THE ROLE OF WATER IN THE GROWTH OF THE TEA (*CAMELLIA SINENSIS*) CROP: A SYNTHESIS OF RESEARCH IN EASTERN AFRICA. 1. WATER RELATIONS

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SUMMARY

With a focus on eastern Africa, the results of research on the ecophysiology and water relations of tea are reviewed. In particular, work undertaken at the Ngwazi Tea Research Station (formerly Unit) in southern Tanzania is synthesized and interpreted in relation to work reported from elsewhere in Africa (and beyond where appropriate). Topics covered include factors influencing: the components of yield, yield distribution, root growth, stomatal behaviour, photosynthesis, transpiration, xylem water potential and how cultivars vary in their responses to water stress. A companion paper (Carr, 2010) reviews the results of research on the irrigation of tea, water productivity, and its practical significance to the tea industry and the wider scientific community.

INTRODUCTION

In the equatorial areas of eastern Africa where tea is grown, Kenya, Uganda, northern Tanzania, Rwanda and Burundi, rainfall distribution is bimodal with two dry or less wet seasons (Stephens *et al.*, 1992). Although some tea in these areas may be irrigated, drought mitigation is usually more appropriate and cost effective. Away from the equator, in southern Tanzania, Malawi and countries to the south, there is a single dry season that can last from four to six months. In these areas, tea is often irrigated during the dry season (Carr and Stephens, 1992). The rainfall amount and distribution in many tea locations in Africa is often considerably modified by local physical features such as altitude (tea is found from 600 to 2700 m asl), proximity to a large body of open water (e.g. Lake Victoria) or to mountains (e.g. the Rwenzoris in western Uganda, or Mulanje mountain in southern Malawi). Research priorities at the principal tea research organizations, which are located in Kenya, Tanzania and Malawi, are influenced by these regional differences in rainfall, availability of water for irrigation, expected yield increases and likely financial benefits.

The contribution of research, over the past 40 years, into the water relations and irrigation requirements of tea in eastern Africa to commercial crop management, and to our understanding of the physiology of the crop, is summarized and reviewed in

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this and a companion paper (Carr, 2010). The Tea Research Foundation of Kenya (TRFK; 0°22′S alt. 2200 m), the Tea Research Institute of Tanzania (TRIT, 8°32′S; alt. 1840 m) and the Tea Research Foundation of Central Africa (TRFCA, 16°05′S; alt. 630 m), based in Malawi, have all undertaken fundamental research on these topics. Prior to 1978, the Tea Research Institute of East Africa (TRIEA) served three countries – Kenya, Tanzania and Uganda. Some of the major private tea companies also undertake their own research.

As background to the main theme of this paper (and the companion paper), the origins of tea and centres of production in Africa are first summarized together with genetic variability in existing populations of tea. These are followed by descriptions of the important crop development processes (including roots), which are influenced by (or influence) water availability, plant water relations and gas exchange processes. In the companion paper, crop water use, examples of yield responses to irrigation and drought, dry matter production and partitioning, irrigation systems, modelling and, finally, the practical implications of this research to the tea industries represented are considered. The principal aim of both papers is to review the results of research undertaken at the Ngwazi Tea Research Unit/Station (now the headquarters of TRIT) since 1967, but in the context of other research undertaken in eastern Africa. This paper extends a previous evaluation of the developmental and scientific impacts of research on tea carried out intermittently over a 30-year period in Tanzania (Carr, 1999). Other reviews of aspects of the ecophysiology of tea include those by Carr (1972), Fordham (1977), Squire and Callander (1981), Carr and Stephens (1992), Tanton (1992) and, most recently, De Costa *et al.* (2007).

ORIGINS AND CENTRES OF PRODUCTION

Tea is believed to have originated within the fan-shaped area extending from the Assam/Burma border in the west to China in the east (*ca.* 26°N), and south from this line through Burma and Thailand to Vietnam (*ca.* 14°N) (Kingdon-Ward, 1950; Mair and Hoh, 2009). This is an area of monsoon climates with a warm, wet summer and a cool, dry (or less wet) winter. From the main centres of cultivation in Southeast Asia, tea has been introduced into many other areas of the world and is now grown in conditions that range from Mediterranean-type climates to the hot, humid tropics, from Georgia in the north (42°N) to Argentina (27°S) and New Zealand (37°S) in the south, and from sea level to 2700 m altitude (Carr, 1972).

Commercial tea production in Africa started in the late nineteenth century when missionaries planted seedlings in Malawi. Afterwards (1920s/1930s) tea industries began to be established in Kenya (planted area by 2007 = 150 000 ha, annual production of processed tea = 315 000 t), Uganda (20 000 ha, 35 000 t) and Tanzania (19 000 ha, 31 000 t). These three countries, together with Malawi (18 500 ha, 39 000 t), are still the leading producers in Africa followed by Rwanda (15 300 ha, 19 000 t), Burundi (9000 ha, 7700 t), Zimbabwe (6100 ha, 22 300 t) and Mozambique (5700 ha, 10 500 t). Smaller industries exist in D.R. Congo, Ethiopia, South Africa and Zambia and, in West Africa, in Cameroon and Nigeria. In 2007, Africa produced just under

500 000 t of processed tea, which is equivalent to about 13% of the total world production (FAOSTAT, 2008).

It is generally believed that existing populations of tea plants are largely derived from two original taxa, which are given varietal status within the species *Camellia sinensis* by Sealy (1958) but specific status by Wight (1962). Wight refers to these species as *C. sinensis* (the China plant, which is a shrub, with small leaves, thought originally to have grown in the open) and *C. assamica* (the Assam plant, which is a small tree, with large leaves, thought to have grown originally in forest). The two species can be distinguished by leaf form and floral characters (Banerjee, 1992; Wight, 1959). Tea is a highly heterogeneous outbreeder, which results in a cline extending from extreme 'China type' plants to those of distinct 'Assam' origin (Wight, 1959). Generally all teas are classified under the name *C. sinensis* (L.) O. Kuntze irrespective of taxonomic variation (Paul *et al.*, 1997).

In Africa, tea plantations were originally established with heterogeneous seedlings derived from seeds imported from India (although in Malawi some seeds were of Chinese origin). From the 1960s onwards, most new plantings were with vegetatively propagated clones selected for superior yield and/or tea making qualities (Ellis and Nyirenda, 1995). Recently, AFLP (amplified fragment length polymorphism) markers have been successfully employed to detect diversity and genetic differentiation among Indian and Kenyan populations of tea. Principal coordinate analysis showed that the Assam genotypes/clones selected in Kenya were indeed of Indian origin (Paul *et al.*, 1997).

