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Responses of tea clones
to drought
in Southern Tanzania

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ABSTRACT

A line-source experiment, planted in August 1988, was used to quantify the yield responses of six tea (*Camellia sinensis*) clones to drought in Southern Tanzania. The selected clones (1, 6/8, SFS150, S15/10, 207 and K35) are scientifically and/or commercially important in eastern Africa. Drought treatments were imposed during the latter part of 1989 and 1990. Soil water deficits were estimated using a water balance model, validated using a neutron probe.

The maximum yield of made tea, from June 1990 to May 1991, was 3760 kg ha⁻¹ for clone S15/10, compared to 2210-2640 kg ha⁻¹ for the other clones. Drought resistances, assessed from the relative yield reduction below the maximum, were greatest for clones 1 and SFS150. The clonal attributes determining these responses were examined in terms of dry matter production and partitioning, components of yield, and plant water status, and were used to determine selection criteria for high yielding and/or drought resistant clones.

The high yield of clone S15/10 resulted from greater partitioning of dry matter to leaf and harvested shoots (51%) than the other five clones (34-39%). The conversion efficiency for four of the fully irrigated clones was 0.33-0.55 g MJ⁻¹ intercepted total solar radiation.

Drought resistance was related with leaf measurements of photosynthetic rate per unit stomatal conductance (A/g). In a comparison of droughted plants, resistance was related to reduced incidence of *Phomopsis theae*, reduced leaf abscission and high xylem water potentials. Measurements of stomatal conductance highlighted calibration problems with transient and steady state porometers.

Clone SFS150 had the lowest base temperature for shoot extension (8.9°C) and therefore a more even seasonal distribution of yield than the other clones. Base temperatures for shoot development were 1.7-3.5°C lower than those for extension. The dry matter content of harvested shoots typically ranged from 24.2% for clone 1 to 20.7% for clone SFS150.

Partitioning of dry matter to leaves and green stem for high yield, a high A/g ratio for drought resistance, and low base temperatures for improved yield distribution are proposed as selection criteria.

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SYMBOLS AND ABBREVIATIONS

A	assimilation rate an area of leaf	($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)
ADC	Analytical Development Company Ltd	
AP3	Automatic porometer mark 3 produced by Delta-T Devices Ltd.	
AWC	available water content. Water held in the soil between ULAW and PWP ($\psi_s = -1500 \text{ kPa}$)	(mm m^{-1})
b_M	relative increase in mass per unfurled leaf	($\text{g g}^{-1} \text{ leaf}^{-1}$)
CD	critical soil water deficit, beyond which transpiration or yield is reduced	(mm)
CO ₂	carbon dioxide	
D	drainage of water below the rooting depth of the crop	(mm)
DM	dry mass	(g)
D_w	diffusion coefficient of water vapour in air	($\text{mm}^2 \text{ s}^{-1}$)
DS	drought stress	
d_c	stem diameter measured at soil surface	(mm)
d_s	stomatal diameter	(mm)
dT	the temperature of the porometer cup minus that of the leaf	(°C)
dt	transit time - time for the relative humidity with a transient porometer to rise by 5%	(s)
E_o	evaporation rate from an open water surface estimated using the McCulloch (1965) version of the Penman equation (1948)	(mm d^{-1})
E_L	transpiration rate from an individual leaf	($\text{mmol m}^{-2} \text{ d}^{-1}$)
E_{pan}	evaporation rate from a screened evaporation pan	(mm d^{-1})
ET_o	potential crop evaporation rate, calculated using the Penman-Monteith equation described by Smith (1991b)	(mm d^{-1}).
ET	actual crop evaporation rate (sum of E_t and E_s)	(mm d^{-1}).
E_t	actual crop transpiration rate	(mm d^{-1}).
E_s	actual evaporation rate of water from the soil surface	(mm d^{-1}).
f_s	proportion of S intercepted by the crop canopy, ie, reflected and absorbed	
f_w	proportion of AWC used by the crop for transpiration	

GC	proportion of ground covered by crop, determined from overhead observation	
g_L	leaf conductance of water vapour	(mmol m ⁻² s ⁻¹ ; mm s ⁻¹)
g_s	stomatal conductance of water vapour	(mmol m ⁻² s ⁻¹ ; mm s ⁻¹)
h_s	depth of a stoma	(mm)
HI	harvest index - the proportion of the total dry matter, including roots, produced by a crop that is harvested to form the economic product	(%)
I	depth of irrigation water applied	(mm)
i	shoot internode length	(mm)
$I_0, I_1, I_2,$ I_3, I_4, I_5	labels for drought/irrigation treatments	
k	extinction coefficient of light for a canopy	
K_c	crop factor used to calculate ET from E_{pan} ($ET = K_c E_{pan}$)	
K_y	relative change in yield per unit increase in DS	
L	shoot length	(mm)
L_f	final length of an axillary shoot when it becomes dormant after a period of extension	(mm)
L_o	initial length of an axillary shoot at time of release from apical dominance	(mm)
LAI	leaf area index (leaf area per unit area of field)	
LAI'	leaf area index (leaf area per unit area of field covered by the canopy)	
LCA-2	porometer (and photosynthesis system) produced by ADC	
M_o	mass of a harvested shoot with no expanded leaves	(g)
M	mass of a harvested shoot	(g)
N	nitrogen	
n	number of treatments	
n_L	number of leaves	
n_s	stomatal density	(mm ⁻²)
ODA	U.K. Overseas Development Administration	
P	probability	
P_a	atmospheric pressure	(kPa)
P_o	atmospheric pressure at sea level	(kPa)
PPFD	photon flux density of photosynthetically active radiation	(μ mol m ⁻² s ⁻¹)
P_{max}	maximum photosynthetic rate at light saturation	(mg CO ₂ m ⁻² s ⁻¹)

PWP	permanent wilting point	
r^2	proportion of variation explained	(%)
R	rainfall	(mm)
RH	relative humidity	(%)
R_s	mean count rate measured with the neutron probe in soil	
R_w	mean count rate measured with the neutron probe in water	
RER	relative extension rate of shoot	(mm mm ⁻¹ d ⁻¹)
S	incident solar radiation (total, as distinct from photosynthetically active)	(MJ m ⁻² d ⁻¹)
se	standard error	
sed	standard error of the difference	
SRC	shoot replacement cycle - time for a shoot released from apical dominance to unfurl three flush leaves	(d)
SWD	soil water deficit	(mm)
SWD _{model}	soil water deficit estimated using the model described in Chapter 4	(mm)
SWD _{np}	soil water deficit estimated from measurements of soil water with a neutron probe	(mm)
T	air temperature	(°C)
T_{mean}	mean air temperature	(°C)
T_{bd}	the base temperature for shoot development - at and below which shoot development, defined in terms of leaf unfurling, does not proceed	(°C)
T_{be}	the base temperature for shoot extension - at and below which shoot extension does not proceed	(°C)
T_c	temperature of the porometer cup	(°C)
T_p	temperature of the calibration plate	(°C)
TAT	The Tea Association of Tanzania	
TRFCA	The Tea Research Foundation of Central Africa	
TRFK	The Tea Research Foundation of Kenya	
TSh	Tanzanian Shilling	
TTA	The Tanzania Tea Authority	
t	time	(d)
U_2	mean day-time (09.00 to 15.00 h) windspeed recorded 2 m above the ground	(m s ⁻¹)
ULAW	upper limit of available water	(mm)
VFC	volatile flavour compounds	
VPD	atmospheric saturation vapour pressure deficit	(kPa)

Y_a	actual yield of made tea	(kg ha ⁻¹)
Y_m	maximum yield of made tea	(kg ha ⁻¹)
ϵ_s	dry matter/intercepted-radiation ratio - the dry mass of plant tissue accumulated over a period of time, divided by the amount of total solar radiation intercepted by the foliage over the same period	(g MJ ⁻¹)
ϵ_w	dry matter/transpired-water ratio - the dry mass of plant tissue accumulated over a period of time, divided by the corresponding amount of water expressed as a volume per unit area	(g mm ⁻¹)
ρ_e	thermal extension rate - increase in relative extension rate per increase in air temperature above T_{be}	(mm mm ⁻¹ d ⁻¹ °C ⁻¹)
ρ_d	thermal development rate - increase in development rate per increase in air temperature above T_{bd}	(d ⁻¹ °C ⁻¹)
θ_v	volumetric soil water content	(mm mm ⁻¹)
χ_c	saturation vapour concentration	(g m ⁻³)
ψ_a	atmospheric water potential	(MPa)
ψ_s	soil water potential	(MPa)
ψ_x	xylem water potential	(MPa)
w	partial vapour pressure of water vapour in air	(kPa kPa ⁻¹)

NOTE ON STATISTICAL ANALYSIS

- 1: Differences between treatments were assumed to be statistically significant at or below a 5% level of probability ($P \leq 0.05$).
- 2: In some of the tables the letters 'a' and 'z' appear to the right of a column of numbers. Those numbers marked with an 'a' are not significantly different from the highest number in the column. Those numbers marked with a 'z' are not significantly different from the lowest number in the column.

CHAPTER 1

INTRODUCTION

Tea (*Camellia sinensis* (L.) O. Kuntze) is a perennial evergreen shrub which is commercially grown for the production of tender shoots usually consisting of two or three expanded leaves and an apical bud. These shoots are harvested by hand at one to three week intervals and are transported on the same day to a tea factory where they are withered, cut and dried to produce made tea, which is sold as a beverage.

Until the 1950s most new areas of tea were planted with transplants grown from seed. Since tea is an outbreeder the resulting seedlings had different genotypes and showed a wide range of morphological and physiological characteristics ranging from 'China' to 'Assam' type. The 'China' type cultivars usually have small, erect, dark green leaves and if allowed to grow naturally can reach a height of about 2 m. The 'Assam' type cultivars, which can grow up to 10 m high, have larger, more horizontal and lighter green leaves than the 'China' types (Hadfield, 1974; Banerjee, 1992a). Research in India, Sri Lanka and Indonesia during the 1930s provided the basis for the introduction of vegetative propagation of tea plants from single node cuttings (Banerjee, 1992b). This enabled producers to plant areas of tea with plants of the same genotype, ie, clonal tea.

The Republic of Tanzania is the third largest exporter of tea within eastern Africa, with production only surpassed by the two neighbouring states of Kenya and Malawi. In 1989/90 there were about 19,000 ha of tea in Tanzania producing approximately 20 million kg of made tea (Ndamugoba, personal communication). Of this about 75% was exported, providing about 4700 million TSh (ISNAR, 1991) or about US\$24 million at 1990 official exchange rates. After coffee and cotton, the export of tea earns Tanzania the largest amount of foreign exchange (TAT, 1989). The tea industry also provides direct income for about 30,000 smallholders and 25,000 tea company employees, as well as contributing significantly to the infrastructure of specific regions.

The first tea in Tanzania was planted in 1904 by German settlers in the Usambaras in Northern Tanzania and in the Rungwe district in the South

(Figure 1.1) (Carr *et al.*, 1988). Whilst both these districts continue to have large areas of tea, tea production has increasingly been centred in the Mufindi district which produced about 45% of the national crop in 1990. With the addition of the tea produced in the Rungwe, Njombe and Tukuyu districts, about 75% of the national crop is produced in Southern Tanzania.

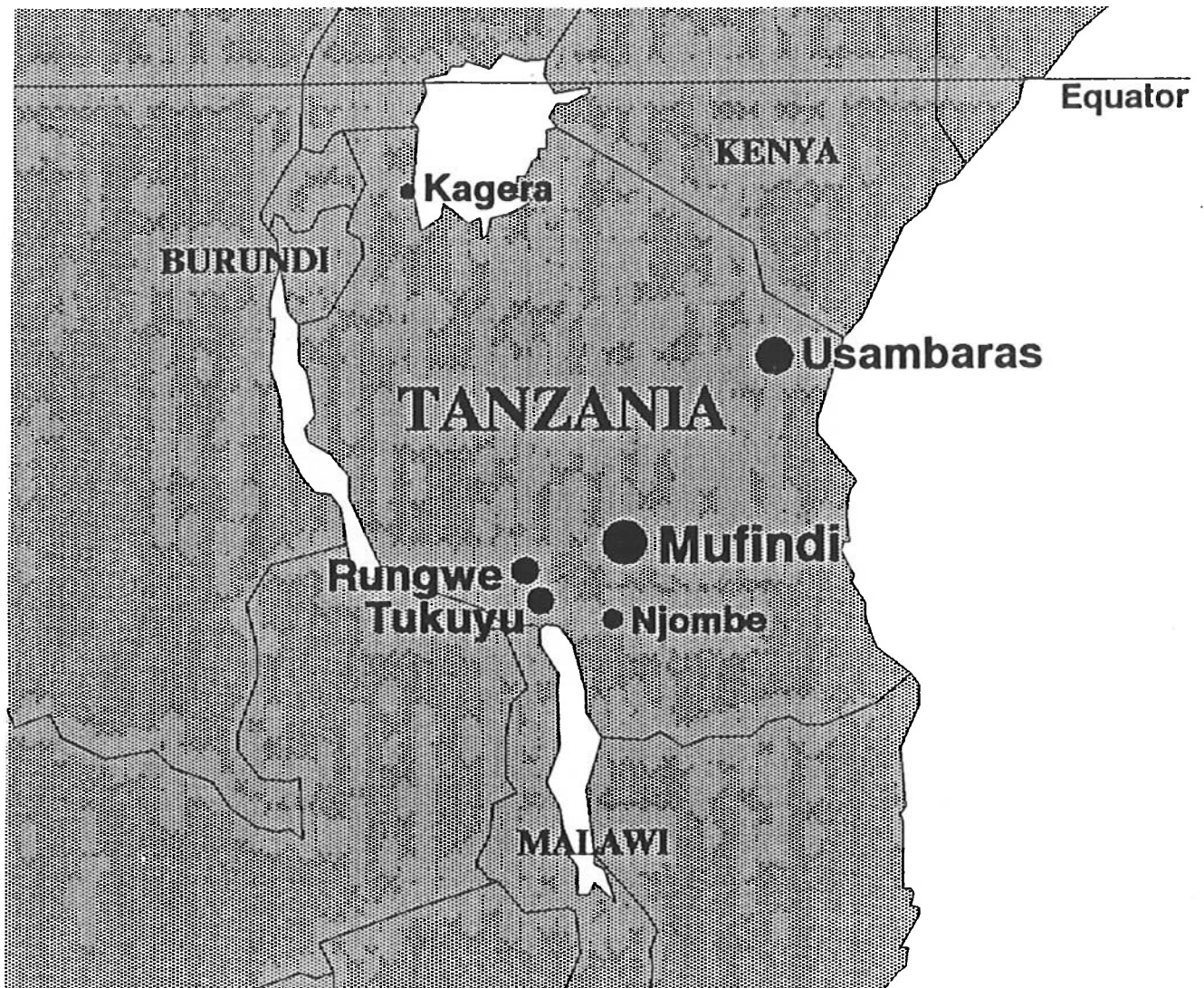


Figure 1.1. Map showing the main tea growing districts of Tanzania.

The climate in the Mufindi district of Southern Tanzania is dominated by the seasonal effects of a single rainy season lasting from November to May, a cool dry season from June to August and a warm dry season from September to the start of the rains during November (Carr and Stephens, 1992). By the end of the dry season the potential soil water deficit below mature tea in this region can exceed 500-600 mm. In the late 1960s Carr (1969; 1974) initiated a series of experiments at Ngwazi in the Mufindi district which showed that irrigation increased yields during the dry season and produced a more even seasonal distribution of crop. On the basis of this work some of the large commercial companies in the area started to irrigate their tea.

Faced with apparently static yields in the mid-1980s Brooke Bond Tanzania Ltd, the largest tea producer in Mufindi, approached Silsoe College to assist in the interpretation of long-term yield data supported with records of irrigation and fertilizer application rates. With the support of the Tanzania Tea Authority and the U.K. Overseas Development Administration this project was extended to investigate the effects of climate on the yield of tea throughout eastern Africa. To provide an experimental basis for this study an irrigation x fertilizer experiment labelled N9 was initiated in 1986 on an established area of clone 6/8 at Ngwazi Tea Research Unit (Plate 1.1). This experiment was managed on-site by Gallus Myinga who was seconded from the Tanzanian Ministry of Agriculture and Livestock Development. The analysis and interpretation of the results was the responsibility of William Stephens, a Research Officer with Silsoe College.

In 1988 a second experiment labelled N10 was initiated by Silsoe College at Ngwazi to determine the irrigation and drought responses of six commercially and scientifically important clones from Kenya, Tanzania and Malawi. The experiment was also designed to allow investigation into those morphological and physiological traits conferring high yield capacity and drought resistance.

In October 1988, subsequent to completing an M.Sc. at Silsoe College, I joined their tea research programme as part of the training component of the ODA Associate Professional Officers Scheme. This training comprised an initial six months at Silsoe College analysing and interpreting data from experiment N9, followed by a posting to Ngwazi from March 1989 to January 1991. At Ngwazi I was responsible for the management and analysis of the work within the unit, with a specific interest in experiment N10. Following my return to Silsoe in February 1991 the data collected from experiment N10 were analysed and interpreted to produce this thesis.



Plate 1.1. Aerial view of Ngwazi Estate during the 1990 dry season showing the lake and the planted tea.

OBJECTIVES

The objectives of the research reported in this thesis are:

1. To quantify the yield responses of six contrasting tea clones to drought in Southern Tanzania.
2. To quantify those attributes of genotype which determine the yield potential and/or drought resistance of six clones.
3. To propose criteria for the selection of high yielding and/or drought resistant clones.

THESIS STRUCTURE

The thesis comprises thirteen chapters which are grouped into four sections. The first comprises this Introduction and the Literature Review. In the Literature Review the major factors affecting tea quality and yield are outlined and a framework is used to review those genotypic traits which determine tea yield.

The second section (Chapters 3 to 5) is concerned with fulfilling objective 1. Chapter 3 describes the design and management of the experiment. In Chapter 4 the drought treatments within the experiment are quantified and the yield responses of the six clones to drought are described in Chapter 5.

The third section (Chapters 6 to 12) consists of an analysis of those genotypic traits which determined the yield responses of the six clones described in Chapter 5. These attributes are examined in terms of dry matter production (Chapters 6 and 7), dry matter partitioning (Chapters 8, 9 and 10) and in terms of plant water status (Chapters 11 and 12).

Dry matter production is related to both light interception (Chapter 6) and transpiration (Chapter 7). Dry matter partitioning is first described in terms of the mass proportioned to leaves, stems and roots (Chapter 8), and secondly in terms of the components of yield. These components are shoot extension and development (Chapter 9) and shoot mass and population density (Chapter 10). The stomatal conductance and xylem water potential of the clones are examined in Chapter 12. However to evaluate the effects of clone on stomatal conductance it was first necessary to evaluate three techniques used for measuring stomatal conductance (Chapter 11). In the final section (Chapter 13) the conclusions of the thesis are synthesized to propose criteria for the selection of high yielding and drought resistant clones. .

