber trees, ahead of the onset of the rains, in contrast to tea, secondary forest and grassland (Guardiola-Claramonte *et al.*, 2008). The predicted mean annual ETc for the northern Thailand site was 1050 mm, about 20% more than the estimate based on crop cover (leaf area index, L). Replacing natural vegetation with rubber trees in these catchments would, by increasing ETc, deplete water storage in the subsoil and reduce discharge from the basin. It is difficult to reconcile the validity of the assumptions made in this analysis, which are open to debate.

Similarly, it is also difficult to judge the validity of the assumptions made by Rodrigo *et al.* (2005) in their estimates of water-use of immature rubber, using the Penman–Monteith equation, grown as a sole crop or intercropped with banana in Sri Lanka. Estimates of transpiration by the sole rubber crop (with a cover crop) were exceptionally low (5 mm per week) even at 122 weeks after planting, when the leaf area index had reached 0.41.

In north-east Thailand (15°16′N 103°05′E), Isarangkool Na Ayutthaya *et al.* (2009) monitored transpiration rate (T) of mature rubber trees (*cv.* clone RRIM 600; the average trunk girth at 1.5 m above soil = 550 mm; maximum leaf area index = 3.9) during the dry season using a modified and successfully calibrated sap flow technique (Do and Rocheteau, 2002). They compared these estimates with others on the basis of changes in soil water content. The sap flow measurements indicated that transpiration declined from about 1.6 mm to 0.4 mm d^{-1} as the dry season progressed. The corresponding estimates based on soil water depletion were of similar orders of magnitude but numerically different at 2.5 mm and 0.1 mm d^{-1}, respectively. The errors associated with each technique were discussed (e.g. calibration, soil evaporation, depth of rooting and water extraction).

As part of the same research, Isarangkool Na Ayutthaya *et al.* (2011a) monitored the effects of intermittent dry periods (up to 20 days) during the rainy season on transpiration rates. When the reference crop evapotranspiration rate (Penman-Monteith) was less than about 2.2 mm d^{-1}, the transpiration rate matched ETo. But when this ETo value was exceeded (maximum 4.2 mm d^{-1}), the transpiration rate fell below ETo even in wet soil (less than 50% depletion of the available soil water, corresponding to a pre-dawn leaf water potential, $\Psi_{\text{predawn}} = -0.45$ MPa). At 70% depletion, the transpiration rate was reduced by 40% and at 90% depletion it was reduced by 80%. Since, regardless of the soil water status, the daytime minimum leaf water potentials on sunny days were relatively stable at *ca* −1.95 MPa ($=\Psi_{\text{critical}}$), the decline in transpiration rates could be explained, using a simple model, on the basis of the hydraulic limitation hypothesis, by reduction in the hydraulic conductance of the whole tree (K_{tree}) and this critical minimum leaf water potential:

$$T = (\Psi_{\text{predawn}} - \Psi_{\text{criitical}}) \times K_{\text{tree}} \times a,$$

where ‘a’ is a coefficient to transform mid-day sap flow densities to total transpiration per day per unit soil area.

This model was tested further during the ‘wintering period’, from the end of the rains through the dry season, when the green leaf area was changing rapidly (defoliation followed by leaf flushing). The validity of this approach to understand how the rubber tree responds to drought (atmospheric or soil-induced) was confirmed (Isarangkool Na Ayutthaya 2010). This whole-tree, hydraulic response approach to estimate transpiration hides the complex short-term (e.g. stomatal closure, xylem cavitation) and long-term (e.g. defoliation, root growth at depth) adjustments that plants make in response to drought.

In south-east Brazil, Mendes *et al.* (1992) found that rainfall interception of five-year-old trees did not exceed 5% of the total rainfall.

Summary: crop water requirements

1. Very little research on the water requirements of rubber has been reported.

2. It is difficult to judge the validity of the assumptions made in some of the reported methodologies.
3. The maximum actual evapotranspiration rates reported are generally lower than might be expected for a tree crop growing in the tropics (<3 mm d^{-1}).

WATER PRODUCTIVITY

Attempts are being made to extend the cultivation of rubber into the North Konkan region (20°N) on the west coast of India. Although the average annual rainfall is 2175 mm, this is concentrated into the June–September period, and there is a long dry season. Potential evapotranspiration over the year is 2250 mm. It was at this location that Vijayakumar *et al.* (1998) attempted to quantify the responses to irrigation of immature clone RRII 105. In a complicated experiment, three levels of basin irrigation (0.5, 0.75 and 1.0 ETc) were compared with three levels of drip irrigation (0.25, 0.5 and 0.75 ETc) and a rain-only control treatment over a three/four-year period (the exact duration of the experiment is not made clear). The Penman equation (modified) was used to estimate potential evapotranspiration, together with a crop coefficient (Kc) for rubber of 1.25 (it is not clear why this value was chosen) to give ETc. Allowance was made for increase in crop cover as the trees matured. (How exactly the quantity of water to apply to each treatment was determined has not been explained clearly.) Tree growth (biomass production) was estimated from measurements of tree girth at a height of 1.5 m above the bud union. With basin irrigation, growth rates were similar at all three water application levels, whereas with drip irrigation both 0.5 ETc and 0.75 ETc treatments outperformed 0.25 ETc. Total biomass production from the best-irrigated treatments was 2.8 times higher than from the rain-only control. Overall, on this oxisol soil, basin irrigation was more effective than drip irrigation. Supporting physiological measurements indicated that osmotic adjustment occurred in the laticifers of trees in drier treatments. The authors concluded that with irrigation the immaturity period in this region could be reduced from more than 10 years to six years. They also stated that the total water requirement in the dry season, once canopy cover was complete, was around 1340 mm (or 33,500 L per tree at 400 trees per hectare) but applying only half of this total could be just as effective. Perhaps this interesting finding was a result of using a high value for the crop coefficient (1.25). Irrigation increased the leaf area index and light interception by the canopy (Devakumar *et al.*, 1998). A similar, but less conclusive, study in the same region of India had been previously reported by Krishna *et al.* (1991).