In Malawi, the most common clones (referred to locally as 'superior cultivars') are SFS150, SFS204 (both field selections, released in the 1970s), PC81, PC105, PC108 and PC110 (selections from crosses in a breeding programme, mostly released in 1981), followed by smaller areas of a large number of more recent releases, including PC122 and PC123 (released in 1994). These clones (and related composites/grafted plants) have all been selected for good field performance and high quality for planting in southern Africa (from 11°S to 32°S) (Ellis and Nyirenda, 1995). Their properties (including observations on drought tolerance) have been described in a catalogue (TRFCA, 2000).

In eastern Africa, the most popular clones include: S15/10, 6/8, 6/10, 31/8, BBK35, TN14/3, BBT207 (all long-established field selections), SC12/28 and the 303 series (selected from crosses, and released in 1987 and 1994 respectively). These clones were selected and evaluated by commercial companies and/or research institutes, usually at single sites. In Kericho, Kenya, four of these clones with contrasting characteristics (S15/10, 6/8, BBK35, TN14/3) were compared at a range of altitudes (1800–2200 m) and significant genotype × environment interactions demonstrated (Ng'etich and Stephens, 2001a) emphasizing the complexity of selection for the diverse geographic locations where tea is grown (Wachira *et al.*, 2002).

In both Malawi and Kenya, grafting of clones onto suitable rootstocks to create higher yielding, high quality composite plants is being promoted as a commercial

practice (Kayange *et al.*, 1981; Tuwei *et al.*, 2008a) and to improve drought tolerance (Tuwei *et al.*, 2008b). Trials on grafting have also been conducted in Tanzania (Mizambwa, 2002).

COMPONENTS OF YIELD[1]

In its natural state, the tea plant grows to become a tree of moderate size (or a shrub); under cultivation, however, it is pruned horizontally (typically at two- to five-year intervals) to form and maintain a low spreading bush. This increases the number of young tender shoots, which supply the produce, and allows them to be removed at relatively frequent intervals. The growth of a plant is therefore continually curtailed by cultural operations that, although familiar to present day tea culture, are alien to the normal growth processes of the tea plant (Carr, 1970).

After planting container-grown rooted plants in the field at commercial densities, usually in the range 10 000–15 000 ha^{-1}, the young plants are encouraged to develop a low spreading frame by a range of techniques, a process known as *bringing into bearing*. These include the removal (or bending) of the dominant shoot (*de-centreing*) to encourage branching, the continuous removal of harvestable shoots above a specified height (*tipping*), pruning of woody branches at one or more fixed heights above the ground (*formative pruning*), and spreading of lateral branches by *pegging*. The aim is to encourage the canopy to cover the ground, to intercept radiation and to come into profitable, commercial production as quickly as possible at least cost. Each method, or combination of practices, has its proponents, but all can have an effect on the shoot or canopy to root ratio and hence the susceptibility to drought of immature tea plants.

There are three principal contributors to the annual yield in tea: 1) the mean *number of shoots* harvested per unit area (N, m^{-2}); 2) the mean shoot *dry mass* at harvest (M, g); and 3) the *number of harvests* in a year. When a shoot is harvested, the uppermost axillary bud on the residual shoot is released from apical dominance and begins to develop into a new shoot. The time taken for this shoot to reach a harvestable size and stage of development (two or three leaves and a terminal bud) is known as the *shoot replacement cycle* (S, d). The annual yield of tea (Y, g m^{-2}) can therefore be expressed in the following way:

$$Y = N \times M \times 365/S$$

However, when tested with experimental data from Tanzania, this simple model consistently overestimated yields in low input plots for no obvious reason, although there was a very good linear relation between predicted and actual yields ($R^2 = 0.83$, $n = 9$) (Stephens and Carr, 1994). It is possible that the number of shoots that reached harvestable size in the low input plots was overestimated. There is the additional complication that more than one shoot can sometimes develop from a residual shoot,

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[1]A glossary of terms commonly used by tea scientists and commercial producers in Africa to describe tea harvesting practices can be found in Carr (2000).

i.e. from secondary and tertiary leaf axils. Each component of yield is now considered in turn.

Number of shoots

This is probably the main determinant of yield. It varies with the clone, inputs such as nitrogen and water, temperature and stage in the pruning cycle. We can define the number of *harvested shoots* (usually those with two or three unfolded leaves and an unopened terminal bud) together with the number of *basal shoots* (small shoots remaining after harvest) as the *total shoot population*. It is also sometimes necessary to differentiate between shoots with terminal buds that are active, and those with buds that are dormant, or *banjhi* (Stephens and Carr, 1990; 1994). For example, in southern Tanzania, the mean annual, basal shoot population density increased from 310 to 560 m^{-2}, averaged across all fertilizer and irrigation treatments, over a three-year period, with peaks of 850 m^{-2} in well-fertilized, well-watered tea (clone 6/8). Applying fertilizer increased the number of shoots harvested in all treatments compared with tea without fertilizer, and the proportion that were actively growing. Irrigation had no effect on the annual mean basal shoot population density, but within seasons there were considerable differences. The main effect of water stress was to delay the peak basal shoot population density from the warm dry season to the early rains, without affecting the annual mean total. Over the period of the experiment, the *shoot replacement ratio* increased from 1:1.1 to 1:1.6 in the high input plots. That is, each harvested shoot was replaced by 1.6 new shoots (Stephens and Carr, 1994).

Shoot mass

The *fresh mass* of an individual shoot increases linearly with the number of leaves on the shoot. The slope of the relationship varies with the clone, season and irrigation (0.16–0.35 g leaf^{-1}) but not with fertilizer level (Burgess *et al.*, 2006; Stephens and Carr, 1994). A shoot with three leaves and a bud can weigh up to 50% more than a shoot with two leaves and a bud. The *dry matter content* of a shoot varies with the season and also with fertilizer and irrigation (range 0.19–0.30; Burgess, 1992b). The product of fresh mass times dry matter content gives the *shoot dry mass*. Processed (or made) teas leaving the factory usually have water contents of 2–4% that is, their mass is 2–4% more than the dry mass.

Shoot replacement cycle

Shoot growth can be considered as a three-stage process. Stage 1 is a long lag phase as the axillary bud slowly expands and the leaf primordia within it develop. Stage 2 is a period of rapid shoot extension and leaf development (the unfolding of leaves). Stage 3 is when the terminal bud becomes dormant. The duration of the shoot replacement cycle (i.e. stage 1 and part of stage 2) is mainly a function of temperature, but it is also influenced by water stress, nutrition and the dryness of the air, and varies between individual clones. To aid our understanding of the processes involved, it is necessary to distinguish between shoot *extension* (increase in length) and shoot *development* (change in appearance). Rates of shoot extension and development are both temperature

dependent. The base air temperature for shoot extension (T_{be}) is in the range 8–13 °C, depending on the clone. The optimum mean temperature is about 24–26 °C, with growth rates declining at temperatures above 30–35 °C. For comparison, the base temperature for shoot development is about 2–3 °C less than that for extension. For this reason, internodes are shorter during the 'winter' months (or at high altitude) than in the 'summer' (or low altitudes), and tea is then more difficult to harvest by hand (Stephens and Carr, 1990; 1993; Burgess and Carr, 1997).