CHAPTER 2

LITERATURE REVIEW

In selecting a clone a commercial grower usually aims to choose that genotype which will produce high yields of high quality tea within a specific environment. In this literature review the major factors determining tea quality and yield are outlined. A framework is then used to review those specific genotypic traits which may determine tea yield.

TEA QUALITY

The quality of made tea has traditionally been determined by tea tasters who subjectively assess value in terms of factors such as the brightness, strength, briskness and flavour of the liquor (Odhiambo *et al.*, 1988). In attempting to obtain a more objective determination of quality, Hilton and Ellis (1972) reported that about 60% of the variation in the sale price of a range of teas from Assam and eastern Africa in 1968 could be related to their theaflavin content. In Kenya the composition of volatile flavour compounds (VFCs) within the tea liquor is also thought to be important in determining market value (Owuor *et al.*, 1988).

Although altered by the manufacturing process, the potential quality of tea is determined in the field (Howard, 1978) by the environment, field management practices and genotype. The effects of environment on quality are usually related to the negative correlation between quality and fast shoot growth (Hilton *et al.*, 1973). As a result quality is usually reduced at high temperatures (Hilton *et al.*, 1973; Owuor *et al.*, 1990) and with high nitrogen applications (Hilton *et al.*, 1973; Cloughley, 1983). Tea quality is also reduced when a high proportion of harvested shoots have three or more expanded leaves, because the proportion of theaflavin (Cloughley, 1983) and desirable VFCs (Owuor and Obanda, 1986) decline as shoots unfurl successive leaves. The composition of VFCs (Takeo and Mahanta, 1983; Owuor *et al.*, 1988) and the theaflavin content (Owuor *et al.*, 1986) are also affected by genotype. However recent work in Kenya has shown that the ranking of clones in terms of quality changes with altitude (Owuor *et al.*, 1990). These changes were possibly linked with genotype x environment interactions on shoot extension rates (Obaga *et al.*, 1988).

YIELD

The annual yield of made tea from the best commercial estates in Southern Tanzania have increased from about 300-400 kg ha⁻¹ in the 1950s (Stephens *et al.*, 1988) to over 3,000 kg ha⁻¹ in 1990. In the same region, under experimental conditions an annual yield of over 5,500 kg ha⁻¹ has been achieved from mature fully irrigated clone 6/8 in the fifth year of prune (Burgess, 1990). The highest reported annual yield of made tea in eastern Africa is thought to be 9,800 kg ha⁻¹ from clone S15/10 within a fertilizer experiment in Kenya (Owuor *et al.*, 1987). Tea yield, like quality, is determined by the interaction of the genotype with the environment (ie, the weather and soil) and field management practices.

The effects of weather have recently been reviewed by Carr and Stephens (1992), who related tea yields within eastern Africa to three major variables: air temperature, soil water deficit (SWD), and vapour pressure deficit (VPD). Yields are positively correlated with air temperature up to about 25°C (Squire, 1979; Tanton, 1982a), and tend to be reduced when the SWD exceeds 40 mm (Stephens and Carr, 1989) or the VPD exceeds about 2.3 kPa (Tanton, 1982b; Carr *et al.*, 1987). Within specific regions yields are also affected by hail damage (Stephens *et al.*, 1992), wind (Carr, 1985) and soil temperature (Othieno, 1982a). The soil environment can also affect the growth and yield of tea through its water holding capacity, nutrient status and pH (Green, 1971; Othieno, 1992).

Some of these environmental effects can be removed or moderated by management. For example the effects of SWD can be removed by irrigation (Carr, 1974; Stephens and Carr, 1991a) and the effects of high VPD can be ameliorated by misting (Tanton, 1982b). Soil temperatures can be altered by mulching (Othieno, 1982a) and mean air temperatures which are below 17-18°C can be increased by using wind breaks (Carr, 1985). Yields can also be increased by applying fertilizer to the soil up to a maximum rate of about 300 kg N ha⁻¹ (Owuor *et al.*, 1987; Stephens and Carr, 1991b).

Harvesting and pruning policy also affects yield. Work in Malawi has shown that yields can be raised by increasing the proportion of shoots that are harvested with three expanded leaves (Cloughley *et al.*, 1983). The harvesting policy also determines how fast the plucking surface rises, and therefore how often the bushes need to be pruned. The pruning of bushes is at best a necessary evil and

results in reduced yield (Stephens *et al.*, 1988) until ground cover and shoot population densities are restored.

In addition to all these factors yields are also determined by the genotype. Each year the various tea research institutes in eastern Africa report the results of their clonal field trials. Whilst these trials enable the ranking of clones within a specific environment, because genotypes can respond differently to the environment, the same ranking need not occur elsewhere (Wickramaratne, 1981; arap Rono *et al.*, 1991). Wickramaratne (1981) compared the stability of yield of a range of clones in four regions within Sri Lanka. Although this analysis gave an indication of the yield stability within Sri Lanka, the results cannot be extrapolated to other regions unless the differences in yield can be related to specific environmental variables such as SWD and temperature.

Little work has been completed on quantifying the differences in the yield responses of tea clones to drought. Although Othieno (1978a) reported variations in the yield responses of five clones to drought in Kenya, he related these to the greater soil water deficits in the 'fully irrigated' treatments for two of the clones. This emphasises the need to ensure that drought stress caused by dry soil is minimised in the 'fully irrigated' treatments. In Malawi clones have been compared under irrigated and unirrigated conditions (Nyirenda, 1988). Although there were clonal differences in yield response, these were not fully quantified.

In quantifying a genotype's response to drought Blum (1983) recommends that it is advantageous to separate the yield potential of the genotype under well watered conditions from its sensitivity to drought (ie, drought resistance). Such an approach has been successfully used in a recently reported breeding programme for pearl millet (Fussell *et al.*, 1991).

GENOTYPIC TRAITS DETERMINING YIELD

Although it is possible to measure empirically the yield responses of particular clones to a quantified drought, this does not indicate which genotypic traits resulted in high yields and/or drought resistance. Such traits may be identified from a systematic analysis of the physiological processes which determine yield. Carr and Stephens (1992) proposed the use of a physiological framework for

analysing the effects of climate on the yield of tea. A modified form of this framework is presented in Figure 2.1.

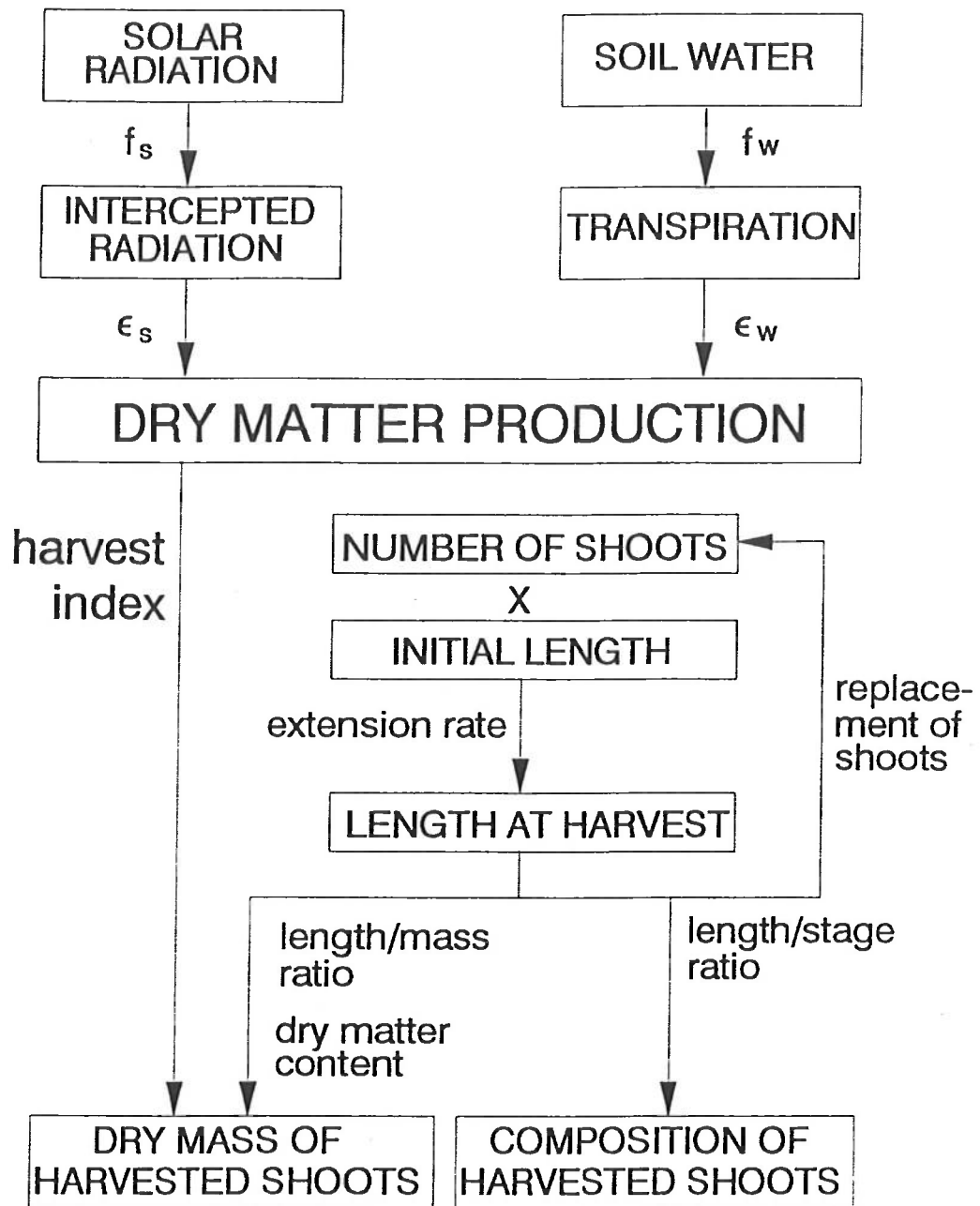


Figure 2.1. Framework for analysing the effects of genotype on the dry mass and composition of harvested shoots.

In many crop production systems, the interception and efficient use of radiation to produce dry matter defines the ultimate potential yield. Therefore the dry matter production (DM; g m⁻²) of tea (Squire, 1985), or any crop, can be determined from the incoming total solar radiation (S; MJ m⁻²), the proportion of radiation intercepted by the canopy (f_s), and the dry matter/light conversion ratio or conversion efficiency (ε_s; g MJ⁻¹) (Equation 2.1).

$$DM = S \cdot f_s \cdot \epsilon_s \quad 2.1$$

Where there is drought limitation, the dry matter produced by a plant can also be related to the efficiency with which it uses the water stored in the soil at the beginning of the dry season (Passioura, 1983). In such systems the production of dry matter can be related to the availability of soil water (AWC; mm m⁻²), the proportion that is transpired (f_w), and the dry matter/transpiration ratio or transpiration efficiency (ε_w; kg mm⁻¹) (Equation 2.2). Where the available water changes due to irrigation or intermittent rainfall it can be easier to analyse the product of AWC and f_w, which is the amount of transpired water (Et; mm m⁻²)

$$DM = AWC \cdot f_w \cdot \epsilon_w \quad 2.2$$

It has been argued that the yield of a tea crop is not primarily limited by the production of dry matter, but by the proportion of the total dry matter which is partitioned to the 'economic yield' of harvested shoots (Tanton, 1979; Squire and Callander, 1981). This proportion is termed the harvest index (HI; %). The partitioning of dry mass to the harvested shoots can also be related to the components of yield. These have been identified as shoot extension rate, the fresh mass and dry matter content of harvested shoots, and the number of shoots per unit area (Tanton, 1979; Stephens and Carr, 1990).

Using the framework in Figure 2.1 possible genotypic traits which may cause differences in yield response and the extent to which they have been quantified for tea are now reviewed.

DRY MATTER PRODUCTION AND LIGHT INTERCEPTION

The annual receipt of total shortwave radiation received at any site is determined by the latitude and the local climate. Within the tea growing regions of eastern Africa the mean annual receipt of total solar radiation varies from about 6500-6700 MJ m⁻² at Mufindi in Southern Tanzania (8°36'S, 35°21'E) and Kericho, Kenya (0°22'S 35°21'E) to 7400 MJ m⁻² y⁻¹ at Mulanje, Malawi (16°05'S, 35°36'E) (Carr and Stephens, 1992). As the annual incidence of solar radiation decreases with increasing latitude (Charles-Edwards, 1982) the lower receipts in Mufindi than Mulanje are probably due to greater cloud cover. Within the year there are also seasonal variations in solar radiation: for example in Mufindi the mean monthly solar radiation increases from about 16 MJ m⁻² d⁻¹ in the wet season to 23 MJ m⁻² d⁻¹ in the dry season (Carr, 1974). Maximum solar radiation levels within East Africa are about 1000 W m⁻² (Squire and Callander, 1981).

Interception of solar radiation

The proportion of solar radiation intercepted by a discontinuous canopy such as young tea is dependent upon the ground cover (GC), the leaf area per unit of area of ground cover (LAI) and the extinction coefficient for light (k) (Equation 2.3) (Jackson and Palmer, 1979)

$$f_s = GC (1 - e^{(-k LAI)}) \quad 2.3$$

At current commercial planting densities of 10,000 to 14,000 plants ha⁻¹, full ground cover is not achieved until at least two years after planting. Until complete ground cover is established those clones with a large bush area usually produce higher yields than clones with less ground cover (Nyirenda, 1987).

Values of the extinction coefficient (k) for crops other than tea range from 0.8 for planophile (flat) leaved canopies to 0.3 for erectophile canopies (Goudriaan and Monteith, 1990). For a given leaf area, clones with horizontal leaves are therefore likely to intercept a greater proportion of light than erect leaved clones (Equation 2.3). However at full ground cover, plants with erect leaves may compensate for this by having a higher LAI. Hadfield (1974) reported that the value of LAI at full ground cover ranged from 4 for 'Assam' type horizontal leaved clones to 8 for the more erect leaved 'China' types.

Conversion efficiency

The potential radiation use efficiency for any crop is determined by the relationship between photosynthesis and light intensity. For tea this is asymptotic, being approximately linear from zero to 300 W m⁻² before reaching a plateau (Squire, 1977) (Table 2.1). Therefore at a typical midday light intensity of about 1000 W m⁻², much of the light intercepted by a single exposed leaf is not effectively used. However because light unused by the upper leaves tends to be reflected into the lower levels of the canopy, the saturation light intensity for the canopy (700 W m⁻²) is greater than that for an individual leaf (Sakai, 1975). This redistribution of light depends upon the canopy architecture, being greatest in clones with erect rather than horizontal leaves. It is probably this better distribution of light that enables clones with erect leaves to maintain a higher LAI at full ground cover than those with horizontal leaves (Hadfield, 1974).

The more even distribution of solar radiation in clones with erect leaves has also been reported to reduce the heat stress on the uppermost leaves (Hadfield, 1974). Whilst this is important at Tocklai, Assam (26°47'N, 94°12'E; altitude 87 m) where maximum air temperatures exceed 28°C for seven months of the year (Barua, 1989), it is unlikely to be influential in areas such as Southern Tanzania where the monthly maximum air temperatures remain below 25°C.

There are substantial variations in the measured maximum gross leaf photosynthetic rates of tea ($P_{\max}$; mg CO₂ m⁻² s⁻¹) as shown in Table 2.1. With the exception of the values of 0.55-0.83 mg CO₂ m⁻² s⁻¹ which were measured on detached leaves in the U.K. (Barua 1953, quoted Barua, 1989), values of $P_{\max}$ for tea have been reported from 0.12 to 0.55 mg CO₂ m⁻² s⁻¹. This range may be caused by differences in measurement technique, VPD (Squire, 1977), temperature, SWD, nutrition (Smith *et al.*, 1991) and leaf age (Sakai, 1975). Whilst it is difficult to compare the values of $P_{\max}$ obtained in different experiments for these reasons, the values for tea appear to be towards the lower end of those recorded for other C₃ species (Table 2.1). Sakai (1975) reported that there were genotypic differences in $P_{\max}$ which were related the 'viability' of the clones. Genotypic differences in leaf photosynthesis have been related to yield in crops like cassava (El-Sharkawy *et al.*, 1990) and therefore important clonal differences in the photosynthetic rate of tea may exist.

Table 2.1. Comparisons of the maximum photosynthetic rates per area of leaf at light saturation for tea and some other C₃ crops.

Crop	Location	Saturation point b	Maximum photosynthetic rate ^a	Source
		(W m ⁻²)	(mg CO ₂ m ⁻² s ⁻¹)	
Tea	Malawi	350-400 300	0.45-0.55 0.20-0.30	Squire (1977) ^{c e} Squire (1977) ^{c e}
	Kenya -		0.12-0.14	Obaga (personal communication)
	Tanzania	480 ^b	0.15	Smith <i>et al.</i> (1991)
	Sri Lanka-		0.23	Roberts and Keys (1978)
	U.K.		0.54-0.83	Barua (1953, quoted Barua, 1989)
Barley	U.K.	500	0.83	Biscoe <i>et al.</i> (1974)
Cassava	Columbia	710 ^b	1.32	El-Sharkawy and Cock (1990)
Cocoa	S. India	190 ^b	0.26	Balasimha <i>et al.</i> (1991)

^a. Conversion: 1 mg CO₂ m⁻² s⁻¹ = 22.7 μmol CO₂ m⁻² s⁻¹ (Pearcy *et al.*, 1989)

^b. Conversion: 1 W m⁻² is approximately equal to 2.1 μmol m⁻² s⁻¹ PPFD.

^c. Wet cool season.

^d. Irrigated tea during dry season.

^e. Although Squire (1977) was unsure whether this was gross or net photosynthesis, it was probably gross photosynthesis (Tanton, 1979).

The actual conversion efficiency for a crop depends upon the sum of total photosynthesis minus respiration losses. Magambo and Cannell (1981) reported that the annual dry matter production including roots of harvested six year old clone 6/8 with full ground cover at high altitude in Kenya was 16.9 t ha⁻¹. Assuming complete interception of the annual total solar radiation receipt of 6700 MJ m⁻² (Stephens *et al.*, 1992) the estimated value of ϵ_s is about 0.25 g MJ⁻¹. This value is substantially lower than those for crops grown under temperate

conditions (1.3-1.6 g MJ⁻¹) and for tropical annual crops (0.6-0.8 g MJ⁻¹), being closest to that reported for natural rain-forest (0.2 g MJ⁻¹) (Table 2.2).