Prior to this experiment, Jessy *et al.* (1994) reported the results of a similar experiment conducted in central Kerala (9°32′N 76°86′E), where there is a similarly extended dry season from December to April. Basin and drip irrigation (fabricated with locally available materials) were compared at two water application rates (30 and 50% replacement of water lost by evapotranspiration) over a five-year period from the year after planting (with clone RRII 105) in 1986 till 1992. Evapotranspiration was estimated using a modified version of the Penman equation (not specified), in which the crop factor was assumed to have a value of 1.0 with an allowance made each year for changes in the crop cover. The soil was a well-drained laterite with a water holding capacity of 77 mm m^{-1}. Drip irrigation was applied daily during the summer, while basin irrigation was applied once a week for the first three years and afterwards every four days. In the fifth year, the application rates were equivalent to 1.5 mm and 2.1 mm d^{-1} for the two deficit irrigation treatments. For comparison, the ETo estimate averaged over the dry season was 5.0 mm d^{-1}. After five years the girth measurements (at a height of 1.5 m above the bud union) were similar in the drip and basin treatments at both watering levels (drip 364 mm; basin 347 mm) and both were significantly greater than the control, unirrigated treatment (300 mm). The implications of these results were not discussed, other than to recommend drip irrigation because of its greater conveyance and application efficiencies. Treatment effects on root distribution to the depth of 0.60 m after four years were described at 0.10, 0.50 and 1.5 m from the trunk in two directions.

Summary: water productivity

1. Virtually no research on the yield responses of rubber to water has been reported.
2. With the crop now being planted in drier regions, this lack of evidence base is surprising.
3. In these drier areas, irrigation can reduce the immaturity period from more than 10 years to six years.
4. Other methods of drought mitigation need to be researched, particularly the selection of drought-resistant composite clones (scions and rootstocks).

CONCLUSIONS

The structure of the industry plays a role in determining research priorities. Viswanathan (2008) reported an interesting detailed analysis of smallholder rubber farming systems in north-east India and southern Thailand. Smallholders dominate rubber production in south-east Asia, with 90% of production reported in Thailand, 89% in India and Malaysia and 83% reported in Indonesia. These four countries together represent 77% by area and 79% by production of the world's rubber industry. Assuming these figures are correct, smallholders in these countries produce about 70% of the world's natural rubber. The average size of a holding (area of rubber) is about 1 ha in north-east India and 2 ha in southern Thailand, and the corresponding yields of rubber are in the range 950 to 1240 kg ha^{-1} (compared with the best commercial yields of 5000 kg ha^{-1}). The number of trees available for tapping is similar across these two regions, averaging about 380 ha^{-1}. The rubber farming systems vary within the south-east Asia region with a predominance of monoculture in Malaysia and southern India, co-existence of rubber and agroforestry in Indonesia and integrated farm livelihood systems (consisting of rice, other crops and livestock with rubber) in Thailand and north-east India. Smallholder rubber monoculture is viable as long as the price is right, though in the integrated systems rubber provides the dominant input to the household income. In so doing it contributes resilience during financial and other crises (i.e. it contributes to sustainable livelihoods). Other issues that affect the viability of smallholder rubber production include land tenure, shared cropping and the marketing of rubber.

An interesting and useful framework for analysing and explaining structural changes in the production of plantation tree crops is the one proposed by Barlow (1997). Using rubber as the case study, he identified five stages of development, beginning with time a plantation crop is first introduced into a subsistence economy (e.g. Malaysia in 1870) and ending with its demise when, as the economy develops a manufacturing base, it is no longer profitable to grow a plantation tree crop in the traditional way except in remote settings, although existing trees may still be exploited (e.g. Malaysia since 1985). Rubber producing countries are at different stages on this continuum with Malaysia and Thailand probably being the most ‘advanced’ nations.

This therefore is the context within which research on the water relations of rubber has to be considered. Income from rubber is central to the livelihoods of several million people. Compared with most of the plantation crops reviewed in this series, very little research has been reported in the literature on the water relations and irrigation requirements of rubber. When the crop was confined to the humid tropics, this may not have been surprising, but with its expansion into regions with extended dry seasons one might have expected more emphasis to be placed on this aspect of agronomy of the crop, especially the selection of drought-tolerant clones. It is not known, for example, what the yield losses are due to drought in different areas where rubber is grown (or conversely the likely benefits from irrigation). This information is essential for rational planning purposes.

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