This approach to understanding the effects of climate and weather on crop developmental processes was reviewed by Carr and Stephens (1992). In summary, Squire (1979) demonstrated a linear relationship between shoot extension rates and mean air temperature over the range 17–25 °C. By extrapolation backwards the base temperature for shoot extension was identified (about 12.5 °C for clone SFS204). Squire (1979) and afterwards Tanton (1982a) then applied the concept of thermal time to predict the time taken for a bud released from apical dominance to reach a harvestable size. Subsequently, a total of 475 day °C became the accepted value (although unconfirmed) in Malawi, summed above a base temperature of 12.5 °C. This has allowed the seasonal effects of temperature on the duration of the shoot replacement cycle to be quantified and geographical sites compared. A limitation to this approach occurs when temperatures exceed the optimum for growth (> 30–35 °C), and/or when the saturation deficit of the air exceeds a value of about 2.0–2.3 kPa (Squire, 1979; Tanton, 1982b). As a practical example of its importance, Carr *et al.* (1987) demonstrated how dry air could limit the responses to irrigation in the hot, dry season in Malawi (at a relatively low altitude, 650 m), but rarely in southern Tanzania (at a relatively high altitude, 1800 m). In other words, irrigation cannot substitute entirely for rainfall.

Subsequently, Stephens and Carr (1990) showed how the apparent base temperature for shoot extension varies between clones, from 14–15 °C (BBT1) to 10.5 °C (clones BBT28 and BBT36) to as low as 7.5 °C (S15/10; Squire *et al.*, 1993). Based on measurements on seven clones in Malawi, Smith *et al.* (1993c) urged caution when taking too simplistic an approach to shoot extension and over reliance on the view that there is an inherent base temperature characteristic of a particular clone. The analysis by Stephens and Carr (1990) also showed how the results of studies like these could be biased by the shoot selection technique employed. If shoots already 30–50 mm long and actively growing are selected for measurement, there is a risk that the growth rates of only inherently fast growing shoots are recorded. To obtain a representative sample it is essential to select axillary buds at random immediately after harvesting for subsequent measurement.

Using this approach, Burgess and Carr (1997), in a comparison of six clones at Ngwazi Tea Research Station (NTRS), found that an exponential function with two constants, an initial shoot length and a relative extension rate (r), provided a realistic description of the length of axillary shoots at the end of the period beginning with the release from apical dominance to the unfurling of three true leaves. Differences between clones in the values of T_{be} (8.9 °C; SFS150 to 11.3 °C; BBK35) and in thermal extension rates (ρ, derived from linear relations between r and the mean

air temperature) could be used to explain seasonal differences in yield in southern Tanzania. The apparent base temperatures for shoot development (T_{bd}, the unfolding of leaves) were consistently 1.7 (BBT207) to 3.4 °C (6/8) below those for extension, an observation supported by the effects of temperature on the length of the internodes. The value of T_{be} for young clone 6/8 plants (9.5 °C) is close to that identified for mature plants of the same clone (10.0 °C), which was also some 2–3 °C above T_{bd} (Stephens and Carr, 1993). Both sets of results apply to well-fertilized, well-watered plants, but nutrition and water supply also influence how shoots respond to the environment. For example, shoots of well-fertilized tea were always longer (at a given stage of development) than those from unfertilized plants, whilst the length of shoots with three leaves and a bud ranged from 15 mm in unirrigated plots at the end of the dry season to 130 mm in high input plots at the start of the rains. Similarly, the duration of the shoot replacement cycle varied from 65 d (warm, wet season) to 95 d (cool, dry but irrigated) for high input plots, and from 75–180 d for unirrigated, unfertilized tea, results that all have commercial implications in terms of the choice of clones, harvesting policies and planning, and yield distribution (Stephens and Carr, 1993).

YIELD DISTRIBUTION

Crop yield is not uniform during the year. Large peaks in production can occur after a limiting factor, such as low temperature or drought, has ended and allowed the accumulated buds of many ages to develop together. This large peak, such as that which follows the start of the rains in southern Malawi, or for irrigated crops the rise in temperatures after the cool winter period in southern Tanzania, can cause major logistical problems for farmers and factory managers. There is then a decline in production until the next generation of shoots has developed. A second, but smaller, peak in production is followed by a third and possibly a fourth until once again drought and/or low temperatures reduce rates of development, and the cycle is repeated. The scale of these oscillations is proportional to the degree of synchronization induced during the period of stress (Stephens and Carr, 1990).

The initial yield peak followed by the subsequent decline is often referred to as the '*Fordham effect*' after the scientist who first described and modelled the process in Malawi. It must be emphasized that the period between peaks is one of active growth and not dormancy (Fordham, 1970; 1977; Fordham and Palmer-Jones, 1977).

To assist growers in Tanzania to plan a harvesting schedule, relationships were derived for six contrasting clones between the 'leaf appearance rate' (leaf d^{-1}, equivalent to the reciprocal of a phyllochron [the interval in days between the unfolding of two successive leaves]) and the mean daily air temperature (range 13–20 °C). It was assumed that the most advanced cohort of shoots remaining on the bush after a harvest has, on average, one unfolded leaf, and that these will form the basis for the next harvest. If the target shoot for harvesting is then three leaves and a bud, the time to the next harvest will be two phyllochrons. A simple procedure has been described for determining harvest intervals from mean air temperature. Allowances can also

be made for the effects of drought using estimates of the potential soil water deficit (Burgess and Carr, 1998).

Burgess (1994) has highlighted the importance of restricting the increase in height of the plucking surface, if potential yields are to be achieved. Each unnecessary 10 mm increase represents an annual yield loss of 70–150 kg ha^{-1}. Growers in Tanzania are recommended to set limits on the maximum allowable annual increases in crop height (not more than 80 mm for Assam-type clones, or 100 mm for China-type clones). This is also very important in research where yield responses to inputs like irrigation and fertilizer can be greatly underestimated if harvesting is not strictly controlled, and crop heights regularly monitored. It also influences the frequency of pruning, allowing pruning intervals to be extended from the conventional 3–4 years to 5 or 6, or even more, as has been possible with many of the irrigation experiments in Tanzania reported in the companion paper (Carr, 2010).