Magambo and Cannell (1981) reported that the total dry matter produced by tea was reduced by harvesting the shoots. They related this to the removal of sinks for photosynthates. However, whilst the ground cover in the harvested tea was the same as unharvested tea, they did not report that the process of harvesting would have altered the bush architecture and distribution of radiation. This could also have decreased photosynthesis. Further work is needed to determine whether the low ϵ_s established for tea in Kenya occurs elsewhere.

Table 2.2. Comparisons of dry matter production per unit of intercepted total shortwave radiation (ϵ_s) for tea, some other crops and natural vegetation fully supplied with water. Those measurements known to include roots are marked with an ^a.

Species	Location	ϵ_s (g MJ ⁻¹)	Source
Tea (harvested) (unharvested)	Kenya	0.25 ^a 0.39 ^a	Magambo & Cannell (1981)
Field crops	U.K.	1.40 ^a	Monteith (1977)
Willow	U.K.	1.58 ^a	Cannell <i>et al.</i> (1987)
Groundnut	U.K.	1.32 ^a	University of Nottingham (1987)
Groundnut	India	0.74 ^a	Azam Ali <i>et al.</i> (1989)
Chickpea	India	0.67	Singh and Sri Rama (1989)
Rain-forest	Amazon	0.20 ^a	Saldarriaga and Luxmoore (1991)

The low value of ϵ_s for tea in comparison to annual crops may also be caused by the high respiration losses from the non-photosynthetic roots and stems. It has been estimated that between 63 and 85% of the total dry matter produced by photosynthesis in tea is respired (Hadfield, 1974; Tanton, 1979; Barua, 1989). A reduction in these losses may offer one way of increasing the yield potential.

DRY MATTER PRODUCTION AND TRANSPIRATION

Transpiration

The potential transpiration from tea, or any crop, depends upon the energy available for evaporation and the VPD between the crop and the surrounding atmosphere. In East Africa the transpiration rate of well watered tea has traditionally been estimated from open water evaporation rates multiplied by a crop factor of 0.8 to 0.9 (Squire and Callander, 1981). More recently equations have been developed which allow the potential transpiration from a crop to be calculated directly from readily available meteorological data and estimates of aerodynamic and canopy resistance (Smith, 1991b). The canopy resistance is dependent upon the total area of leaves and the leaf conductances (Allen *et al.*, 1989). Dagg (1970) showed that the transpiration from a tea bush occurred in direct proportion to the ground cover. Therefore clonal attributes which increase ground cover should also increase transpiration. Leaf conductances of water vapour are determined from the sum of the cuticular and stomatal conductances. Because the conductance of a tea leaf cuticle is low (8-16 mmol m⁻² s⁻¹; Nagarajah, 1979), the diffusion of water vapour out of the leaf is primarily determined, as in most crops, by the stomata.

Stomatal conductance in well watered tea

There are substantial variations in the reported values and the diurnal changes of stomatal conductance determined using transient porometers (Table 2.3). Values for mature clone SFS204 during the wet season in Malawi closely followed solar radiation levels with midday maxima (Squire, 1978). By contrast the stomatal conductance of well-watered clonal 'Assam' type tea in Kenya was highest in the morning and then declined during the day (Callander and Woodhead, 1981). This diurnal change corresponded to simultaneous micro-meteorological determined estimates of canopy conductance which responded to both radiation and VPD. Similar morning peaks between 08.00 and 09.00 h followed by a steady decline during the day have also been reported for potted tea plants grown in greenhouses in Sri Lanka (Sandanam *et al.*, 1981; Nagarajah, 1981).

Table 2.3. Stomatal conductances of mature leaves of tea measured using transient porometers.

Source	Location and altitude	Type of clone	Soil water status	Time (h)	Stomatal conductance ^a	
					(mm s ⁻²)	(mmol m ⁻² s ⁻¹)
Squire (1978)	Malawi (630 m)	mature clone SFS204	wet	06.00	10 - 20	39-78
			wet	12.00	40 - 60	154-232
			dry	12.00	20 - 40	78-156
Callander and Wood-head (1981)	Kenya (2150 m)	'Assam' type clone	wet	09.00	60	198
			wet	12.00	24	77
Sandanam <i>et al.</i> (1981)	Sri Lanka (1200 m)	three potted clones	wet	07.00	7 - 10 ^b	23- 35
			wet	09.00	20 -50 ^b	70 - 175
			wet	12.00	10 - 20 ^b	35 - 70
			dry	12.00	2 - 5 ^b	9 - 18
Nagarajah (1981)	Sri Lanka (1200 m)	potted clone	wet	06.00	4 - 8	14 - 29
			wet	08.00	33	121
			wet	12.00	13	48

^a: Conversion of conductances to mmol m⁻² s⁻¹ based on temperature of 20°C (or 25°C if marked with a ^b), and the mean atmospheric pressure for the altitude of the site (Doorenbos, 1976).

Using the infiltration score technique on well watered tea during the dry season Carr (1971a) in Tanzania, and Othieno (1978b) during the dry season in Kenya, also reported widest stomatal opening in the early morning followed by closure towards midday. However in contrast to the porometry measurements, the infiltration score readings indicated distinct stomatal opening in the afternoon. These inconsistencies in reported stomatal behaviour could be a result of differences between the clones, the environment, or the measurement procedure. Before any conclusions can be drawn it is obviously necessary to evaluate and compare the measurement techniques.

Clonal differences in the mean day-time stomatal conductance (g_s ; mm s^{-1}) of well watered tea plants have been reported by Squire (1976) and Sandanam *et al.* (1981). These are probably the result of either differences in stomatal density (n_s ; mm^{-2}), diameter (d_s ; mm) or depth (h_s ; mm) (Monteith and Unsworth, 1990; Equation 2.4). The value of D_w , the diffusion coefficient of water vapour in air ($\text{mm}^2 \text{s}^{-1}$) is increased at high air temperatures and low atmospheric pressures (Parkinson, 1985), but within a given location it should be relatively stable.

$$g_s = \frac{n_s \pi d_s^2 D_w}{4 (h_s + \pi d_s/8)} \quad 2.4$$

Stomata are only present on the abaxial side of the tea leaf, typically at a density of between 150 and 300 mm^{-2} (Fordham, 1971; Squire, 1976; Nagarajah, 1981). Sandanam *et al.* (1981) reported that there were clonal differences in stomatal density, ranging from 158-293 stomata mm^{-2} for one clone to 210-420 stomata mm^{-2} for another. Stomatal density also varies with leaf age, with Sandanam *et al.* (1981) reporting that it decreased as a leaf grew, whilst Saikia and Dey (1987) found that it was highest in older leaves.

The mean length of a tea stoma is about 10 μm with an estimated depth of 20 μm (Squire, 1978). Clonal differences in the area of the stomatal guard cells from 230 to 323 μm^2 were reported by Sandanam *et al.* (1981), and from 1,110 to 1,340 μm^2 by Mazumder and Bezbaruah (1978). The area of the stomatal guard cells is generally larger in old than young leaves and this moderates the effects of changes in density with leaf age on stomatal conductance (Sandanam *et al.*, 1981).

Stomatal conductance and available soil water

Stomatal closure occurs when tea is subjected to soil drought stress (Carr, 1971b; Squire, 1978), and this has been related to concurrent changes in the xylem water potential (ψ_x ; MPa) (Carr, 1977b). However there is also increasing evidence, reviewed by Turner (1991), that stomatal conductance can be reduced by dry soil independently of ψ_x due to changes in the balance of phytohormones produced by the roots. The effects of available soil water and ψ_x on stomatal conductances are now considered in more detail.

High stomatal conductances can be maintained during a dry season by ensuring there is readily available water within the rooting depth of the crop. This can be

provided by irrigation, but the available water content can also be increased by selecting clones with roots which spread deep and proliferate evenly through the soil. The greater drought resistance of mature tea compared to newly established tea is at least partly due to the greater spread and depth of the roots, which can sometimes extend to below 5.5 m (Stephens and Carr, 1991a). Clonal differences in the proportion of roots below a depth of 0.3 m in one to two year old tea were reported by Cannell *et al.* (1990) and clone SFS204, which is known to be drought susceptible, was particularly shallow rooting. Both Nyirenda (1987; 1990) and Nagarajah and Ratnasuriya (1981) have identified a deep root system as an important clonal characteristic for drought resistance.

Stomatal conductance and xylem water potential

The relationships between stomatal conductance and ψ_x are less well defined than those between stomatal conductance and soil water status. During the wet and cool seasons in Malawi, afternoon values of ψ_x in the highest yielding of five clones (clone SFS42) were approximately 0.2-0.4 MPa below those of the lowest yielding (Squire, 1976). Because the leaf area of these clones were similar the lower values of ψ_x in SFS42 were expected to be the result of a high stomatal conductance, but in fact this clone had the lowest conductance. Squire (1976) suggested that the lower values of ψ_x in clone SFS42 were therefore due to lower leaf osmotic potentials drawing water from the xylem, and proposed that a low ψ_x was related to high productivity.

Although Squire (1976) related low values of ψ_x to high yield during the wet season, during the dry season in Kenya both Carr (1977b) and Othieno (1978b) found that the afternoon values of ψ_x were lowest in the most drought susceptible clones, assessed by visual observation and reputation (Othieno, 1972). Carr (1977b) proposed that drought resistance could be related to the slope of the line relating the ψ_x of individual cultivars to an environmental mean. Those clones with a shallow slope were drought resistant. This technique successfully ranked three clones and using the same procedure Renard *et al.* (1979) were able to successfully classify the drought resistance of twenty four clones in Burundi.

Othieno (1978b) related the lower values of ψ_x in the drought susceptible clones in his experiment to wide open stomata. Sandanam *et al.* (1981) also reported that for three clones grown in pots of dry soil, the most drought susceptible clone had the highest stomatal conductance. However in contrast with these results, Carr (1977a; 1977b) found that at high SWDs stomata tended to be more closed in drought susceptible than drought resistant clones. Based on his findings, Carr

(1977b) proposed that the relative drought resistance of the selected clones could correspond to the value of the slope relating the individual infiltration scores to an environmental mean. He also examined the value of the slope of the infiltration scores against the values of ψ_x for each clone. However both of these techniques were less successful in determining drought resistance than the technique using ψ_x alone.

Transpiration efficiency

For a range of crops under conditions of drought stress de Wit (1958) showed that there were linear relationships between dry matter production and transpiration. The physiological basis for the relationship at a leaf level is that the stomata which can determine the rate of diffusion of water vapour out of the leaf can also control the rate of diffusion of CO₂ into the leaf (Bierhuizen and Slatyer, 1965). At a whole plant level this ratio also tends to remain stable because factors such as high temperatures, solar radiation and leaf area, which increase transpiration, also tend to increase photosynthesis.

No measurements of ϵ_w have been reported for tea, but the transpiration ratio for yield (yield/transpiration; kg ha⁻¹ mm⁻¹) of a mature stand of clone 6/8 in Southern Tanzania was reduced by nutrient and drought stress, and was lower in the cool than the warm season (Stephens and Carr, 1991b). It was not possible to determine from this experiment whether these reductions were primarily a result of reduced values of ϵ_w , or a lower harvest index.

DRY MATTER PARTITIONING AND THE COMPONENTS OF YIELD

Harvest index

The assimilates produced by photosynthetically active leaves can be relocated within the plant and used for leaf, stem or root growth and development. It has been argued that it is the proportion of dry matter partitioned to harvested shoots that is the major factor determining low yields (Tanton, 1979; Squire and Callander, 1981). Certainly the harvest index of tea (7-16%) is lower than that for cereals and soyabean (33-50%) (Table 2.4).

Murty and Sharma (1986) comparing two clones, between one and four years old, found that the harvest index of the lowest yielding was 6.9% compared with 16.0% for the highest yielding. The annual dry matter production at 8.7-10.4 t ha⁻¹ were similar, so the clonal difference in harvest index resulted in an increase in annual yield of made tea from 0.6 to 1.7 t ha⁻¹.

Table 2.4. Comparisons of the total dry matter production, yield, and harvest index of tea with some other crops.

Crop	Location	Age (years)	Dry matter production (t ha ⁻¹ y ⁻¹)	Dry mass of yield (t ha ⁻¹ y ⁻¹)	Harvest Index (%)	Source
Tea	Kenya	1-4	7.6-12.0	0.8-1.4	8.1-13.7	Othieno (1982b) ^a
	Kenya	6	16.9	1.4	8.3	Magambo & Cannell (1981)
	Assam	1-10	12.5-29.3	1.3-3.1	8.9-12.0	Barua (1989) ^b
	Assam		10.0-14.0	1.2-1.8	12.0-13.0	Hadfield (1974)
	S. India	1-5	8.7-10.4	0.6-1.7	6.9-16.0	Murty and Sharma (1986) ^c
Barley					33-42	Wahbi & Gregory (1989)
Soyabean					50	Huck <i>et al.</i> (1986)
Oil palm			29.0	5.0	17	Corley <i>et al.</i> (1971)
Rubber			26.0	2.0	8	Shorrocks (1965) quoted Corley (1983)

^a: range of five clones

^b: range of six clones

^c: range of two clones

Components of yield

The factors determining partitioning can also be examined from an analysis of the components of yield: shoot extension rates, the fresh mass and dry matter content of harvested shoots and shoot numbers.

Shoot extension

Most shoots originate from axillary buds where extension is initially inhibited by the apical dominance of a terminal bud. When the terminal bud is removed the axillary bud starts to expand and the gradual expansion of cells behind the growing point results in the unfurling of successive leaves. The first two leaves are usually deciduous cataphylls or bud scales which fall away (Bond, 1945). These are followed by a small and usually unserrated 'fish' leaf and then a series of 'flush' leaves until the growing point becomes dormant.

The length of a shoot between the release of apical dominance and the time when it becomes dormant was first mathematically described using a logistic equation (Bond, 1945). During the central part of this growth curve the extension rate is approximately constant (Squire, 1979; Stephens and Carr, 1990). However if shoot length is described from the release of apical dominance to the unfurling of three leaves then an exponential model is more appropriate (Tanton, 1979). If a description of shoot length is required beyond this time then a Gompertz (Smith *et al.*, 1990) or logistic curve (Bond, 1945) is usually needed.

Table 2.5. Comparisons of the estimated base temperatures for shoot extension (T_{be}) and thermal extension rates (ρ_e) for a range of clones.

Clone	T_{be} (°C)	Thermal extension rate ρ_e (mm mm ⁻¹ d ⁻¹ °C)		Source
SFS204	12.8	-	0.0090	Tanton (1982a)
SFS150	10.4	-	0.0091	Cannell <i>et al.</i> (1990)
K35	14.8	-	0.0130	
6/8	14.9	-	0.0121	
1	12.8-14.5	0.76-1.01	-	Stephens and Carr (1990)
28	11.1	0.89	-	
36	10.8	0.55	-	

Using these models a mean extension rate (mm d^{-1}) or relative extension rate (RER; $\text{mm mm}^{-1} \text{d}^{-1}$) can be calculated to describe clonal differences in shoot extension. By determining the linear relationship between these rates and the air temperature, it is usually possible to define a base temperature for extension (T_{be} ; $^{\circ}\text{C}$) and a thermal extension response (ρ_e ; $\text{mm d}^{-1} \text{ }^{\circ}\text{C}^{-1}$ or $\text{mm mm}^{-1} \text{d}^{-1} \text{ }^{\circ}\text{C}^{-1}$) (Obaga and Squire, 1992). Tanton (1982a) reported that clone SFS204 in Malawi had a value for T_{be} of 12.8°C and a thermal extension rate of $0.009 \text{ mm mm}^{-1} \text{d}^{-1} \text{ }^{\circ}\text{C}^{-1}$. Since then the values of T_{be} (range: $10\text{--}15^{\circ}\text{C}$) and ρ_e (range: $0.009\text{--}0.0130 \text{ mm mm}^{-1} \text{d}^{-1} \text{ }^{\circ}\text{C}^{-1}$) have been shown to vary with clone (Cannell *et al.*, 1990; Stephens and Carr, 1990) (Table 2.5). In areas where there is a pronounced cool season, such as in Tanzania, selection of clones with a low T_{be} may allow a more even seasonal distribution of yield (Stephens and Carr, 1990)

Fresh mass and composition of harvested shoots

The fresh mass of harvested shoots has been considered as an independent component of yield (Stephens and Carr, 1990). However if shoots are harvested on the basis of length, then it can be advantageous to determine shoot fresh mass from the relationship between shoot fresh mass and length (Palmer-Jones, 1974). Smith *et al.* (1990) reported that the relationship between shoot dry mass and length was exponential and that the constants for this relationship varied with clone.

As stated earlier the composition of harvested shoots is important in determining the quality of tea. It is also possible to relate the length of a shoot to the development stage, defined by the number of expanded leaves. Cannell *et al.* (1990) used a crude conversion of one leaf per 50 mm length for shoots growing during the rainy season in Malawi. If shoots are harvested on the basis of length, then from a knowledge of shoot extension rate and the position of the shoot relative to the plucking surface, the composition of shoots can be simulated for a specified harvesting interval (Cannell *et al.*, 1990). Using a model such as that proposed by Cannell *et al.* progress can be made in determining the differences between clones in the composition of harvested shoots.

Dry matter content

The relationship between the dry and fresh mass of a harvested shoot is expressed as a dry matter content (%). This is often assumed to be a constant 22.5 (TRFK, 1990) or 22.0% (Cloughley 1981), but Cloughley (1981) showed that the mean dry matter content of shoots harvested in Malawi from mid-January to

mid-June varied from 19.8% from one clone to 22.9% for another. The dry matter content can also be increased by low temperatures (Cloughley *et al.*, 1983), drought and poor nutrition (Stephens and Carr, 1992a).

Shoot population density

The number of shoots per bush has been identified in Malawi as an important selection criterion for high yielding clones (Nyirenda and Ridpath, 1984; Nyirenda, 1989). Whilst this variable may be important during establishment, once full ground cover has been established shoot numbers are more easily calculated on a per unit area basis (shoot population density; shoots m⁻²). Clonal differences in annual yield have largely been considered to be due to differences in shoot population density (Squire and Callander, 1981; Stephens and Carr, 1990). Increases in shoot population density, unlike increased shoot extension rates also tend to maintain the final quality of tea (Kayange *et al.*, 1981)

The proportion of shoots that are active is also important, as there is little advantage in increasing shoot density if all the shoots are dormant (Banerjee, 1992b). Since the proportion of active shoots can vary during the year (Stephens and Carr, 1990), it is important that clonal differences in the proportion of active shoots are substantiated over several months.

CONCLUSIONS

The quality and yield of made tea is determined by the interaction of the genotype with the environment and field practice. The evaluation of the same clones at different locations can enable an estimation of the stability of yield between sites, but wider benefit can be derived if changes in ranking can be related to specific environmental variables such as SWD.

Little work has been reported on quantifying clonal differences in the yield responses of tea to drought. In such analyses it can be advantageous to separate the yield of the clone under well watered conditions (ie, the maximum yield) from the response to drought (ie, drought resistance).

Although the maximum yield and drought resistance of specific clones can be quantified, this does not aid the identification of future high yielding and/or drought resistant clones. Using a physiological framework some of the possible genotypic traits conferring high yield and drought resistance can be determined.

Such a framework can comprise two sections: the use of solar radiation and soil water to produce dry matter, and the partitioning of that dry matter to produce yield.

There is evidence that the conversion efficiency of tea is low compared with other crops. Little attempt has been made to quantify the relationship between dry matter production and transpiration. These are two important areas requiring research.

The harvest index of tea is also low compared to many crops. Methods for increasing the harvest index can be investigated by an examination of partitioning to leaves, stems and roots. An alternative method is to analyse the dry mass of the harvested shoots in terms of the components of yield. These components are shoot extension and development, the fresh mass and dry matter content of shoots and the shoot population density.

Although stomatal conductance affects transpiration efficiency, it is an area that requires specific analysis. There are conflicting interpretations of diurnal stomatal behaviour and different understandings about how stomatal conductance and xylem water potential are related to drought resistance. In order to resolve these issues an evaluation of the techniques used to measure stomatal behaviour is required. This will help to elicit the implications of clonal differences in stomatal conductance and xylem water potential on yield.

The use of the framework provides a means of identifying and quantifying in a systematic way those genotypic traits which determine the potential yield and drought resistance for a specified environment. Those traits which are positively correlated with yield may provide future clonal selection criteria. These issues are now explored further during the presentation of the results of the research in the following chapters.

CHAPTER 3

SITE AND METHODOLOGY

In the Literature Review possible mechanisms by which clones respond differently to the environment were identified. These theories were tested in a clone x drought experiment labelled N10 at the Ngwazi Tea Research Unit, Mufindi in Southern Tanzania. This chapter describes the site and climate at Ngwazi and the design and management of the experiment.

SITE AND CLIMATE

Ngwazi Tea Research Unit (8°32'S, 35°10'E, altitude 1840 m) lies about 20 km north-west of the ridge of the Uzungwe escarpment along which is centred the main tea growing region in Southern Tanzania. Annual rainfall at the escarpment edge can exceed 1600 mm, but declines moving north-west so that the annual rainfall at Ngwazi ranges from 800 to 1100 mm with the majority falling between mid-November and May (Stephens *et al.*, 1988). In 1988 there was 16 ha of mature tea at Ngwazi including the fertilizer x irrigation experiment labelled N9 described by Stephens and Carr (1991a). A 500 ha perennial freshwater lake directly to the north-west of this area provided a source of water for irrigation.

Experimental site and soil

In April 1988 a fallow area of one hectare adjacent to the existing area of tea and about 400 m from experiment N9 and 150 m from the lake was identified for experiment N10. This site had a gentle gradient (less than 3%) towards the lake and had previously been used for maize production. Soil samples obtained to a depth of 0.6 m within the site had a pH of 5.1-5.3, which is within the range normally considered optimal for tea (Othieno, 1992). The levels of nitrogen (0.06-0.11%) and exchangeable potassium (0.20-0.44 mmol 100 g⁻¹) were low in comparison to other tea soils in eastern Africa (Othieno, 1992). The depth of the water table determined to one side of the site was below 6 m.

In 1990 the soil profile at a site between experiments N9 and N10 was described to a depth of 5 m. Soil samples were taken between 0.15 and 4.0 m and were

analysed by the Soil Survey and Land Research Centre, U.K. (Appendix A). The soil was classified as a Xanthic ferralsol (FAO-UNESCO, 1988), with the texture of a sandy clay above 0.15 m and of a clay below (Table 3.1). Despite the high proportion of clay the soil was friable. This is explained by the low activity of the clay and the low effective cation exchange capacity ($< 16 \text{ mmol } 100 \text{ g}^{-1}$ of clay).

Table 3.1. Particle size distributions of soil from six depths at Ngwazi Tea Research Unit (analysed by the Soil Survey and Land Research Centre, U.K., 1990).

Particle size	Proportion of total dry mass (%)				
	Sand			Silt	Clay
	600 μm - 2 mm	200- 600 μm	60- 200 μm	2- 60 μm	< 2 μm
Depth (m)					
0-0.15	11	34	15	8	38
0.15-0.7	8	26	12	2	52
0.7 -1.6	2	12	12	4	70
1.6 -2.0	6	6	9	10	69
2.0 -2.6	5	8	11	10	66
2.6 -4.0	5	7	11	23	54

The volumetric water content of the soil at a water potential of -10 kPa, corresponding to field capacity (El-Swaify, 1980), increased with depth from 24.7% in the top 0.15 m to 32.5% at a depth of 1.80 m (Figure 3.1) where the silt and clay content was higher. These are low water contents for clay soils, being more typical of a sandy loam (Campbell and Campbell, 1982).

The available water content held between field capacity (-10 kPa) and permanent wilting point (-1500 kPa) ranged from 110 to 122 mm m⁻¹ in the top 2 m of soil to 93 mm m⁻¹ at 2.70 m. These values are similar to those (80-140 mm m⁻¹, also between soil water potentials of -10 and -1500 kPa) reported for Ngwazi by Carr (1974).

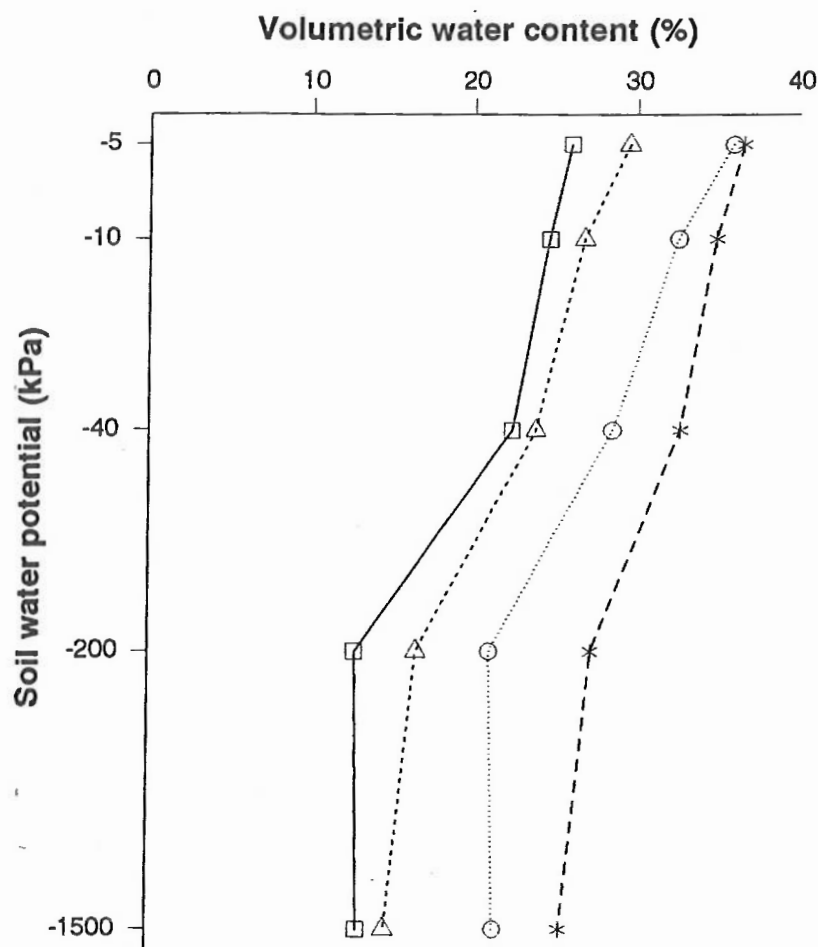


Figure 3.1. Water release curves for soil at Ngwazi Tea Research Unit at four depths: 0.15-0.20 m :—□—, 0.55-0.60 m:---△---, 1.80-1.85 m:○....., 2.70-2.75 m -*- - .

Meteorological measurements

Daily weather data were recorded in an area of well watered short grass about 800 m from experiment N10 and about 50 m from the windward side of the lake. Rainfall was measured using a standard cylindrical 127 mm diameter gauge with a receiving surface about 300 mm above ground level. Daily evaporation (E_{pan} ; mm) was calculated from the change in water level within a sunken 1.8 x 1.8 m British evaporation pan, which was screened with a wire mesh.

Maximum, minimum, dry bulb and wet bulb air temperatures, all within a white Stevenson screen, were recorded at 09.00 h each day. Dry bulb and wet bulb temperatures were also recorded at 15.00 h to calculate the mid-afternoon saturation vapour pressure deficit (VPD; kPa).

Daily measurements of total shortwave solar radiation (300-3000 nm) were recorded using a Gunn Bellani pyranometer, which was calibrated on site against a Kipp pyranometer, loaned from Silsoe Research Institute, Bedford, U.K. Daily wind-run was also measured at 09.00 h with a 2 m high anemometer linked to a trip counter. From 1 June 1989 the wind-run was also recorded at 15.00 h, to allow calculation of the day-time (09.00-15.00 h) wind-speed.

During the two years 1989-1990 the mean annual rainfall at Ngwazi was 982 mm of which over 95% fell between mid-November and the end of April (Figure 3.2; Table 3.2). These values were similar to previous annual rainfalls measured at the same site of 924 mm (1955-65) and 976 mm (1967-70) (Carr, 1974). Monthly means for each individual year are presented in Appendix B. The rains finished in mid-April in 1989 and at the beginning of May in 1990, starting again on 28 November in 1989 and 23 November in 1990.

Table 3.2. Summary of meteorological observations at Ngwazi Tea Research Unit (8°32'S, 35°10'E, altitude 1840 m), 1989 to 1990.

Month	Monthly totals		Monthly means of daily values					
	Rain (mm)	E _{pan} (mm)	Air temperature		Mean (°C)	Solar radiation (MJ m ⁻²)	Wind run (km)	VPD 15.00h (kPa)
			Max (°C)	Min (°C)				
January	201	95	22.2	13.6	17.9	13.9	100	0.69
February	214	92	22.7	13.8	18.3	13.7	122	0.76
March	212	100	22.7	13.6	18.1	16.3	100	0.72
April	112	87	21.8	13.9	17.8	15.6	113	0.74
May	27	74	19.7	12.7	16.2	14.1	137	0.69
June	4	82	19.1	10.3	14.7	16.5	136	0.88
July	2	86	18.6	8.7	13.6	17.0	139	0.93
August	0	93	18.7	10.0	14.4	17.2	153	0.93
September	1	120	21.5	11.0	16.3	20.8	160	1.16
October	0	147	23.4	11.6	17.5	22.7	153	1.48
November	69	124	23.6	12.9	18.2	18.8	143	1.15
December	140	100	23.2	13.5	18.4	15.1	102	0.83
Total	982	1200						
Mean			21.4	12.1	16.8	16.8	130	0.91

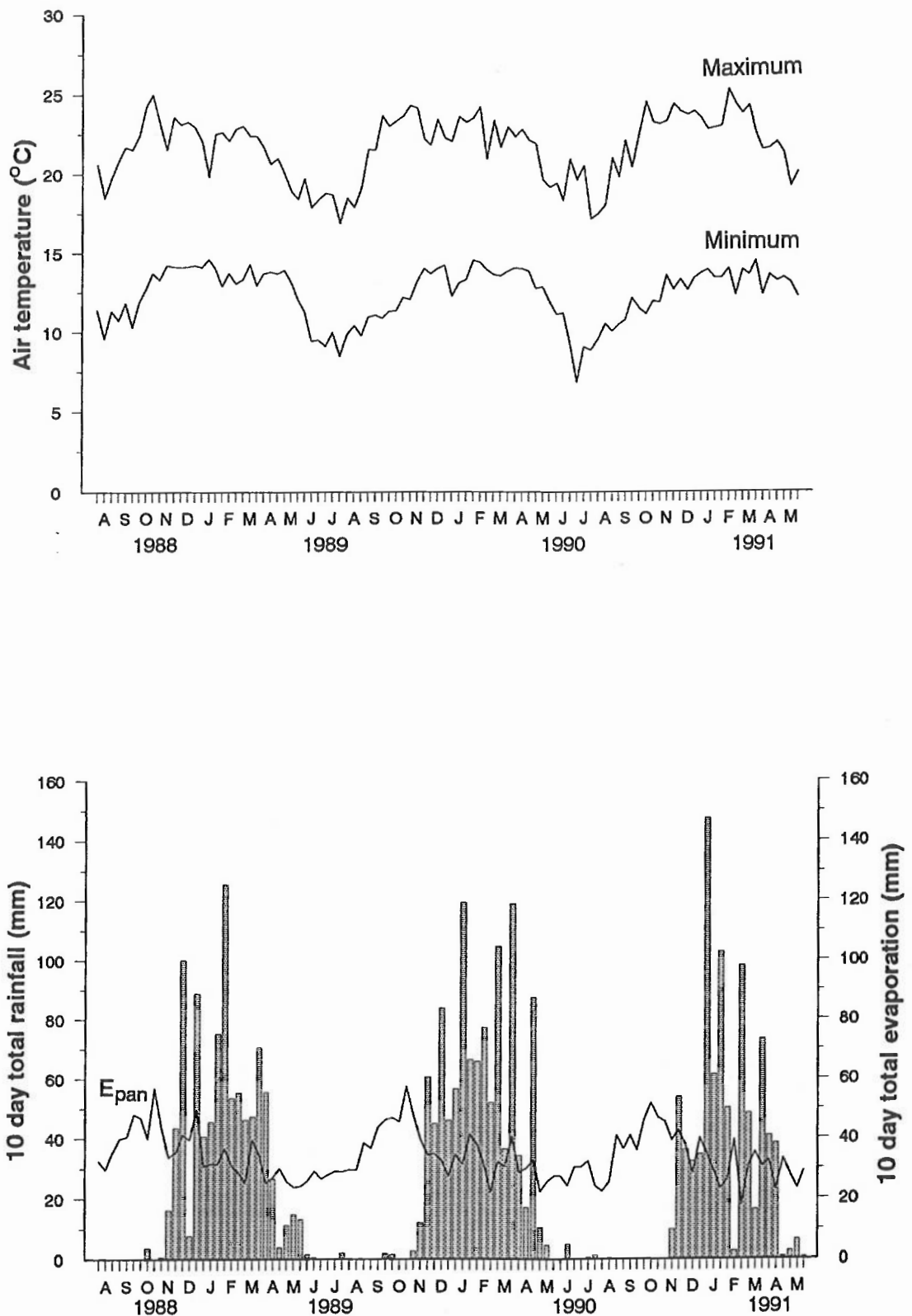


Figure 3.2. Maximum and minimum air temperatures, rainfall and pan evaporation at Ngwazi Tea Research Unit, Mufindi, August 1988 to May 1991.

Maximum temperatures ranged from 21-24°C during the wet season to a low of 18.6°C in July. Minimum temperatures also declined over the same period from 13-14°C to 8.7°C. In some years between June and August it is possible for frost to damage young tea shoots (Stephens and Carr, 1989), but there was no severe frost damage during 1989 or 1990. After July air temperatures rose steadily until the start of the rains.

Mean daily solar radiation averaged 13.7-16.3 MJ m⁻² during the wet season and increased gradually during the dry season to 22.7 MJ m⁻² in October. The daily wind-run also increased from 102-122 km during the wet season to 153-160 km between September and October. These increases in radiation, windspeed and also the steady rise in temperature meant that the mean 15.00 h VPD (1.48 kPa) and daily evaporation rate (4.7 mm d⁻¹) were highest in October.

EXPERIMENTAL DESIGN AND METHODS

Clones

Six clones were chosen on the basis of their commercial and scientific importance in Kenya, Tanzania and Malawi and because they showed contrasting morphological and physiological traits. Those selected were clones 1, 6/8, SFS150, S15/10, 207 and K35 (Table 3.3) (Plate 3.1).

Clone 1 is a small leaved 'China' type clone with dark erect leaves. It has a high base temperature for shoot extension (12.8-14.5°C) (Stephens and Carr, 1990) and is considered drought resistant because it can maintain ground cover when drought stressed (Carr, 1971a). It produces high yields under experimental conditions because it has a large shoot population density (Stephens and Carr, 1990), but the small and fibrous shoots can be difficult to harvest by hand.

Clone 6/8 is a medium-sized leaf clone originally identified in the Nandi Hills region of Kenya (Carr, personal communication) and is now widely grown in Kenya and Tanzania. It is reported to be drought susceptible (Othieno, 1972; 1978a) and has been used to study tea physiology (Magambo and Cannell, 1981; Cannell *et al.*, 1990) and quality (Owuor *et al.*, 1988). In Kenya it is used as a control against which the yield and quality of new clones are compared (Owuor and Njuguna, 1990). The yield, water use and components of yield of this clone

when mature have recently been quantified at Ngwazi (Stephens and Carr, 1991a, 1991b, 1992a, 1992b).

Table 3.3. Leaf type, origin and reported base temperatures for shoot extension (T_{be}) for each of six clones.

Clone	Leaf type	Origin	T_{be} (°C)
1	'China'	Mufindi, Tanzania (8°33'S; 1800-1950 m)	12.8-14.5 (Stephens and Carr, 1990)
6/8	hybrid	Nandi Hills, Kenya (0°S; 1800-2000 m)	14.9 (Cannell <i>et al.</i> , 1990)
			10.0 (Stephens and Carr, 1992a)
SFS150	'Assam'	Mulanje, Malawi (16°5'S; 650 m)	10.4 (Cannell <i>et al.</i> , 1990)
S15/10	'Assam'	Kericho, Kenya (0°22'S; 1800-2200 m)	7.5-11.9 (Obaga and Squire, 1992)
207	'China'	Mufindi, Tanzania (8°33'S; 1800-1950 m)	-
K35	'Assam'	Kericho, Kenya (0°22'S; 1800-2200 m)	14.8 (Cannell <i>et al.</i> , 1990)

Clone SFS150 is a large leaved clone, originally selected by the Tea Research Foundation of Central Africa in Malawi, where it is considered drought resistant and shows quick recovery from pruning (Nyirenda and Grice, 1989). It has a low base temperature for shoot extension (10.4°C) (Cannell *et al.* 1990) and in Malawi it is used as a control to compare the yield of new clones (Nyirenda, personal communication).

Clone S15/10 has large pubescent leaves and was originally selected by the African Highlands Company in Kericho, Kenya. It has achieved an annual yield of made tea of over 9,800 kg under experimental conditions in Kenya (Owuor *et al.*, 1987). It has also been used to determine the effects of nitrogen on quality (Owuor *et al.*, 1991).

**Clone 1****Clone 6/8****Clone SFS150****Clone S15/10****Clone 207****Clone K35**

Plate 3.1. Representative plants of each of six clones in April 1989, eight months after field planting.