The impact of harvesting method and timing on yields of contrasting clones is illustrated in the results of a long-term experiment in Tanzania (Burgess *et al.*, 2006), whilst Mouli *et al.* (2007) have emphasized the importance of specifying the 'intensity of harvest' (IoH) if rational comparisons are to be made between different harvesting methods. The IoH is defined in terms of the number of leaves (or axillary buds) left behind after a shoot is harvested. Since yields increase with more intense (harder) harvesting, Mouli *et al.* (2007) recommended that IoH should be measured routinely in experiments with tea. For example, specifying only the duration of the interval between harvests limited the value of a long-term (10 year), multi-site, single clone (BBK35), harvesting frequency experiment in Kenya (Owuor *et al.*, 2009).

<div align="center">R O O T S</div>

Root depth

In Malawi, roots of mature seedling tea have been found at depths of at least 5.5 m, with evidence of water extraction during the dry season at that depth (Laycock and Wood, 1963). At TRFCA, the soils are deep (>5 m), well-drained Latosols, classed as clays to sandy-clays with a water-holding capacity of about 130 mm m^{-1} (Carr *et al.*, 1987; Willatt, 1970). Similarly in Kenya, Kerfoot (1961; 1962) observed roots of seven-year-old seedling tea at depths of 3 m. He also reported that roots of tea had been exposed at depths of more than 6 m elsewhere in east and central Africa. Later in Kericho, Kenya, Cooper (1979) traced roots of 17-year-old seedling tea to depths below 6 m, The soil at this site is a deep and red, freely draining friable clay (Humic Ferrasol) with an available water-holding capacity of about 215 mm m^{-1}. In southern Tanzania, roots of eight-year-old seedling tea were found at 4.5 m (Carr, 1969), and those of a 23-year-old clone (6/8) at >5 m, both irrigated (Nixon *et al.*, 2001). Here the soil is classified as a Xanthic Ferrasol, with brown, medium- to fine-textured topsoil over a deep, very light coloured, unmottled clay subsoil. The available water holding capacity averages about 100 mm m^{-1} (Baillie and Burton, 1993; Carr, 1974). In Africa, tea is definitely not a shallow rooted crop!

Table 1. *Examples of factors influencing the maximum rooting depth of tea at different locations in Africa.*

Site	Cultivar	Age (years)[†]	Depth (m)	Treatments	Source
Kericho, Kenya	Clone 12/12	3	0.72	Pegged; rainfed	Carr (1976)
			0.94	Pruned; rainfed	
	Clone 6/8		1.43	Pegged; rainfed	
			1.17	Pruned; rainfed	
	Seedlings	9	1.4–1.6	Rainfed	
	Clones 6/8, 6/10, 6/11	7	3.0	Rainfed	Carr (1977a)
	Clone 6/8	3	0.6–>1.2 m	Depending on the mulch used; rainfed	Othieno (1977)
	Seedlings	17	>6.0	Rainfed	Cooper (1979)
	Clones 6/8, S15/10, TN14/3, BBK35	<3	1.2–1.5	Rainfed	Ng'etich and Stephens, (2001b)
Ngwazi, Tanzania	Clones BBT1, 6/8, SFS150, S15/10	2.25	1.4–1.7	Irrigated and part irrigated	Burgess and Carr (1996)
	Clone S15/10	4	2.8	Irrigated	
	Clone 6/8	23	>5.0	Irrigated	Nixon *et al.*, (2001)
		4–5	>3.0		
	Seedlings	8	4.5	Part irrigated	Carr (1974)
	Clone S15/10	3	2.3	Irrigated	Kigalu (1997)
	Clone BBK35		1.7		
	Clone S15/10	6	3.6–4.3	Plant density/water variables	Kigalu (2002)
	Clone BBK35		2.5–3.0		
Marikitanda, Tanzania	Clone BBK35	4	1.5	Rainfed	Sanga and Kigalu (2006)
Mambilla, Nigeria	Clone 31/8	2	0.6–0.8	Rainfed	Carr, personal observation (1978)
Mulanje, Malawi	Clones MT12, SFS204, SFS371	0.75	0.54–0.60	Irrigated	Willatt (1970)
			0.45	Rainfed	

[†]Time from planting in the field.

In Malawi, Willatt (1970) illustrated the beneficial effects of irrigation on root depth and distribution of four clones in the first year after field planting. By contrast, grass mulches reduced the dry root mass (by 20%) and rooting depth (from 1.20 m in the control to 0.60–0.90 m depending on the mulch used) and influenced root distribution in three-year-old plants (clone 6/8) in Kenya (Othieno and Ahn, 1980). These, and other, examples are summarized in Table 1. They include observations of the root systems of two rainfed three-year-old clones brought into bearing by pegging or pruning at TRFK, Kericho, Kenya. Pruning appeared to reduce the size of the root system compared with pegging (Carr, 1976).

Detailed observations made at NTRS in southern Tanzania on irrigated tea are also summarized. For example, Burgess and Carr (1996) showed how the maximum rooting depth of four irrigated (and mulched) clones (BBT1, 6/8, SFS150 and S15/10)

increased linearly with time after field planting (from 12 to 48 months) at similar rates (averaging $2.0 \pm 0.11\,\mathrm{mm\,d^{-1}}$), reaching 2.8 m depths within four years (clone S15/10). By contrast, comparisons of four clones at four rainfed sites in Kericho, Kenya, showed roots reaching depths of 1.0–1.5 m three years after planting (averaging $1.0\text{–}1.2\,\mathrm{mm\,d^{-1}}$), depending on site (Ng'etich and Stephens, 2001b). The relationship between rooting depth and time from planting was, however, in this case best described by an exponential equation. Clone S15/10 had the shallowest roots at each site and TN14/3 the deepest: clones 6/8 and BBK35 were intermediate. Maximum rooting depths for each clone increased linearly with the mean air temperature over the range 16 to 19.5 °C. Previously, Othieno and Ahn (1980) had demonstrated the positive influence of soil temperature (16–22 °C) on root mass.

Root distribution

In order to help to explain differences in response to irrigation by young and mature tea, a detailed comparison of root distribution of 'young' (six years after field planting) and 'mature' (23 years) clone 6/8 plants was undertaken at NTRS, Tanzania, in 1994 (Nixon *et al.*, 2001). Both crops had been irrigated since planting. Sampling was restricted to the top 3.0 m, although roots of both crops went deeper than this. The total dry mass of structural roots ($>1.0\,\mathrm{mm}$ diameter) to 3.0 m depth was four times greater in the mature crop ($5.82\,\mathrm{kg\,plant^{-1}}$) than the young crop ($1.56\,\mathrm{kg\,plant^{-1}}$), and for fine roots ($<1.0\,\mathrm{mm}$) eight times greater (1.86 and $0.24\,\mathrm{kg\,plant^{-1}}$ respectively). For both crops, over 85% of the structural roots (dry weight, $\mathrm{g\,l^{-1}}$) were found in the top 0.40 m of soil, but the absolute weights again differed by a factor of four. The corresponding shoot:root ratios (dry mass) were about 1:1 and 2:1 for 'old' and 'young' plants respectively.