Clone 207 is a small leaved 'China' type clone originally selected in Mufindi, Tanzania. It has been widely planted in this region because it establishes easily and gives a high yield.

Clone K35 has large leaves and was originally selected and used by Brooke Bond Kenya Ltd in Kericho. In recent years it has also been planted in Southern Tanzania. Cannell *et al.* (1990) reported that in Malawi it has a high base temperature for shoot extension (14.8°C).

Experimental design

The experimental area was planted in August 1988 using sleeved transplants of the six clones grown in a nursery from single node cuttings. The experiment followed a line-source design (Hanks *et al.*, 1976) consisting of two 24 x 38.4 m blocks either side of a central path (Figure 3.3). Within each block a 24 x 6.4 m plot, running perpendicular to the path, was randomly allocated to each clone. A total of 160 plants was planted at a spacing of 1.2 x 0.8 m in these plots with the outer edge of plants forming a guard row, making an effective treatment area of 21.6 x 4.8 m (108 plants). These clonal plots were then split into six contiguous drought treatment sub-plots (3.6 x 4.8 m with 18 plants), labelled from I_5 (full irrigation) closest to the path to I_0 (rain only) at the extreme sides of the experiment.

Because similar drought treatments were spatially grouped together significant 'drought effects' could be caused by a fertility trend across the experiment. This led Hanks *et al.*, (1980) to conclude that the effects of drought could not be statistically tested with this design. However this is an extreme position provided that the site, as in this case, is selected to avoid a fertility trend symmetrical to the central path. The effects of a possible linear fertility trend across the experiment were removed by an analysis of covariance (Morgan and Carr, 1988).

On the side of the main-experiment nearest the lake, an observation block was planted comprising a 24 x 4 m plot (100 plants) of each clone (Figure 3.3). These plants were treated similarly and received the same drought treatments as those in the main experiment. An 18 to 19 m wide perimeter of clone K35 was planted around the experiment.

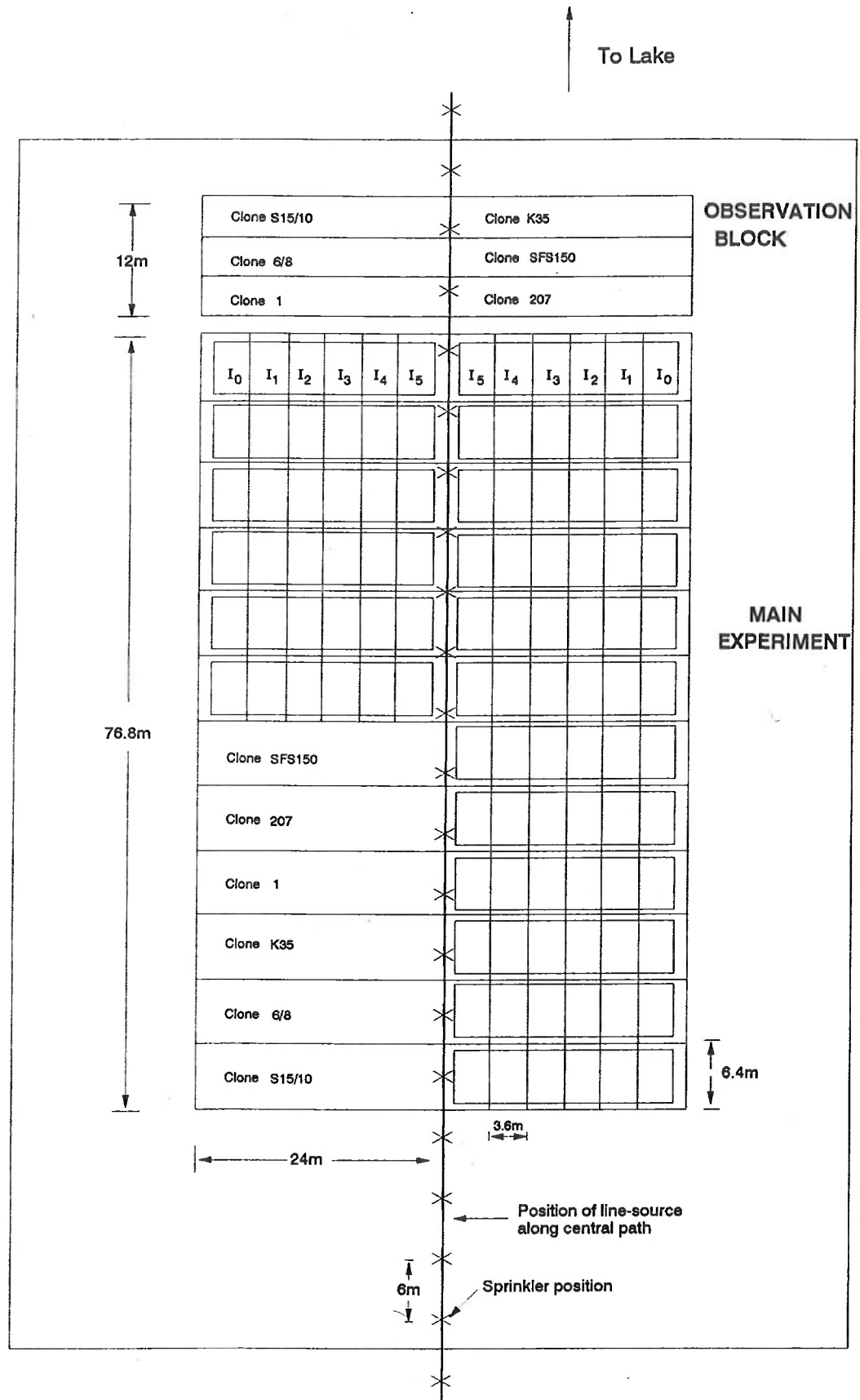


Figure 3.3. Plan of experiment N10.

Irrigation scheduling

Irrigation was scheduled with the aim of preventing yield loss due to high SWD in the fully irrigated (I_5) sub-plots. The critical SWD for the dry season yield of mature clone 6/8 at Ngwazi is between 40 and 100 mm, corresponding to about 12-30% of the extractable water (330 mm) over a 5.5 m rooting zone (Stephens and Carr, 1990). In August 1989 the rooting depth of the tea in experiment N10 was about 0.6 m, suggesting an AWC of about 72 mm and a critical deficit of 9-22 mm. In practice a compromise between choosing a low deficit and the need to share the irrigation equipment, meant that in 1989 irrigation was scheduled to bring the I_5 treatment sub-plots to field capacity whenever the SWD reached about 35 mm. The yield results collected in early 1990 (cf Chapter 5) suggested that this level of drought did not reduce yields. In the following dry season beginning in April 1990 the rooting depth had increased to about 1.2 m and irrigation was scheduled when the SWD in the I_5 sub-plots reached about 45 mm.

The SWD in the I_5 sub-plots was calculated daily using a simple soil water balance (Equation 3.1):

$$SWD_i = SWD_{i-1} - R_i - I_i + D_i + ET_i \quad 3.1$$

where R_i is the rainfall, I_i is the irrigation, D_i is the drainage and ET_i is the crop evapotranspiration all recorded on the i th day and measured in mm. The value of I_i on each date of irrigation was recorded in 48 catch cans spaced systematically across the experiment. Any irrigation or rainfall received when the soil was at field capacity, ie, $SWD = 0$, was assumed to drain instantly through the profile. Any likely movement of surface water between treatments was prevented by micro-catchments dug between the bushes.

The value of ET_i was estimated from the daily evaporation pan measurements (E_{pan} ; mm) multiplied by a crop factor K_c . The value of E_{pan} measured at Ngwazi gives a good estimate of the water loss from a mature stand of clone 6/8 with complete ground cover at the same site (Stephens and Carr, 1990a; 1990b). Until the end of the dry season in the year of planting (August to November 1988) and from April to August 1989, the value of K_c was assumed to be 1. Whilst this overestimated the value of ET_i , it ensured that the soil was always returned to field capacity at each irrigation.

Following an analysis of soil water measurements taken with the neutron probe between April and August 1989 (cf Chapter 4), the approach for calculating the SWD was refined by considering soil evaporation and transpiration separately. Losses due to transpiration were assumed to be in direct proportion to the ground cover, and on the day of irrigation K_c was assumed to equal 1 due to soil evaporation losses (Dagg, 1970). To account for the continued soil evaporation during the week immediately following irrigation (Ritchie, 1972), the value of K_c was steadily reduced over seven days from 1 to a value based on ground cover (Table 3.4). The largest ground cover within any individual sub-plot in October 1989 was 36%, so the minimum value of K_c was fixed at 0.4. In 1989 this empirical model was used for estimating the SWD from mid-August to the end of the dry season in November.

In 1990 the highest ground cover within a fully irrigated sub-plot ranged from 63% in April to 80% in November. To ensure that the water loss from these sub-plots was not underestimated K_c was assumed to equal 1 throughout the dry season.

Table 3.4. Crop factors (K_c) used to calculate the crop evaporation from August to November 1989.

Days from irrigation	0	1	2	3	4	5	6	7	8	9
K_c	1.0	1.0	1.0	0.8	0.8	0.6	0.6	0.4	0.4	0.4

Drought/irrigation treatments

Because young tea is particularly sensitive to drought, the experiment and the surrounding area of clone K35 were uniformly irrigated during the dry season from August 1988 immediately after planting, from the beginning of the dry season in April until 8 October in 1989, and from May until 26 July in 1990. This was to ensure that sufficient plants survived to maintain the long term viability of the experiment. The irrigation water was applied from twenty Wright Rain Lancer sprinklers, with 13/64" (5.1 mm) and 1/8" (3.2 mm) spreader nozzles, spaced at 19.2 x 18.0 m with the laterals laid perpendicular to the central path

(Plate 3.2). To uniformly irrigate the complete area required three movements of the laterals.

Differential drought treatments were imposed for the first time between 9 October and 27 November in 1989 using a line-source arrangement of twenty two Bauer B90Z sprinklers, with 7 mm range and 3.5 mm spreader nozzles, spaced at 6 m intervals along the central path. Equal water pressures (± 35 kPa) at each sprinkler along the line-source were achieved by pumping the water first to the highest end. This arrangement provided uniform application rates parallel to the line-source, but in a perpendicular direction water application declined symmetrically from a maximum in the I_5 sub-plots to zero in the I_0 sub-plots at a distance of 18 m from the lateral (Figure 3.4a). Although the distribution was symmetrical the depths of irrigation water applied to the two drought treatments (I_4 and I_5) nearest the lateral were similar. The differentiation between these treatments was increased in 1990 (Figure 3.4b) by alternating at each irrigation the twenty two Bauer sprinklers with twenty two Wright Rain Lancer sprinklers.

In 1990 drought treatments were imposed on 27 July and continued until 18 November. Because of the severe symptoms of drought stress shown by clone 207 the experiment was uniformly irrigated on 19 November, before the start of the rains. The mean depths of irrigation water applied to each drought treatment in 1989 and 1990 are presented in Table 3.5.

Table 3.5. Mean depths of rainfall, the sprinkler arrangement and mean depths of irrigation water applied to drought treatments between 1 June and 30 November in 1989 and 1990.

	Rainfall (mm)	Sprinkler arrangement	Irrigation (mm)					
			Drought treatment					
			I_5	I_4	I_3	I_2	I_1	I_0
1989								
1 Jun-8 Oct	7	Uniform	357	357	357	357	357	357
9 Oct-27 Nov	14	Line-source	143	140	99	33	3	0
28-30 Nov	60	Uniform	0	0	0	0	0	0
1990								
1 Jun-26 Jul	6	Uniform	175	175	175	175	175	175
27 Jul-18 Nov	11	Line-source	481	404	356	70	9	0
19-30 Nov	54	Uniform	67	58	62	57	56	64

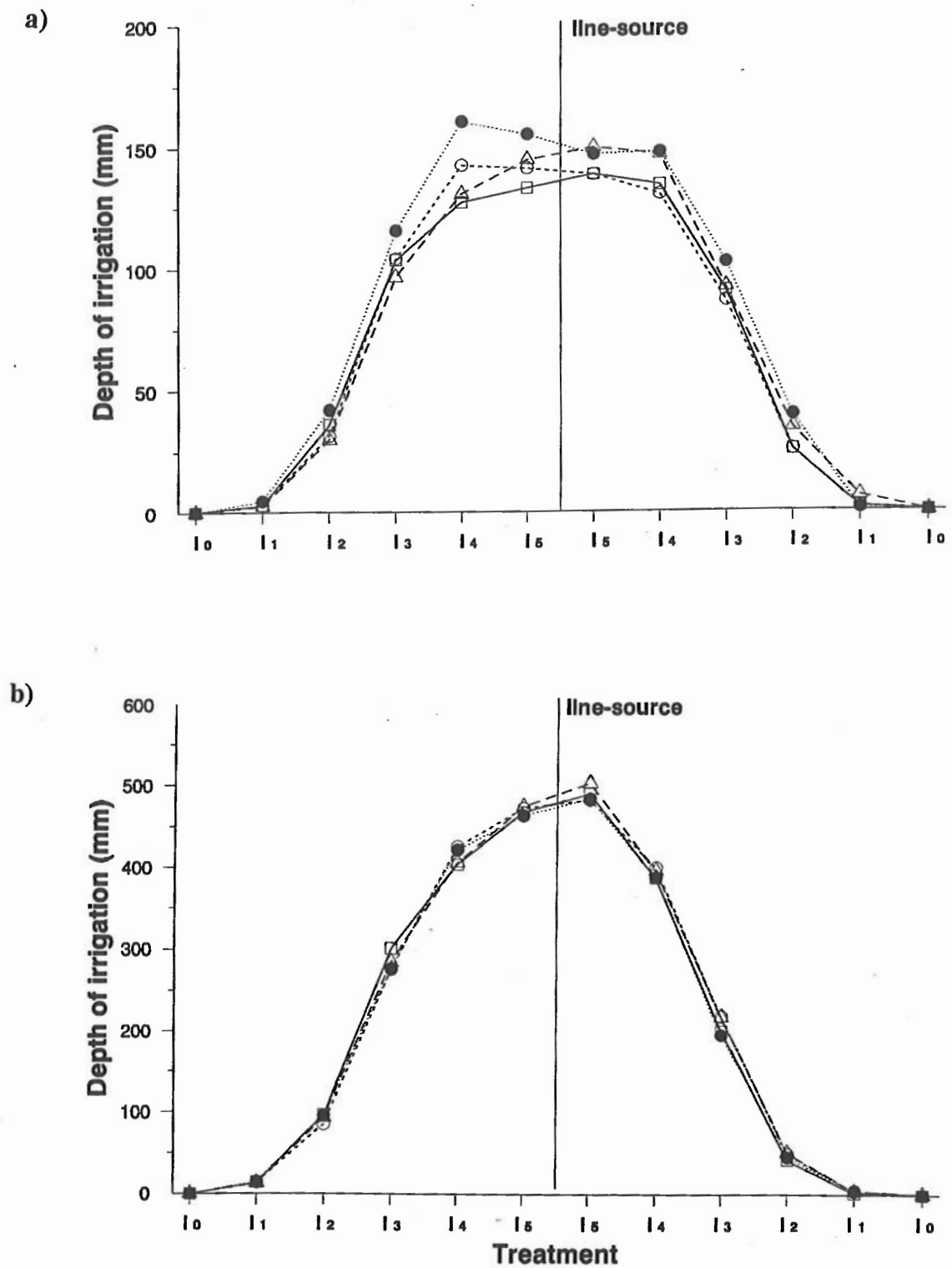


Figure 3.4. Distribution and depths of irrigation water applied either side of the line-source during the imposition of differential drought treatments in a) 1989 and b) 1990.



Plate 3.2. View across experiment N10 showing uniform irrigation in May 1989, nine months after field planting.



Plate 3.3. View across experiment N10 in December 1990, twenty eight months after field planting. The line-source is being used to irrigate an area of new tea planted adjacent to the far side of the experiment.

Crop management

The experiment was mulched with Napier grass (*Pennisetum purpureum*) at planting in August 1988 and in April 1989, and with Guatemala grass (*Tripsacum laxum*) in October 1990. The principal aim of laying these mulches was to reduce soil evaporation (Othieno, 1980). These mulches should also have improved the nutrient status of the top soil (Othieno, 1978c).

The fertilizer policy broadly followed that recommended for newly planted tea by the Tea Research Foundation of Kenya (TRFK, 1986). An ammonium sulphate, triple superphosphate and potassium sulphate mixture was applied at the rate of 3.2 g N plant⁻¹ (33 kg N ha⁻¹) at planting in August 1988, followed by 2.1 g N plant⁻¹ (22 kg N ha⁻¹) of ammonium sulphate in November. After these initial applications, which included sulphur, all the fertilizer used comprised N:P:K in a 2:1:1 ratio. Because it was easy for nitrogen to be leached out of the shallow rooting zone in the first year after planting, fertilizer was applied in regular but small quantities with third and fourth applications in January (21 N kg ha⁻¹) and April 1989 (31 kg N ha⁻¹). In the second year after planting (August 1989 to 1990) a total of 135 kg N ha⁻¹ was applied in three applications at the end of September, December and March. In the third year (August 1990 to August 1991) 200 kg N ha⁻¹ was applied in two equal applications in August prior to the first peak in yield from the irrigated treatments, and in December prior to the second peak. In the unirrigated (I₀) sub-plots all the fertilizer was applied in December after the start of rains.

The experiment was kept free of weeds by regular hand weeding and selective application of herbicides. A two metre high windbreak of Napier grass (Plate 3.2) was constructed in 1988 across the centre and both ends of the experimental area perpendicular to the line-source to reduce wind damage during the cool season. The central windbreak was removed in July 1989 prior to the start of differential irrigation.

Because of the natural upright growth habit of the tea bush, branches need to be trained to grow laterally to achieve full ground cover quickly at current commercial plant spacings. In Southern Tanzania this is usually achieved by cutting back all the branches above a certain height to promote the growth of new wider spreading shoots. However this process not only reduces light interception in the short term but can cause weaker root development (Carr, 1976). In order to bring the tea into production as early as possible the plants were 'pegged' by bending branches growing from the base of the plant outwards

and securing them into position with wooden pegs. This began in April 1989, eight months after field planting, and continued as needed until October in that year.

Shoots and branches above a height of 0.45 m from the ground were removed or 'tipped' on 7 November 1989 to produce a level plucking surface. The first shoots for manufacture were harvested on 4 December, sixteen months after planting. At subsequent thirteen to fifteen day intervals extending up to twenty four days during the cool season, all the shoots above the plucking surface with at least two expanded leaves were harvested by hand. The mass of these shoots and other measurements taken within the experiment are reported in the succeeding chapters.

CHAPTER 4

SOIL WATER DEFICITS

INTRODUCTION

The amount of irrigation water applied to the different treatments in the clone x drought experiment were described in Chapter 3. However it is often advantageous to describe crop responses, not to the irrigation water applied, but to a soil water deficit (SWD). The actual SWD below mature tea has been measured by gravimetric sampling (Willatt, 1971) and with a neutron probe (Stephens and Carr, 1991b). However such techniques are either time-consuming or require specialised equipment. The actual SWD can also be estimated by keeping a daily soil water balance (Stephens and Carr, 1991b). The SWD on the i th day can be related to the value of the existing SWD and subsequent rainfall (R), irrigation (I), drainage (D) and crop evaporation (ET) (cf Equation 3.1). When analysing the SWD in crops with incomplete ground cover it is advantageous to separate ET into losses from transpiration (E_t) and soil evaporation (E_s) (Equation 4.1).

$$SWD_i = SWD_{i-1} - R_i - I_i + E_{t_i} + E_{s_i} + D_i \quad 4.1$$

By separately determining each component of Equation 4.1 it is possible to estimate the SWD, the total water use of the crop and more specifically the transpiration. As reviewed in Chapter 2, the dry matter production of a crop can be related to the transpiration (Passioura, 1983). The components of Equation 4.1 are now considered in turn.

The SWD within a soil water balance model is often fixed at zero immediately after an irrigation event which saturated the soil (Jensen, 1972). However if the soil water content was measured at this time, there would be substantial variation because of differences in the amount of water draining through the profile. A more stable measure can be obtained by measuring the soil water content two to three days after irrigation and adding back the estimated water lost through evaporation and transpiration. The resulting water content has been termed the upper limit of available water (ULAW) (Wilcox, 1962). In a sandy free draining soil this estimate of soil water content is likely to be similar to field capacity. This is the water content of a soil where evaporation and

transpiration is prevented and drainage has materially ceased (Veihmeyer and Hendrickson, 1931).

Potential transpiration rates for mature tea in East Africa have been related to the McCulloch (1965) version of Penman's (1948) formula for estimating open water evaporation (Squire and Callander, 1981). However a recent international conference concluded that transpiration was most accurately calculated using a version of the Penman-Monteith equation (Smith, 1991b). The use of such an equation has also been recommended for Tanzania by Stigter (1978). The actual transpiration rate is reduced below potential transpiration when the tea crop has incomplete ground cover (Dagg, 1970), when the SWD exceeds a critical level (Willatt, 1971; Stephens and Carr, 1991b), and/or when the vapour pressure deficit is high (Callander and Woodhead, 1981).

Once a SWD develops soil evaporation and drainage from a mature tea crop with full ground cover may be negligible (Stephens and Carr, 1991b). However in tea with incomplete ground cover soil evaporation can be significant when the surface is wet (Dagg, 1970). Cooper (1979) also showed that under a tea crop in Kenya, when transpiration and soil evaporation were prevented, drainage continued at a rate of 2.5 mm d⁻¹ for the first 40 days and then continued at an average rate of 0.7 mm until 100 days after saturation of the soil.

Apart from the work of Dagg (1970) in Kenya few attempts have been made to quantify the water use of young tea plants. Within the experiment described in Chapter 3 a neutron probe was used to establish the soil water content within the profile at the ULAW, and to measure changes in the SWD within selected clone x drought treatments. This chapter describes these measurements and the independent development of a soil water balance model to estimate the SWDs within the other treatments. The model was validated using the measured soil water contents.

METHODOLOGY

Field measurement of soil water content

During 1989 and 1990 the soil water content of selected treatments within experiment N10 were measured with a Wallingford neutron probe (Didcot Instruments Ltd).

Calibration of the neutron probe

The neutron probe was calibrated in July 1989, using two access tubes located in dry soil and one sited in wet soil adjacent to the experimental site. For each tube the mean count rate in the soil (R_s) to a depth of 3.1 m was measured in 0.05 m increments and expressed as a ratio of the standard water count (R_w). R_w was determined from the mean of ten 16 s readings in an access tube installed in the centre of a 200 l drum filled with water. Once these measurements were completed, four soil cores of known volume (mean: 130 ml) were taken at six to nine depths between 0.2 and 3.0 m and weighed (± 0.1 g). These samples were oven dried to determine the mean volumetric water content (θ_v). The best fit linear calibration between θ_v (range: 0.17-0.37) and the ratio R_s/R_w was:

$$\theta_v = 0.58(\pm 0.057) \cdot R_s/R_w - 0.03(\pm 0.03) \quad (n=21, r^2=83\%) \quad 4.2$$

The slope of this line is much lower than that found for temperate soils with the same textural classification (Bell, 1976). However the slope also depends upon the chemical composition of the soil (Greacen *et al.*, 1981).

Field measurements

On each day when the soil water content was measured in the experiment a mean standard water count (R_w) was first recorded. One 16 s reading (R_s) was then taken at depths of 0.25, 0.40, 0.55 and 0.70 m and thereafter at 0.2 m increments to 1.8 m in each of the selected treatments. The water content over each depth was calculated using Equation 4.2 and summed to calculate the total water content within the upper 1.8 m of soil.

From May to September 1989 the soil water content was measured at distances of 0.15 m and 0.45 m from the base of a single fully irrigated plant of clones 1, 6/8 and K35. There were two replicates, hence a total of twelve access tubes. Clones 1 and 6/8 were chosen because it was believed they were respectively drought resistant and drought susceptible. Clone K35 was chosen as a representative large-leaved clone.

Differential drought treatments were imposed from 9 October 1989. Between September and November soil water content was measured within new access holes installed in the fully irrigated (I_1), partially irrigated (I_2) and unirrigated

(I₀) sub-plots. Measurements were taken 1-2 days before and 2-3 days after each irrigation. Three replicates of three clones (1, 6/8 and S15/10) were examined in each of the three selected drought treatments. Clone S15/10 was chosen in preference to clone K35, because the August 1989 dry matter study showed that clone S15/10 partitioned a smaller proportion of its dry mass to roots than the other clones (cf Chapter 8). The earlier measurements taken between May and September showed no significant effect of the distance of the access hole from the plant on the measured soil water content, so all the new access holes were positioned an equal distance (0.4 m) from the base of two plants. A shortage of aluminium tubes meant that it was only possible to line the holes in one replicate of each clone x drought treatment. The remaining holes were only lined over the top 0.5 m.

No measurements were taken between June and September 1990 because the neutron probe was out of order. However during this time new access holes were installed so that the water use by clone SFS150 and within the partially irrigated I₃ sub-plots of each of the four clones could be sampled. The number of replicates was increased to four and all the access holes were unlined below 0.5 m. Measurements of soil water content started again in September and continued 1-2 days before and 1-3 days after each irrigation until mid-November. During 1990 sixteen out of the sixty four access holes within the experiment became clogged as soil fell from the unlined sides. The incidence of failure was apparently random and affected no more than two replicates of any clone x drought treatment. Values from these holes were removed from the data base before statistical analysis.

Upper limit of available water

The upper limit of available water was determined from neutron probe measurements in the fully irrigated (I₅) sub-plots one to three days after irrigation, plus an addition of the water lost by evaporation and transpiration in the intervening period. Between June and August 1989, the ULAW to a depth of 1.8 m was 503 ± 2 mm ($n=7$). Measurements taken between September and November 1989 also indicated an ULAW of about 500 mm to a depth of 1.8 m.

By contrast in 1990 the ULAW over the 1.8 m deep profile in the I₅ sub-plots was estimated to be 480 ± 3 mm ($n=5$). Although the water contents in the top 0.5 m were similar to those observed in 1989, they were less below this depth. Because the soil in these sub-plots was saturated at each irrigation in both 1989

and 1990 the lower readings below 0.5 m in 1990 were probably due to a systematic bias in the measurement. Whilst all the access holes were lined when the measurements were taken between June and August 1989, the holes were only lined within the top 0.5 m during 1990. The lack of a lining below 0.5 m could have caused a systematic reduction in the value of R_s due to the looser fit of the radioactive source and detector in the hole. Measurements made between September and November 1989 showed that, although only significant at the 10% level, the mean water contents over the top 1.8 m depth of soil measured in the unlined holes were 10 mm (sed = 16 mm) lower than those measured in holes lined with an aluminium tube. As a result it was assumed that all estimates of water content over the upper 1.8 m of soil were underestimated by 23 mm during 1990.

Development of the soil water balance model

A soil water balance model based on Equation 4.1 was developed to estimate the SWD and crop water use in 1989 and 1990. The model required separate estimates of transpiration, soil evaporation and drainage.

Transpiration

Transpiration was assumed to be dependent upon potential crop evaporation (ET_o), the ground cover (GC) and the SWD. ET_o was calculated using the Penman-Monteith equation described by Smith (1991b) assuming a canopy resistance of 69 s m^{-1} and an aerodynamic resistance of $100/U_2 \text{ s m}^{-1}$, where U_2 is the mean day-time (09.00 to 15.00 h) windspeed (m s^{-1}) measured at a height of 2 m. Linear regression showed that the relationship between monthly values of ET_o and $0.85 E_o$ during the dry season in 1989 and 1990 ($n=12$) was not significantly different from a 1:1 line passing through the origin (Equation 4.3):

$$ET_o = 1.07(\pm 0.06).(0.85 E_o) - 0.28(\pm 0.21) \quad (r^2=97\%) \quad 4.3$$

The ratio of actual transpiration to ET_o was assumed to be directly proportional to the ground cover of the crop (GC). Although the actual transpiration also depends upon the transfer of energy between the soil and the canopy (Shuttleworth and Wallace, 1985), such an analysis was beyond the scope of this study. The simpler linear relationship has been verified for tea by Dagg (1970)

and has been used successfully to estimate transpiration from other crops such as groundnut (Simmonds and Azam-Ali, 1989).

Transpiration is also modified by the SWD. In the model transpiration was assumed to continue at the value of ET_o modified by GC, until the SWD exceeded a critical deficit (CD). At this point transpiration was assumed to decline linearly with increasing SWD to zero when the soil within the maximum depth of rooting reached permanent wilting point, ie, when the total available water content (AWC) within the root zone had been extracted. The AWC within the top 1.8 m of soil was calculated from the ULAW estimated using results obtained with the neutron probe between September and November 1989 and the soil water content at permanent wilting point ($\psi_s = -1500$ kPa) determined from the soil water release curves described in Chapter 3 (Table 4.1).

Table 4.1. Available water contents (AWC) for incremental soil depths of 0.2 m between 0 and 1.8 m. The upper limits of available water (ULAW) were established from neutron probe measurements between September and November 1989. Permanent wilting point (PWP) values ($\psi_s = -1500$ kPa) were interpolated from soil samples taken in 1990.

Depth (m)	Water content		
	ULAW (mm m ⁻¹)	PWP (mm m ⁻¹)	AWC (mm 0.2 m ⁻¹)
0.0-0.20	295 ^a	129	33 ^a
0.20-0.40	285	139	29
0.40-0.60	280	149	26
0.60-0.80	272	159	23
0.80-1.00	257	168	18
1.00-1.20	261	178	17
1.20-1.40	280	188	18
1.40-1.60	280	198	16
1.60-1.80	291	208	17

^a. Includes an estimated 5 mm transpired between the date of irrigation and the time of measurement.

The value of CD was assumed to equal 18% of the AWC within the rooting depth of the crop, which was the ratio determined for a mature stand of clone 6/8 within 400 m of the experiment (Stephens and Carr, 1991b). The calculation of transpiration (E_t) is summarised by Equation 4.4:

If $SWD_{(0-1.8\text{ m})} \leq CD$:

$$E_t = GC.ET_o$$

If $CD < SWD_{(0-1.8\text{ m})} < AWC$:

$$E_t = GC.ET_o \cdot \frac{(AWC - SWD_{(0-1.8\text{ m})})}{(AWC - CD)}$$

If $SWD_{(0-1.8\text{ m})} \geq AWC$

$$E_t = 0$$

4.4

Soil evaporation and drainage

Estimates of soil evaporation and drainage were based on three independent sets of neutron probe measurements from replicated ($n = 2$ to 4) bare soil sites adjacent to the experiment in 1989 and 1991. These sites were covered with a mulch of Napier grass and were kept clear of weeds. Despite the mulch, each of these sites showed substantial soil water loss either through evaporation or drainage. To separate the water lost through evaporation from that lost through drainage the soil water contents within these plots were expressed as soil water potentials to determine the zero flux plane (Figure 4.1). The values of ψ_s were estimated using the soil water release curves in Figure 3.1. There was evidence of a zero flux plane at 0.4 m indicating that, in the absence of a crop, water loss above this level was due to soil evaporation and below due to drainage.

Mean daily evaporation, drainage and water contents above and below the 0.4 m zero flux plane were calculated for the three sets of measurements. As expected these showed that evaporation and drainage declined as the soil dried (Table 4.2).

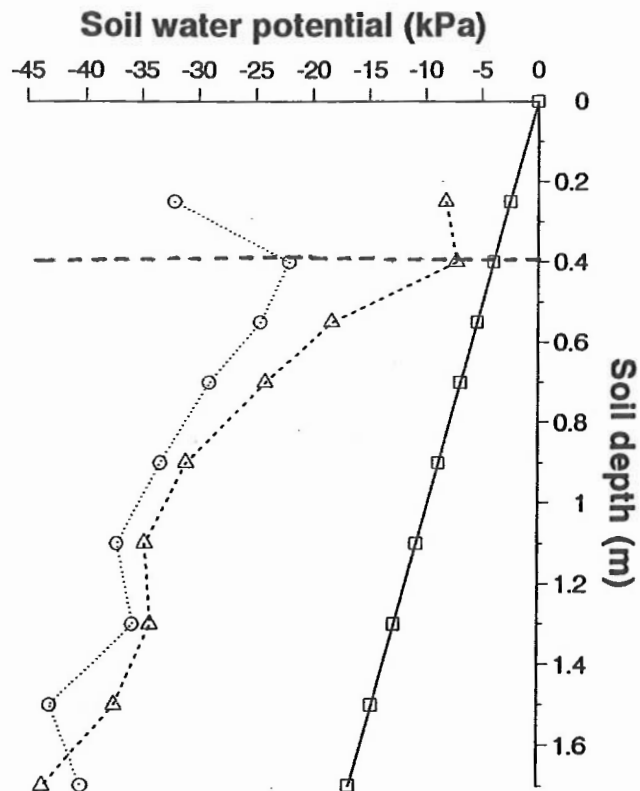


Figure 4.1. Changes in the soil water potential with depth below bare soil one day: $\circ$ and ten days: $\triangle$ after irrigation. Also shown are the unit gradient: $\square$ and the zero flux plane: - - - .

Table 4.2. Mean daily evaporation, daily drainage and soil water content at depths of 0 to 0.4 m and 0.4 to 1.8 m from bare soil with a surface mulch of Napier grass.

Depth of soil		0-0.4 m		0.4-1.8 m	
Sample	n	Mean water content (mm)	Mean evaporation (mm d ⁻¹)	Mean water content (mm)	Mean drainage (mm d ⁻¹)
Sept-Oct 89	8	83	0.25 (± 0.12)	338	0.65 (± 0.10)
May-Aug 89	12	103	0.42 (± 0.21)	371	0.98 (± 0.25)
July 1991	23	109	1.25 (± 0.25)	378	1.25 (± 0.31)

The relationship between soil evaporation (E_s) and the volumetric water content of the top 0.4 m of soil ($\theta_{v(0-0.4 \text{ m})}$) was assumed to be linear (Simmonds and Williams, 1989). Although the correlation coefficient was low ($r^2=20\%$), the best fit linear relationship (Equation 4.5) predicted a sensible value for E_s of 1.2 mm d⁻¹, when the value of $\theta_{v(0-0.4 \text{ m})}$ was at the upper limit of 115 mm (Table 4.1). Equation 4.5 also predicts that E_s becomes zero when the value of $\theta_{v(0-0.4 \text{ m})}$ is 77 mm, which is equivalent to a SWD over the top 0.4 m of soil of about 40 mm.

$$E_s = 0.031(\pm 0.025) \cdot \theta_{v(0-0.4 \text{ m})} - 2.4(\pm 2.5) \quad (n=3, r^2=20\%) \quad 4.5$$

Assuming a mean ET_o of about 3 mm d⁻¹ between May and October, the maximum value for E_s of 1.2 mm d⁻¹ below a mulch is equivalent to about 40% of ET_o . If the total value of E_s is also assumed to be dependent upon the proportion of ground not covered by the crop (1-GC) (Dagg, 1970) then it can be shown that:

If $SWD_{(0-0.4 \text{ m})} < 40 \text{ mm}$:

$$E_s = 0.4 \cdot (1-GC) \cdot ET_o \cdot (40 - SWD_{(0-0.4 \text{ m})}) / 40$$

If $SWD_{(0-0.4 \text{ m})} \geq 40 \text{ mm}$:

$$E_s = 0 \quad 4.6$$

A linear relationship was assumed between drainage (D) and the soil water content between depths of 0.4 and 1.8 m ($\theta_{v(0.4-1.8 \text{ m})}$; mm). The best fit straight line relationship between D and $\theta_{v(0.4-1.8 \text{ m})}$ using the three values shown in Table 4.2 had a correlation coefficient of 83% (Equation 4.7):

$$D = 0.01377(\pm 0.0040) \cdot \theta_{v(0.4-1.8 \text{ m})} - 4.03(\pm 1.50) \quad (n=3, r^2=83\%) \quad 4.7$$

This equation shows that at the upper limit of available water, when $\theta_{v(0.4-1.8 \text{ m})}$ is 385 mm (Table 4.2), the rate of drainage was 1.27 mm d⁻¹. Drainage then continued until the value of $\theta_{v(0.4-1.8 \text{ m})}$ was equal to 293 mm, which corresponds to a SWD between 0.4 and 1.8 m of 92 mm. Equation 4.7 can therefore be rewritten:

If $0 < \text{SWD}_{(0.4-1.8 \text{ m})} < 92 \text{ mm}$:

$$D = 1.27 \cdot (92 - \text{SWD}_{(0.4-1.8 \text{ m})}) / 92$$

If $\text{SWD}_{(0.4-1.8 \text{ m})} \geq 92 \text{ mm}$:

$$D = 0$$

4.8

Because E_s was related to $\theta_{v(0-0.4 \text{ m})}$ and D was related to $\theta_{v(0.4-1.8 \text{ m})}$ it was necessary to calculate separate values of the SWD for each of the two layers of soil.

Use of the soil water balance model

The soil water model described by Equation 4.1, where E_t is defined by Equation 4.4, E_s is defined by Equation 4.6 and D is defined by Equation 4.8, was used to calculate the SWD within the fully irrigated (I_5), partially irrigated (I_3 and I_2) and unirrigated (I_0) sub-plots within the experiment on each day during the dry season (1 June to 30 November) in 1989 and 1990. Rainfall amounts were taken from the daily meteorological measurements and the depths of irrigation were derived from the actual depths of irrigation measured within the experiment using catch cans.