By contrast, the concentration of fine roots (sampled towards the end of the dry season) was much lower in the corresponding mature clone 6/8 plants that had not been irrigated for the previous nine years ($0.13\,\mathrm{g\,l^{-1}}$, to 3 m depth) compared with the equivalent for well-irrigated plants ($0.53\,\mathrm{g\,l^{-1}}$). The weight and distribution of the structural roots, and the shoot (or canopy):root ratios (1:1), were, however, similar under both water regimes (Nixon and Sanga, 1995).

Root depth and distribution were monitored in selected treatment combinations in a plant density × drought × clone experiment at NTRS. There were six spacings, giving densities ranging from 8333 (D1) to 83333 (D6) plants $\mathrm{ha^{-1}}$ (Kigalu, 1997) of which three only are considered here. By August 1995, 32 months after planting (and mulching), roots of well-watered clone BBK35 had reached depths of 0.9 m (D1) to 1.1 m (intermediate density, D3 = 16 667 $\mathrm{ha^{-1}}$), and those of clone S15/10 from 1.5 m (D1) to 2.1 m (D3). Roots in treatment D6 went less deep than those in D3. The largest effect of plant density on root distribution occurred in the top 0.2 m where root density increased with plant density for both clones. Below this depth the largest root density occurred with treatment D3, followed by D6 (S15/10 only), and then D1. S15/10 had more fine roots below 0.2 m than K35 at all three densities. The corresponding rates of increase in root depth equated to about $0.9\text{–}1.1\,\mathrm{mm\,d^{-1}}$ (BBK35) and $1.6\text{–}2.2\,\mathrm{mm\,d^{-1}}$ (S15/10).

It is of interest to note that relative differences between clones in rooting depth were not consistent between sites. Thus, roots of three-year-old BBK35 plants were shallower than those of S15/10 in Ngwazi, but deeper in Kericho.

The treatment effects on root depth and distribution were again investigated at NTRS in early 1999, six years after field planting and four years after differential irrigation/drought treatments had first been imposed. This time the two extreme densities were compared (high, D6, and low, D1) at each of the two extreme drought treatments: I0 (most droughted, a total of 40 weeks without irrigation/rain), and I6 (well-irrigated since planting) for both clones. Three plants from each treatment combination were excavated at 0.20 m depth increments. The results were not easy to interpret. Although, on average, roots of clone S15/10 reached depths (4.0 m, equivalent to about $1.8 \, \mathrm{mm \, d^{-1}}$) substantially greater than those of BBK35 (2.8 m, $1.3 \, \mathrm{mm \, d^{-1}}$), the effect of water regime was not consistent between the two clones. For S15/10, dry conditions (I0) resulted in deeper rooting (4.3 m, $2.0 \, \mathrm{mm \, d^{-1}}$) than with well-watered plants (3.6 m, $1.6 \, \mathrm{mm \, d^{-1}}$). For clone BBK35 the situation was reversed, with droughted plants rooting less deep (2.5 m, $1.1 \, \mathrm{mm \, d^{-1}}$) than those watered well since planting (3.0 m, $1.4 \, \mathrm{mm \, d^{-1}}$). The effect of plant density was more complicated: for S15/10 roots of high density plants were about 0.2–0.4 m shallower than those grown at low density; by contrast, for BBK35, although roots of droughted plants were 0.8 m shallower at low density, they were 0.2 m deeper when irrigated (Kigalu, 2002).

In terms of root distribution, there were more fine roots (<1.0 mm) at the low plant density than at the high density (expressed as $\mathrm{g \, l^{-1}}$ soil). For droughted plants this difference extended to depths of 2.0 m with both clones, but to only 0.5–1.0 m for irrigated bushes (Kigalu, 2002). In all four treatment combinations, BBK35 had fewer fine roots than S15/10, low density plants had more than high density and, with one exception (S15/10, high density), droughted plants more than those well irrigated. The largest differences (averaged over 1.0 m depth only) in fine root densities for (a) BBK35 were between low plant density, well irrigated ($0.4 \, \mathrm{g \, l^{-1}}$) and low density, droughted ($1.5 \, \mathrm{g \, l^{-1}}$), and for (b) S15/10 between high density both droughted and well irrigated ($0.9 \, \mathrm{g \, l^{-1}}$) and low density, droughted ($2.0 \, \mathrm{g \, l^{-1}}$).

The canopy:root ratios (dry mass), as calculated from the slope of the linear relationship between the cumulative totals recorded in sequential whole plant harvests over the three years following planting, were independent of plant density but were consistently less for BBK35 (3:1) than for S15/10 (5:1) (Kigalu, 1997).

Root extension

The growth of tea (white, unsuberized) feeder roots was observed and monitored against glass in several simple underground root chambers over a 21-month period 1968–1970 at Ngwazi, Tanzania (Carr, 1969; 1971a). The principal observations were:

- Roots of irrigated China-type BBT1 grew throughout the 'winter' months (June–September) when shoot growth was negligible.

- Roots of previously unirrigated BBT1 began to grow only after the first 'flush' of shoot growth was coming to an end, six to eight weeks after water was first added to the soil.
- Roots of two Assam-type clones (BBT28 and BBT36) grew only slowly during the 'winter' although some shoots continued to grow, albeit slowly.

In a similar study in southern Malawi, Fordham (1972) observed roots of both young clones (SFS204, MT12 and MFS76) and mature seedling tea under irrigated field conditions in simple root observation trenches. For the clones, periods of maximum shoot growth were associated with minimal root growth. For mature tea, there was a similar reduction of root growth during a period of intense shoot growth. Pruning caused roots to stop growing for approximately three months. Herd and Squire (1976) also observed a stimulation of root growth in the 'winter' months in Malawi.

Summary: roots

Although studying roots is not easy, the following broad conclusions can be reached, nearly all of which influence water availability and crop responses to drought and to irrigation:

1. The roots of tea can extend to considerable depths (5–6 m), providing that there are no physical restrictions.
2. Roots extend in depth at rates of between 1 and $2\,\mathrm{mm\,d^{-1}}$ (temperature dependent), reaching 1.0 m in about 18–36 months after planting in the field.
3. About 85% of the structural roots (by mass) occur in the top 0.4 m of soil, regardless of the plant age.
4. The density of roots continues to increase at all depths with age from planting.
5. The canopy:root ratio (by mass) decreases with plant age.
6. Clones differ in the depth and distribution of roots, but not consistently across sites.
7. Methods of bringing young tea into bearing can influence the form of the resultant root system in young tea. Pruning results in the cessation of root growth.
8. There is no consistent evidence that irrigation reduces the size or depth of a root system (indeed there is some evidence for the opposite).
9. Grass mulches can reduce the depth and mass of root systems of young plants.
10. Planting density can also influence root depth and distribution, but the effects are complex, and appear to vary with clone and watering regime.
11. Roots can continue growing during 'winter' months when shoot extension rates are slow.
12. There is evidence of periodicity of root growth, with root growth alternating with active shoot growth.