The model also required estimates of the value of GC, and the maximum rooting depth of the crop to calculate the AWC. The value of GC on any particular day was interpolated from measurements of mean ground cover for each drought treatment reported in Chapter 6. The values selected for rooting depth were derived from measurements reported in Chapter 8. For the 1989 dry season a constant rooting depth of 0.62 m was chosen, based on the mean maximum rooting depth in September. This value corresponded to an AWC within the root zone of 90 mm (Table 4.1). In the 1990 dry season a constant rooting depth of 1.30 m was selected, again based on the mean maximum rooting depth in September. This depth corresponded to an AWC within the root zone of 155 mm. Because it was necessary to calculate a separate SWD for the two soil strata, it was also important to partition the source of the water that was used for transpiration. In 1989 it was assumed that all the transpired water came from the top 0.4 m of soil. In 1990 the source of water for transpiration was partitioned between the two strata in direct proportion to the mean distribution of thin roots (cf Chapter 8), which was 43% in the top 0.4 m and the rest below.

The values of SWD estimated with this model ($\text{SWD}_{\text{model}}$) were compared with those measured using the neutron probe (SWD_{np}) on corresponding dates and within corresponding drought treatments.

RESULTS

Measured soil water deficits

Following the imposition of differential drought treatments on 9 October 1989, the mean values of SWD within the unirrigated (I_0) sub-plots were consistently greater than those within the fully irrigated (I_5) sub-plots, being significantly ($P \leq 0.05$) larger after 23 October. On 13 November, two days after the experiment had been differentially irrigated, the mean SWD was 93 mm in the I_0 treatments, 68 mm in the I_2 treatments and 23 mm in the fully irrigated (I_5) treatments. The standard error of the difference for these measurements was 16 mm ($n=9$).

In 1990 differential drought treatments were imposed from 27 July. After the neutron probe had been repaired the first measurements were taken on 26 September 1990. On this date a SWD of 117 mm had developed in the unirrigated (I_0) sub-plots. On 16 November, the last measurement before the start of the rains, the SWD had only increased by a further 10 mm to reach 127 mm. Over the same period (26 September to 16 November) the SWD increased from 97 mm to a maximum of 110 mm in the I_2 treatments and ranged from 0 to 39 mm in the fully irrigated (I_5) sub-plots. The maximum SWD in the I_3 treatments was 85 mm. By 29 November after the start of the rains there were no significant differences in the SWD (range: 0-32 mm) between any of the drought treatments.

The change in soil water content with depth for the four drought treatments on 2 November 1990, about two days after the last differential irrigation, is shown in Figure 4.2. The water contents in the fully irrigated (I_5) treatments were close to the laboratory determined value of water content at a ψ_s of -0.1 MPa. The soil within the fully irrigated treatment was wetter ($P \leq 0.05$) than that in the partially irrigated (I_3) treatment to a depth of 1.0 m, and wetter ($P \leq 0.05$) than that in the unirrigated (I_0) sub-plots to a depth of 1.8 m.

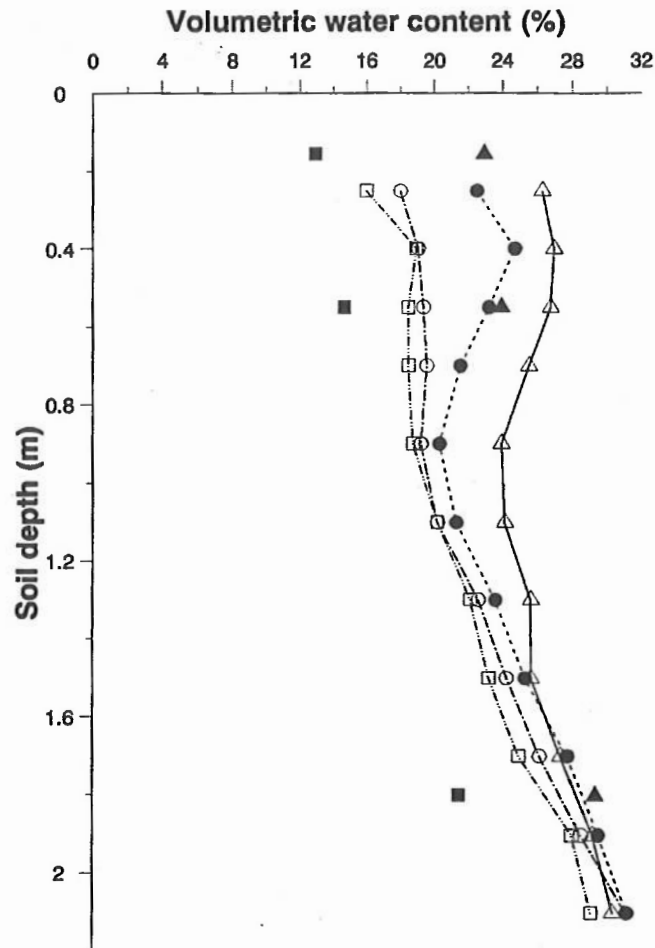


Figure 4.2. Changes in the volumetric soil water content with depth on 2 November 1990 (2 days after an irrigation) for each of four drought treatments: fully irrigated I_5 :—△—, partially irrigated I_3 :—●— and I_2 :—○—, and unirrigated I_0 :—□—. Laboratory determined values for field capacity ($\psi_s = -10$ kPa): ▲, and permanent wilting point ($\psi_s = -1500$ kPa): ■ are shown for three depths.

Clonal differences

During the dry season in 1989 there were no significant differences in the values of the SWD over the depth range 0-1.8 m for clones 1, 6/8 and S15/10. During the dry season in 1990 there were again no significant differences in the SWDs for clones 1, 6/8, SFS150 and S15/10 except on one occasion. On 2 November the soil water content below clone SFS150 was higher ($P \leq 0.05$) than that under clones 1, 6/8 and S15/10. Because this difference (although not significant) continued into the wet season it was probably the result of a systematic error. The access holes for clone SFS150 were installed approximately a year later than most of those used for monitoring the other clones and they were therefore

probably less eroded. This would have led to systematically higher measured values of water content.

Calibration of the soil water balance model

The model was first used to estimate the SWD between 1 June and 30 November in 1990 in each of the four selected drought treatments. Over this time the model overestimated the SWD as determined with a neutron probe (range: 0-127 mm) by about 12% (Equation 4.9). This was equivalent to a maximum error of about 15 mm.

$$\text{SWD}_{\text{model}} = 1.12(\pm 0.02) \cdot \text{SWD}_{\text{np}} \quad (n=42, r^2=97\%) \quad 4.9$$

A possible reason for this small error was a overestimate of water loss by drainage. Whilst the zero-flux plane remained stable at 0.4 m depth beneath a bare soil, it can descend rapidly through the soil profile when a crop is extracting water (Cooper, 1979). It is also possible that two zero-flux planes may be created within the soil profile. Therefore the drainage rate not only depends upon the water content of the soil, but also on the position(s) of the zero-flux plane(s). These effects may explain why Stephens and Carr (1990b) were able to assume that there was negligible drainage below mature fully irrigated tea with complete ground cover once the SWD was larger than zero. This effect of crop water use on drainage was incorporated into the model by assuming that drainage was linearly related to the proportion of the ground not covered by the crop (1-GC) (Equation 4.10):

If $0 < \text{SWD}_{(0.4-1.8 \text{ m})} < 92 \text{ mm}$:

$$D = 1.27 \cdot (1-\text{GC}) \cdot (92 - \text{SWD}_{(0.4-1.8 \text{ m})}) / 92$$

If $\text{SWD}_{(0.4-1.8 \text{ m})} \geq 92 \text{ mm}$:

$$D = 0 \quad 4.10$$

Using Equation 4.10 in place of Equation 4.8, the values of the SWD for the selected treatments in 1989 and 1990 were recalculated. The value of r^2 for the linear relationship between $\text{SWD}_{\text{model}}$ and SWD_{np} in both years was 97%. In 1989 the model underestimated SWD_{np} in the range of 0 to 93 mm by about 14%

(Equation 4.11; Figure 4.3). This was equivalent to an error of 13 mm at the largest SWD, which was within the precision of the neutron probe.

$$\text{SWD}_{\text{model}} = 0.86(\pm 0.023) \cdot \text{SWD}_{\text{np}} - 3.2(\pm 1.08) \quad (n=42, r^2=97\%) \quad 4.11$$

In 1990 the relationship between $\text{SWD}_{\text{model}}$ and SWD_{np} was not significantly different from a 1:1 line passing through the origin (Equation 4.12; Figure 4.4).

$$\text{SWD}_{\text{model}} = 1.04(\pm 0.026) \cdot \text{SWD}_{\text{np}} + 1.6(\pm 2.07) \quad (n=42, r^2=97\%) \quad 4.12$$

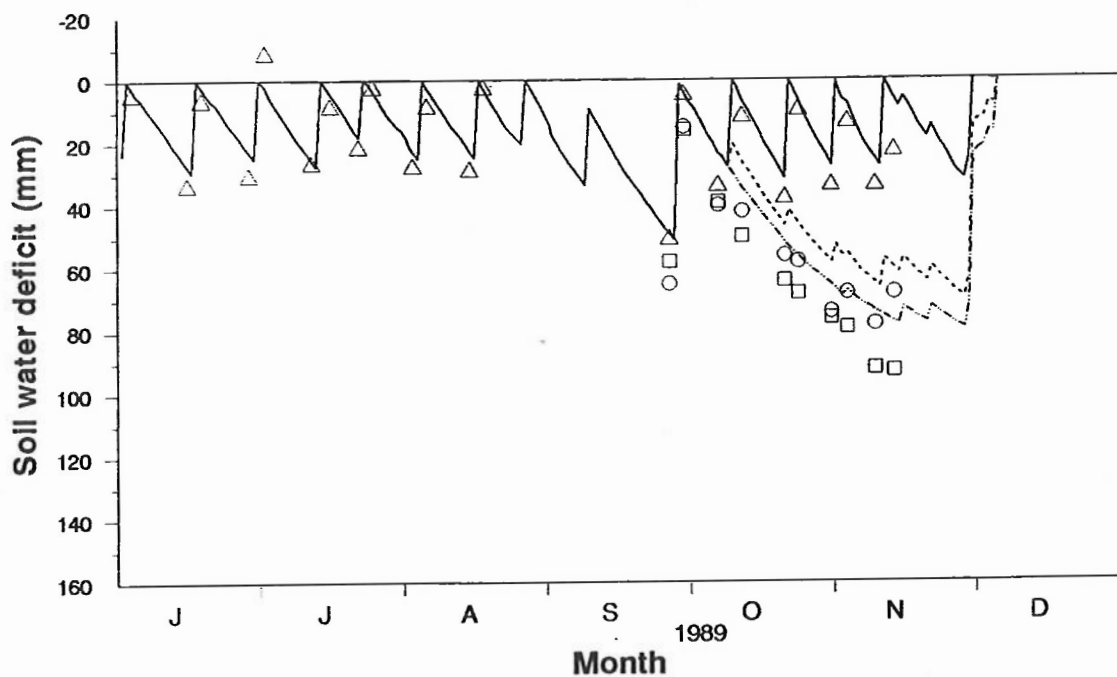


Figure 4.3. Predicted changes in the soil water deficit within each of three drought treatments during the 1989 dry season using the soil water balance model: fully irrigated I_5 : —, partially irrigated I_2 : and unirrigated I_0 : ----. The symbols indicate the measured soil water deficit using a neutron probe I_5 : Δ I_2 : $\circ$ I_0 : $\square$.

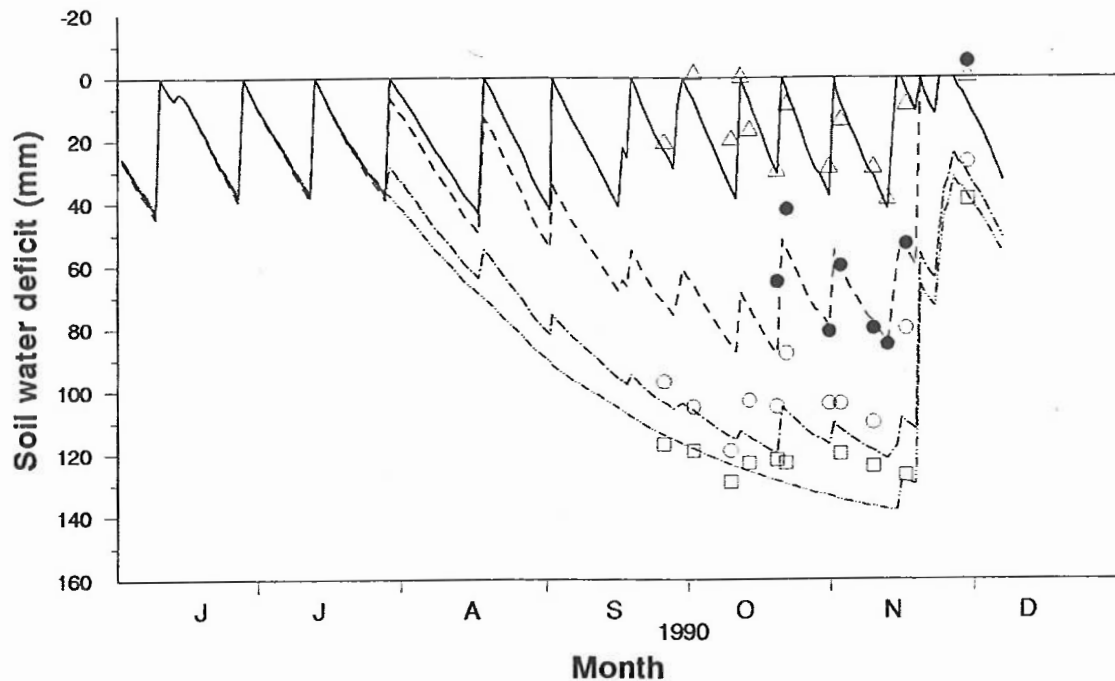


Figure 4.4. Predicted changes in the soil water deficit within each of four drought treatments during the 1990 dry season using the soil water balance model. Fully irrigated I_5 : —, partially irrigated I_3 : ----, I_2 : - · - · and unirrigated I_0 : The symbols indicate the measured soil water deficit using a neutron probe I_5 : Δ I_3 : $\bullet$ I_2 : $\circ$ I_0 : $\square$.

DISCUSSION

Precision of measurements

Both the neutron probe measurements and the soil water balance method required an estimate of the ULAW ie, the soil water content when the SWD = 0. This was determined from *in-situ* measurements of water content one to three days after excess irrigation with an allowance for Es and Et over the intervening period. In 1989 over the top 1.8 m depth of soil this corresponded to about 500 mm. The precision of this value is determined primarily by the intercept of the neutron probe calibration (Equation 4.2) which had a standard error of ± 30 mm m^{-1} . The corresponding water content over the same depth of 1.8 m at a soil

water potential of -10 kPa, estimated from undisturbed soil samples, was about 480 mm. Thus a soil water potential of -10 kPa appears to be an appropriate value for determining the ULAW for soils like those at Ngwazi. In order to relate measurements of SWD more closely to the corresponding soil water potentials in the future, the precision of the neutron probe calibration curve needs to be improved.

It was easier to derive precise estimates of the changes in soil water content than the absolute values using the neutron probe, as these estimates depend primarily on the slope of the calibration curve (Equation 4.2). The ratio of R_s to R_w over the upper 1.8 m depth of soil ranged from 0.38 to 0.51 in 1990, which corresponds to a standard error of only ± 13 mm for the changes in water content over the full 1.8 m. The estimate also depended upon the standard error of the field measurements, which for this experiment over the upper 1.8 m of soil was about ± 10 mm. In view of the problems with the unlined access holes and sampling variations in a crop with incomplete canopy and root development these errors are quite small.

The soil water balance model

The soil water balance model provided a good description of changes in the SWD in 1989 when the ground cover of the crop was below 20%. Between 1 June and 30 November 1990 when the mean ground cover for the six clones ranged from 34 to 65% the model provided a very good estimate of the SWD as measured using a neutron probe. If the model is extrapolated to calculate the SWD below a crop with full ground cover ($GC = 1$) then, because E_s and D then equal zero, the model is identical to that presented by Stephens and Carr (1991b). Using this specific form of the general model presented here, they were able to determine accurately the water use of a mature stand of clone 6/8. The model can therefore be used with confidence to determine the actual crop water use and the resulting SWD below immature and mature tea at Ngwazi with and without irrigation.

Because the model partitions crop water use into transpiration, soil evaporation and drainage it can also be used to estimate the total transpiration of the crop. The effects of clonal differences in ground cover and maximum rooting depths on transpiration can also be estimated. Because the model was developed using the Penman-Monteith estimate of potential crop evaporation, the model can

also potentially be used to determine the effects of changes in canopy conductance.

Clonal differences in crop water use

The measurements of water content with the neutron probe indicated that the SWD below clones 1, 6/8, SFS150 and S15/10 between September and November 1990 were similar. This was despite the mean ground cover in the unirrigated sub-plots ranging from 25-38% for clone 6/8 to 38-55% for clone S15/10.

To determine the reasons for this, the soil water model was used to calculate changes in SWD and crop water use of unirrigated clones 6/8 and S15/10 from the beginning of June to mid-November 1990 before the experiment was uniformly irrigated. The values of GC were derived from the interpolation of actual measurements of ground cover within the experiment (cf Chapter 6). A constant rooting depth of 1.30 m (AWC = 155 mm) was assumed for each clone during this period.

Table 4.3. Estimated changes in the soil water deficit (SWD) using a soil water balance model for unirrigated clones 6/8 and S15/10 from 1 June to 14 November 1990.

	Increase in soil water deficit (mm)	
	clone 6/8	clone S15/10
Initial SWD	25	25
uniform irrigation	-175	-175
rainfall	-7	-7
(Inputs of water)	-182	-182
drainage	133	106
soil evaporation	51	36
transpiration	108	155
(Outputs of water)	292	297
Final SWD	135	140

Like the values of SWD measured using the neutron probe, the model also indicates that the estimated SWD in the unirrigated sub-plots of these two clones were similar at the end of the dry season on 14 November 1990. Although this is expected since the model assumes that each clone can only dry the soil within a specified rooting depth to permanent wilting point, the results show that there were in fact substantial clonal differences in transpiration. In this example total transpiration ranged from 108 mm for clone 6/8 to 155 mm for clone S15/10. This indicates that for plants of a similar rooting depth increased ground cover will improve the proportion of water that is transpired and correspondingly reduce soil water losses through drainage out of the root zone and evaporation from the soil surface. The lack of clonal differences in the actual SWD also means that a single value can be used to describe the actual SWD in each drought treatment.