PLANT WATER RELATIONS

The water relations of tea have been studied at all three East African research sites. Emphasis has been on measurements of stomatal behaviour, photosynthesis,

transpiration and xylem water potential in attempts to understand better how the crop responds to its environment (in order to inform field management practices), and to find ways of identifying drought-resistant cultivars at an early stage in the selection process.

Stomatal behaviour

Stomata occur only on the lower (abaxial) surface of the leaf at an average density reported as about 190 mm^{-2} (Fordham, 1971), 130 mm^{-2} (Squire, 1976) and 150–200 mm^{-2} (Olyslaegers *et al.*, 2002; Samson *et al.*, 2000). By contrast, Ng'etich and Wachira (2003), in a comparison of common cultivars grown in Kenya (all diploid), reported densities in the range 240–312 mm^{-2} with significant differences between individual clones (triploid and tetraploid cultivars had smaller densities).

A range of techniques has been used to monitor the behaviour of tea stomata. These include the infiltration score technique, the pressure drop porometer, the steady state constant flow porometer, the non-ventilated transient (or dynamic) porometer and direct observation. Unfortunately, they have not always given results that are consistent or directly comparable.

In early work in Tanzania and Kenya, the infiltration technique, based on isopropyl alcohol was used to study stomatal behaviour (i.e. a measure of the degree of opening of the widest stomatal pores) in relation to environmental variables, and specifically to water stress. Preliminary measurements showed that the most consistent estimates were obtained from healthy, fully grown, yet still supple leaves that were fully exposed to sunlight (Carr, 1971b). In Tanzania, partial stomatal closure was observed during the middle of the day on nearly all occasions when diurnal assessments were made (Carr, 1968). Similar diurnal patterns of stomatal opening were observed during dry weather for a selection of clones in Kenya. Stomata were always wider open in the rains than during the dry season in both (previously) irrigated and unirrigated plants. Differences in the dryness of the air (saturation deficit) were believed to be largely responsible for both the diurnal and seasonal differences in the degrees of stomatal opening observed (Carr, 1977a; Othieno, 1978).

In Malawi, Fordham (1971) used a pressure drop porometer as well as the infiltration method to measure both diurnal and seasonal changes in stomatal opening of mature Assam-type seedling plants. Progressive closure of the stomata was observed from midday onwards in both irrigated and unirrigated tea, and there were marked seasonal changes associated with the dry season. Also in Malawi, Squire (1976) using a diffusion porometer in the cool dry season, showed leaf conductances (measured on the second leaf of an actively growing shoot of several clones) increasing from low values in the morning, peaking during the middle of the day, and declining throughout the afternoon. Later, Squire (1977) used silicone rubber impressions of leaves to estimate stomatal opening in the wet season. Again, the stomata were wider open at midday (3.5–4 μm) than at dawn or dusk (2 μm).

By contrast to these observations in Malawi, diurnal changes in stomatal conductances recorded in Sri Lanka (6°55′N; alt. 1382 m) were similar to those

summarized above using the infiltration technique. In the early morning, conductances (clone TRI 2025, measured with a portable infra red gas analyser on recently mature leaves) were large, they decreased towards midday and increased again in the afternoon (Mohotti and Lawlor, 2002). The pattern was the same regardless of the degree of shade or nitrogen level. There were negative linear relations between conductance and leaf temperature (range 16–33 °C), saturation deficit of the air (range 0.5–3.8 kPa) and illuminance (range 0–2000 μmol m^{-2} s^{-1}).

Burgess (1992a) attempted to make direct comparisons of diurnal patterns of stomatal behaviour using steady state and transient porometers and the infiltration technique. The absolute and relative measures of stomatal conductances of six irrigated clones were also compared with the corresponding infiltration score. Despite taking all the precautions possible (for example, in the calibration of the porometers), it was difficult to reconcile the results obtained. Relationships between conductance (transient porometer) and the infiltration score were linear but varied with the clone. As a result of this experience, Smith *et al.* (1993a) urged caution when using the results of porometry to identify drought-tolerant clones.

In an interesting short-term pot experiment in Colombia, Hernandez *et al.* (1989) demonstrated convincingly the relative sensitivity of tea stomata (and also coffee and cacao) to the dryness of the air. Conductances of all three species (shaded) declined rapidly as the saturation deficit increased from 0.5 to 4.0 kPa, whilst transpiration rates were reduced when the saturation deficit exceeded 1.0–1.5 kPa. By comparison, sunflower stomata (not shaded) were less sensitive to the dryness of the air, and transpiration continued to increase over the range 0–4.0 kPa.

Photosynthesis

Using a portable gas exchange system, photosynthetic rates (A) of individual mature leaves (clone 6/8) at the surface of the canopy were monitored during the warm dry season in southern Tanzania (Smith *et al.*, 1993b). Rates increased up to an illuminance (photon flux density) of about 1000 μmol m^{-2} s^{-1}, but above this value they remained relatively constant. There was a quadratic relationship between A and stomatal conductance (g), with A increasing with g over the range 8–100 mmol m^{-2} s^{-1}, but with minimal changes in A when g exceeded 100 mmol m^{-2} s^{-1}. Irrigation and fertilizer increased photosynthetic rates both by increasing A per unit leaf area and by increasing the proportion of light intercepted by photosynthetically efficient leaves. Although there was a broad temperature (air and leaf) optimum for photosynthesis (range 20–36 °C), irrigation induced increases in A could be accounted for by increases in g and associated reductions in leaf temperature. The effects of fertilizer were more complicated.

By comparison, Barman *et al.* (2008) at Tocklai in North East India (26° 47′N; alt. 97 m) identified for a selection of tea clones an optimum illuminance for A of about 1200 μmol m^{-2} s^{-1} (possible range 1000–1400), whilst the optimum leaf temperature was considered to be about 26 °C (range 25–30), values comparable with those reported by Smith *et al.* (1993b). Similarly, in Sri Lanka Mohotti and Lawlor (2002)

found, at a high elevation site (1400 m), that A increased rapidly from zero at dawn to a maximum between 08:00 and 09:00 hours, followed by a progressive decrease during the remainder of the (bright and sunny) day, even when the environmental conditions were ameliorating during the late afternoon (irradiance, temperature and saturation deficit declined). Photoinhibition was implicated in the (complicated) explanation put forward to explain this diurnal pattern in A, linked to the corresponding diurnal pattern in stomatal conductances summarized above.

Previously, Squire (1977) had monitored representative diurnal changes in photosynthesis in the wet, cool and dry seasons in southern Malawi using the ^{14}C technique. Photosynthesis of leaves on the bush surface was light-saturated when irradiance reached 350–400 W m^{-2} (equivalent to an illuminance of about 800–900 μmol m^{-2} s^{-1}). Declines in photosynthesis observed in the afternoon appeared, in large part, to be closely related to falls in the xylem water potential (range -0.4 to -1.5 MPa, measured with a pressure chamber). Photosynthesis did not decrease at the start of the cool season when the yield of tea declined, whilst irrigation in the dry season had little immediate effect on shoot growth, but increased photosynthesis. These observations are important to our understanding of the allocation of assimilates within the tea plant and seasonal yield distribution.

As De Costa *et al.* (2007) concluded in their detailed review of the photosynthetic process: 'the photosynthetic apparatus and partial processes of tea show specific adaptations to shade. Maximum light saturated photosynthetic rates are below the average for C3 plants and photoinhibition occurs at high light intensities. These processes restrict the source capacity of tea.'

Transpiration

Although portable gas analysers have been used to monitor instantaneous rates of transpiration (Smith *et al.*, 1994), they do not allow whole plant water use to be determined. Accurate estimates of transpiration are needed when scheduling irrigation for immature tea or, for example, comparing the water use of different clones. Kigalu (2007) has described the successful use of sap flow meters, based on the stem heat flow method, for measuring transpiration rates of individual plants in a plant density experiment (three years after field planting) in Tanzania. There were differences in water use (on a per unit leaf area basis) between the two well-watered clones, with S15/10 (with a spreading habit) transpiring faster for most of the day than BBK35 (more upright). Similarly, there were differences in diurnal patterns of water use between plants (both clones) grown at low density (8333 ha^{-1}) or at very high density (83 333 ha^{-1}). The same method was used by Samson *et al.* (2000) to compare the responses of four clones to atmospheric water stress in South Africa with some success.

Xylem water potential

The Scholander pressure chamber has proved to be a useful way of measuring the water status of tea in the field. It was first used by Carr (1971a; 1971b; 1976; 1977a; 1977b) in Tanzania and Kenya; and by Williams (1971) and Fordham (1977)
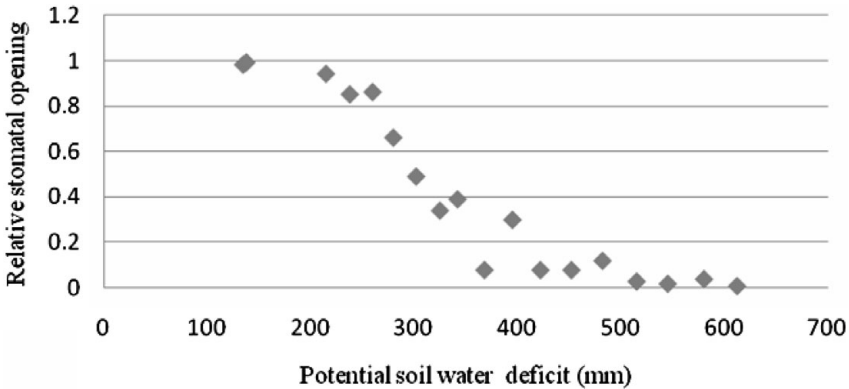
Figure 1. Relation between relative stomatal opening (ration infiltration score unirrigated to irrigated tea, clone BBT1) and potential soil water deficit.

in Malawi; and subsequently by Squire (1977; 1979) in Malawi; Othieno (1978; 1980) and Odhiambo *et al.* (1993) in Kenya; Renard *et al.* (1979) in Burundi and Olyslaegers *et al.* (2002) in South Africa. The technique has been variously used to identify the critical values of xylem water potential (Ψx) that limit the growth of shoots and yield (−0.7 to –0.8 MPa) in relation to potential soil water deficits (SWDs) and saturation deficits of the air, to explain the seasonality of yield, to understand the effects of shelter from wind and mulches on crop water use, to determine the relationship to stomatal behaviour, to compare clones for drought tolerance, to assess the relative yield potential of clones, to evaluate the effects of methods of bringing tea into bearing on crop water status, and to compare the responses of seedling tea bushes and their clones to water stress. These issues are considered in more detail, under the appropriate headings, elsewhere in this and the companion paper (Carr, 2010).

Cultivar comparisons

In Tanzania, differential stomatal closure between well-irrigated plants (cv. BBT1) and unirrigated plants was first observed when the potential SWD exceeded about 200–300 mm (Carr, 1968; 1969). There was then a progressive decline in relative opening until the potential SWD reached about 500 mm, followed by all day closure (Figure 1). BBT1, a China-type cultivar, is unusual in many respects, being very drought tolerant on an annual yield basis, but responsive to irrigation in the short term. Because of these properties, it is worthy of study.

The slope of the linear relationship between Ψx and the infiltration score is a possible indicator of drought tolerance. For example, compared with heterogeneous, mature seedling tea, the stomata of BBT1 are relatively insensitive to large changes in the shoot water potential (range −0.1 to −1.5 MPa). Thus, there was an eight-fold difference in the slopes of the regression line for seedling tea (−0.71) and BBT1 (−0.09) (Carr, 1971b). A follow-up study during dry weather in Kenya confirmed that there were differences between clones in the slope of this relationship, with clone 6/127 being classified as relatively drought tolerant and a seedling population as drought sensitive,

but with none as extreme as BBT1 (Carr, 1977a). As the soil dried (to a maximum potential SWD of 300 mm), the daily minimum shoot water potentials declined (to −2.0 MPa), more in some clones than others. There was some evidence of a genotype × environment interaction for both variables. The infiltration score and the xylem water potential were both negatively correlated with air temperature (range 13–28°C) and the saturation deficit (0.06–2.5 kPa).

In a related study again in Kenya during the same dry season (1971), similar comparisons were made between the responses of seedling plants and the clones derived from them (Carr, 1977b). There was no evidence to suggest that the response of a clone to drought could be predicted from that of its seedling 'parent' (ortet). It was postulated that, since the original seedlings were originally identified in a field on account of their comparative vigour, they must have been able to compete effectively with their neighbours for water. This advantage would not be maintained when clonal plants were competing with neighbouring plants that were genetically identical. Using the same criteria as described above (the Ψx/infiltration score relationship), clone 7/4 was considered to be relatively *drought tolerant*. The stomata of this clone remained open during the dry season, and the shoot water potential remained high, suggesting a very efficient root and water transport system throughout the plant (or possibly changes in osmotic potential, as suggested by Karunaratne *et al.*, 1999). By contrast the stomata of clone 7/14 began to close early in the dry season and were slow to reopen when the rains began (an example of *drought avoidance*).

In Malawi, Squire (1976) found that the Ψx, measured in the cool and rainy seasons, was least in clones that gave the largest yields (recorded over a full year), and postulated that measurements of Ψx with a pressure chamber might be used to screen new clones for high productivity at an early stage of growth, although the physiological link between Ψx and yield was not obvious. In a comparison of six irrigated clones in Tanzania, Smith *et al.* (1993a) were not able to confirm this relationship.

In a detailed comparison of six young (<3 years) contrasting clones in southern Tanzania, Smith *et al.* (1994), using a portable gas analysis system, found that stomatal conductances (g) of clones S15/10 and 6/8 were consistently at least 10% higher than those of clones BBT1 and BBT207 (both China-type). The rates of photosynthesis (A) in clones BBT1, SFS150, S15/10 and 6/8 were always greater than those in BBT207. Irrigation increased g, A and the A/g ratio (a measure of instantaneous water use efficiency) in all six clones. Clones also differed in the relationship between leaf temperature and A. By contrast to the results summarized above (under photosynthesis) for 'mature' clone 6/8 plants, irrigation also increased the temperature optimum for photosynthesis, and reduced photoinhibition at high illuminance (Smith *et al.*, 1993b).

In the same experiment, clones BBT1 and SFS150 were classified as 'drought resistant' (based on the relative annual yield loss) although different mechanisms were involved (see Carr, 2010). Drought resistance for both these clones, and also for the high yielding S15/10, were strongly related to high Ψx values (less negative) in the dry season. Smith *et al.* (1993a) were of the view that 'there is now sufficient accumulated evidence for the relationship between drought resistance and Ψx (measured with

a pressure bomb) to be used to help to identify drought resistant clones during a dry season'. They also believed that further investigations were justified into establishing the relationships between A and A/g and an appropriate measure of drought resistance. Subsequently, in an evaluation of the effects of grafting in Kericho, Kenya, on drought tolerance (based on an index derived from the ratio of yields in a drought year with those in the previous or subsequent year, or equivalent period, with only a mild drought) Tuwei *et al.* (2008b) considered that Ψx measurements (least negative) of a clone under well-watered conditions may be related to its drought tolerance as a rootstock, and could be helpful in a selection programme. By contrast, the performance of clones as drought-resistant scions, based on visual symptoms, was correlated with stomatal conductance values.

Among the morphological leaf traits studied by Olyslaegers *et al.* (2002) in South Africa, stomatal density, pore diameter and pore depth were not linked consistently to stress tolerance. Cuticle thickness was also not a good indicator. In contrast, leaf conductances were greater and leaf water potentials lower in two clones considered to be sensitive to very dry air (PC113 and SFS204) compared with two clones thought to be tolerant (PC114 and SFS150), but this observation was site dependent. Previously, Samson *et al.* (2000), in a comparison of the same four clones under controlled conditions, considered leaf-related sap flow measurements (which are related to transpiration rate) to be a possible promising discriminator for identifying clones sensitive to drought stress induced by dry air conditions (considered to be an important limiting factor to tea production in South Africa), in contrast to daytime stomatal conductance. Similarly, Nijs *et al.* (2000) compared PC113 and PC114 using a canopy level energy balance approach together with measurements of stomatal conductance and leaf water potential of individual leaves. Neither approach could distinguish clearly between the two clones, which visually differed considerably in their response to water stress. PC114 (tolerant) did though exhibit greater stomatal control in young leaves, and associated higher (less negative) water potentials, than (susceptible) PC113.

Summary: plant water relations
1. Stomata only occur on the abaxial surface of the leaf.
2. A range of techniques has been used to monitor stomatal behaviour, but results are not always directly comparable.
3. In particular, evidence for diurnal changes in stomatal opening is inconsistent, partly depending on the technique used.
4. Nevertheless, it appears that stomata are sensitive to temperature and/or dry air.
5. Rates of photosynthesis increase up to an illuminance of about $1000\ \mu mol\,m^{-2}\,s^{-1}$, and then remain relatively constant.
6. The optimum leaf temperature for photosynthesis is about 25–30 °C.
7. Rates of photosynthesis can vary between clones but are not linked directly with yield.
8. Sap flow meters have been used with apparent success to monitor actual transpiration by young clones.

9. Measurements of xylem water potential with a pressure chamber have proved to be a very useful way of quantifying plant water status, and possibly drought resistance, in the field.
10. The sensitivity of stomata to changes in xylem water potential varies between clones, and this may also offer a drought tolerance/avoidance selection procedure.
11. There is no apparent direct relationship between the responses of a clone to water stress and that of its ortet.
12. Caution is urged when using porometry for identifying drought resistant clones.

CONCLUSIONS

Research institutes serving an industry such as tea face difficult challenges. Namely, the producers who are funding the research, often through a statutory levy, as well as donors, usually want answers to short-term problems that are often time and location specific. At the same time, researchers are meant to serve an industry located in diverse ecological areas, with both large-scale and small-scale producers, often with conflicting and constantly changing priorities and resources. Fundamental information is needed to enable results of experiments to be extrapolated from one location to another where conditions may be very different. It is also necessary for researchers to anticipate future problems and not to concentrate only on the immediate challenges facing the industry. Somehow a balance has to be struck within the financial and skill constraints available.

Researchers at the Ngwazi Tea Research Station (now TRIT) set themselves three objectives:

1. To answer questions of immediate practical importance to the industry.
2. To understand, where possible, the mechanisms responsible for the observed responses so that the results can be applied with confidence elsewhere.
3. To communicate the results of the research to the industry, and to the scientific community, in the most appropriate ways.

This paper provides a synthesis of some of the fundamental studies conducted within eastern Africa, which contribute to point 2 above, whilst the companion paper is more focused on point 1. Both contribute to point 3.

Despite continuing uncertainties over funding, progress has been made in understanding the fundamentals of the water relations of the tea plant, and how it responds to its immediate environment. This, in turn, has fed back into practical advice to the industry. In particular, our understanding of the role temperature plays in determining shoot growth rates and yield distribution, and the controlling effect of dry air on photosynthesis rates and shoot growth has contributed to ways of predicting harvest intervals, responses to irrigation and, by understanding limiting factors, site selection. In addition some progress has been made in identifying drought-tolerant cultivars at an early stage in the selection process. All this knowledge crosses national boundaries and is not location or time specific.

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