CONCLUSIONS

The SWD within selected clone and drought treatments of young tea were measured using a neutron probe. A soil water balance model was also developed based on measurements of soil evaporation and drainage from bare soil sites adjacent to the experiment. This model was used to predict the values of SWD within selected treatments of the experiment, using measured values of rainfall, irrigation, potential crop evaporation, ground cover, the available water content of the soil and the maximum rooting depth.

The agreement between the values of SWD estimated with the model and those measured using the neutron probe was good. The model can therefore be used with confidence to estimate the SWD in treatments where the neutron probe was not used.

By partitioning water loss into transpiration, soil evaporation and drainage, the model can also be used to predict transpiration from each treatment. The model indicated that for clones of a similar rooting depth, greater ground cover increased the proportion of water that was transpired. However because larger ground cover also reduced drainage and soil evaporation, the net effect on the SWD was moderated. In fact both the neutron probe and the soil water balance model suggest that the total water use and the SWD within each drought treatment was similar for each of these clones, which were all planted at the same time.

CHAPTER 5

YIELD AND YIELD DISTRIBUTION

INTRODUCTION

New areas of tea in Southern Tanzania are usually planted with vegetatively propagated clones which have been grown from cuttings in a nursery for 12 to 18 months. It can then take another one to two years before the first shoots are harvested, and a minimum of a further three years for yields to stabilise.

Both the initial and longer term yields are affected by the choice of clone. Each of the national and regional tea research institutes in eastern Africa report the results of their clonal field trials (eg, Ndamugoba, 1989; Njuguna, 1989; Nyirenda, 1987). Although these trials are sometimes done in only one location, the results usually need to be extrapolated to different environments. In Southern Tanzania a major variable determining yield is the degree of drought stress as the actual SWD under mature tea can exceed 300 mm (Stephens and Carr, 1991b). Whilst the larger tea companies are able to reduce such soil water deficits by irrigation, virtually all the smallholders in this region rely only on rainfall. Both Othieno (1978a) in Kenya and Nyirenda (1988) in Malawi have reported that clones vary in their yield responses to drought.

The yield responses of any crop to dry soil can be described by a) the maximum yield where the soil is kept fully wet and b) the stability of that yield as the soil dries (Ludlow and Muchow, 1990). The maximum yield for a crop under well watered conditions for a specific environment and management regime (Y_m ; kg ha⁻¹) can be determined experimentally. The stability of yield with increasing drought stress can be expressed as the absolute difference between Y_m and the actual yield (Y_a ; kg ha⁻¹) (Blum, 1983; Fussell *et al.*, 1991). However because yields tend to converge towards zero at increased stress, there is a tendency for cultivars with high maximum yields to be more sensitive in absolute terms to drought than clones with low maximum yields. This link between Y_m and drought sensitivity can be minimised by considering the responses of yield to drought in relative terms (Doorenbos and Kassam, 1986). Thus the value of Y_a can be related to Y_m , the drought stress (DS) and a relative yield response factor to drought stress (K_y) (Equation 5.1).

$$Y_a = Y_m \cdot (1 + K_y \cdot DS) \quad 5.1$$

In this chapter the total annual yields, and their seasonal distribution for each of the six tea clones are examined under varying drought regimes. The yield response for each clone is described in terms of a maximum yield (Y_m) and a relative yield response to drought (K_y).

METHODOLOGY

A clone x drought experiment (described fully in Chapter 3) comprising of six clones: 1, 6/8, SFS150, S15/10, 207 and K35 was planted at the Ngwazi Tea Research Unit in August 1988. The dry season at Ngwazi usually begins in April or May and continues until the start of the rains at the end of November. The first half of the dry season up to August is cooler than the second half from September to November.

To prevent complete loss of the plants, the experiment was uniformly irrigated during the early part of the dry season in the first two years after planting. In 1989 differential drought treatments were only imposed from 7 October to the end of November, and in 1990 from 27 July until 15 November.

As reported in Chapter 4 there were no significant differences between clones in the measured SWD within any of the drought treatments. As a result the same values of SWD can be used for all clones. Using the soil water balance model described in Chapter 4, daily values of SWD were calculated for each drought treatment in 1989 and 1990. These values were then used to calculate the mean SWD in each drought treatment for the six months from 1 June to 30 November corresponding to the dry season. Using the same time period allowed meaningful comparisons to be made between the two years. A mean value was used so that each daily SWD throughout the dry season received equal emphasis (Table 5.1).

Plant survival

Any plants that died within the experiment were uprooted and replaced with healthy sleeved transplants of the same clone. Replacements within the unirrigated treatments were watered by hand during the dry season.

Table 5.1. Mean and maximum soil water deficits within each drought treatment (Explained in Table 3.5 on page 37) during the dry seasons from 1 June to 30 November in 1989 and 1990.

	Drought treatments					
	I ₅	I ₄	I ₃	I ₂	I ₁	I ₀
Year 1989						
mean SWD (mm)	16	16	20	27	29	30
maximum SWD (mm)	51	51	51	69	78	79
Year 1990						
mean SWD (mm)	19	22	42	66	74	74
maximum SWD (mm)	43	51	88	121	133	138

Yield measurements

In early November 1989, fifteen months after planting, shoots above a height of 0.45 m from the ground were removed or 'tipped' to produce a level plucking surface. The first shoots sent for manufacture were harvested in early December 1989. Subsequent harvests took place at thirteen to fifteen day intervals extending up to twenty four days during the cool season. At each of these harvests the people harvesting the tea were instructed to remove all the shoots above the plucking surface with two or more expanded leaves.

The total fresh mass of the shoots removed from each of the four replicates of each clone x drought treatment was weighed at each harvest. The dry mass of these shoots was estimated from the fresh mass using a conversion factor derived from an analysis of samples taken during 1990 which were oven dried (cf Chapter 9). The conversion factor accounted for the effect of seasonal temperature changes by reducing the dry matter content by 0.36% points for each °C rise in air temperature in the two months prior to harvest. There were also clonal differences in dry matter content. If these are standardised to a temperature of 17°C, which is close to the mean air temperature at Ngwazi, the dry matter content ranged from 20.7% for clone SFS150 to 24.2% for clone 1 (Table 5.2). Although the dry matter content increased at high values of SWD, the net effect of this on total yield was negligible because so few shoots were harvested at this time.

Table 5.2. Mean dry matter contents of shoots harvested from each of six irrigated clones, standardised to growth at an air temperature of 17°C.

Clone	1	6/8	SFS150	S15/10	207	K35
Dry matter (%)	24.2	20.9	20.7	22.3	22.3	22.3

The variance of yield was constant across the treatments and it was not necessary to transform the yield data. The yields were not corrected for plant deaths which are reported separately. The yields of made tea from each clone over the first six months of harvest (December 1989 to May 1990) were related to the SWD in the preceding 1989 dry season. The yields of made tea from each clone for the twelve months from June 1990 to May 1991 were related to the SWD in the 1990 dry season. For the full twelve months, and also the dry (June to November 1990) and the wet season (December 1990 to May 1991) the maximum yields (Y_m) and the relative yield responses to drought (K_y) were determined for each clone (Equation 5.1).

RESULTS

Responses of fully irrigated clones.

Plant survival

From April to August 1989 there were more deaths ($P \leq 0.05$) of clone 6/8 (7%) than clones 1, 207 and SFS150 (all below 1%). This continued into the second year after planting (August 1989 to July 1990) when more plants ($P \leq 0.05$) of clone 6/8 again died (5%) than clones 1, SFS150 and 207 (all below 1%). Clones K35 and S15/10 were intermediate in response. Within the third year after planting (August 1990 to May 1991) the survival of the fully irrigated clones were similar.

Maximum yield of made tea

Surprisingly between December 1989 and May 1990 the mean yields from the I_4 treatments (578 kg made tea ha^{-1}) were higher ($P \leq 0.05$) than those from the fully irrigated I_5 treatments (521 kg made tea ha^{-1}). This was not a result of over-

irrigation as the depths of water applied to both treatments during the 1989 dry season were similar (Table 3.5). One minor reason for this lower yield was the removal of approximately twenty shoots 90-120 m in length from within each I_5 (and also I_0) sub-plot for measuring xylem water potential between June and November 1989 (cf Chapter 12). Allowing for the removal of these shoots which would have been equivalent to 9 kg ha⁻¹, the mean yields from the I_5 and I_4 treatments were no longer significantly different. In the subsequent dry season the shoots used to measure xylem water potential were only obtained from the guard-rows. Over the twelve months from June 1990 to May 1991 the yields of made tea of the fully irrigated I_5 treatments (2590 kg ha⁻¹) were not significantly different from those of the fully irrigated I_4 sub-plots (2680 kg ha⁻¹). However to maintain consistency between the seasons the maximum yield (Y_m) was determined from the I_4 sub-plots.

Table 5.3. Yields of made tea from each of six fully irrigated (I_4) clones for each three month period from December 1989 to May 1991.

		Yield of made tea (kg ha ⁻¹)							
		Wet season		Dry season		Wet season		Annual	
		warm	warm	cool	warm	warm	warm		
		Dec 89- Feb 90	Mar 90- May 90	Jun 90- Aug 90	Sep 90- Nov 90	Dec 90- Feb 91	Mar 91- May 91	Jun 90- May 91	
Clone	1	240 az	291 z	172 z	495 z	892 z	920 z	2480	z
	6/8	202 z	286 z	260 a	657	921 z	798 z	2636	z
	SFS150	236 az	300 z	324 a	561	840 z	785 z	2510	z
	S15/10	307 a	497 a	308 a	828 a	1376 a	1248 a	3761	a
	207	287 a	359 z	237 z	483 z	949 z	817 z	2285	z
	K35	192 z	273 z	186 z	436 z	847 z	748 z	2216	z
mean		244	334	248	577	971	886	2681	
sed (n=4)		29	36	25	30	69	81	166	

The yields from each of the fully irrigated clones as expected increased as the plants grew larger. For example the mean yield of made tea during the first three months of the wet season from December to February was only 244 kg ha⁻¹ in 1989/90 compared to 971 kg ha⁻¹ for the same period a year later (Table 5.3).

Over the twelve months between June 1990 and May 1991 the yield of made tea from fully irrigated clone S15/10 (3761 kg ha⁻¹) was substantially higher ($P \leq 0.01$) than from each of the other clones. This is a very large annual yield for a clone less than three years after field planting. There were no significant differences in the yields of made tea from the other fully irrigated clones, which ranged from 2216 kg ha⁻¹ for clone K35 to 2636 kg ha⁻¹ for clone 6/8.

Seasonal yield distribution

Against the trend of a steady increase, the mean yields of made tea in the fully irrigated I₄ sub-plots declined from 334 kg ha⁻¹ over the three months from March to May 1990 to 248 kg ha⁻¹ in the following cool season (June-August 1990). Lower yields during the cool season are associated with reduced rates of shoot extension (Carr and Stephens, 1992). However there were clonal differences in the response at this time as shown for clones 1 and SFS150 in Figure 5.1.

Before the start of the cool season the yields of fully irrigated clones 1 and SFS150 were similar, and both showed yield reductions when temperatures declined in June and July. However this reduction was greater and more sustained for clone 1 than for clone SFS150. The yields from clone SFS150 started to rise in late August, but the yields from clone 1 only increased after late September. Therefore the cool season yield of made tea from clone SFS150 (324 kg ha⁻¹) was higher ($P \leq 0.01$) than that from clone 1 (172 kg ha⁻¹).

However later in the year towards the end of the warm dry season and into the wet season the weekly yields from clone 1 were generally greater than those from clone SFS150. This meant that by the end of May 1991, the annual cumulative yields of both clones were the same (2410-2430 kg ha⁻¹) (Figure 5.1b). Clones 6/8 and S15/10 tended to show a seasonal yield distribution similar to that for clone SFS150 (Figure 5.2), whilst clones 207 and K35 behaved more like clone 1 (Figure 5.3).

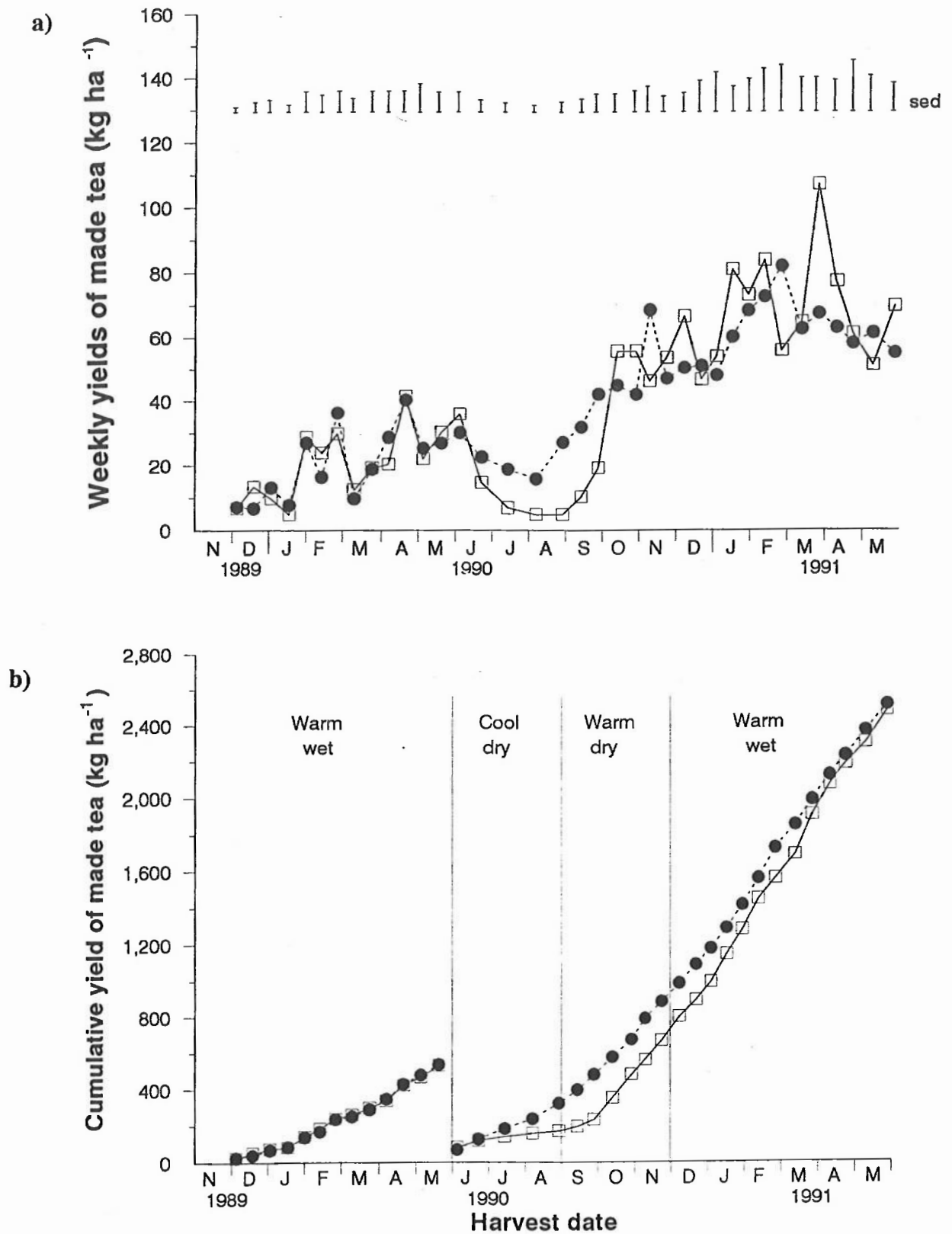


Figure 5.1. Seasonal distribution of a) weekly and b) cumulative yields of made tea from fully irrigated (I_4) clone 1: $\square$, and clone SFS150: $\bullet$.

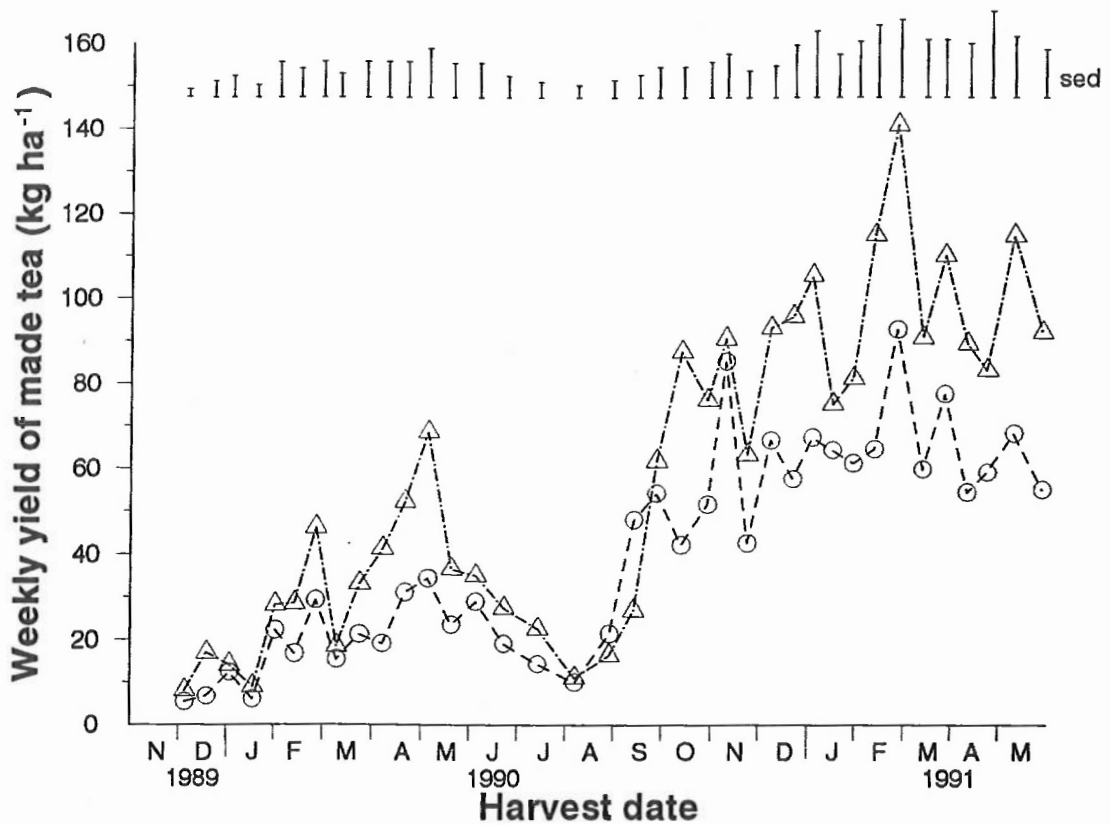


Figure 5.2. Seasonal distribution of the weekly yields of made tea from fully irrigated (I_4) clones 6/8: $--\bigcirc--$, and S15/10: $--\triangle--$.

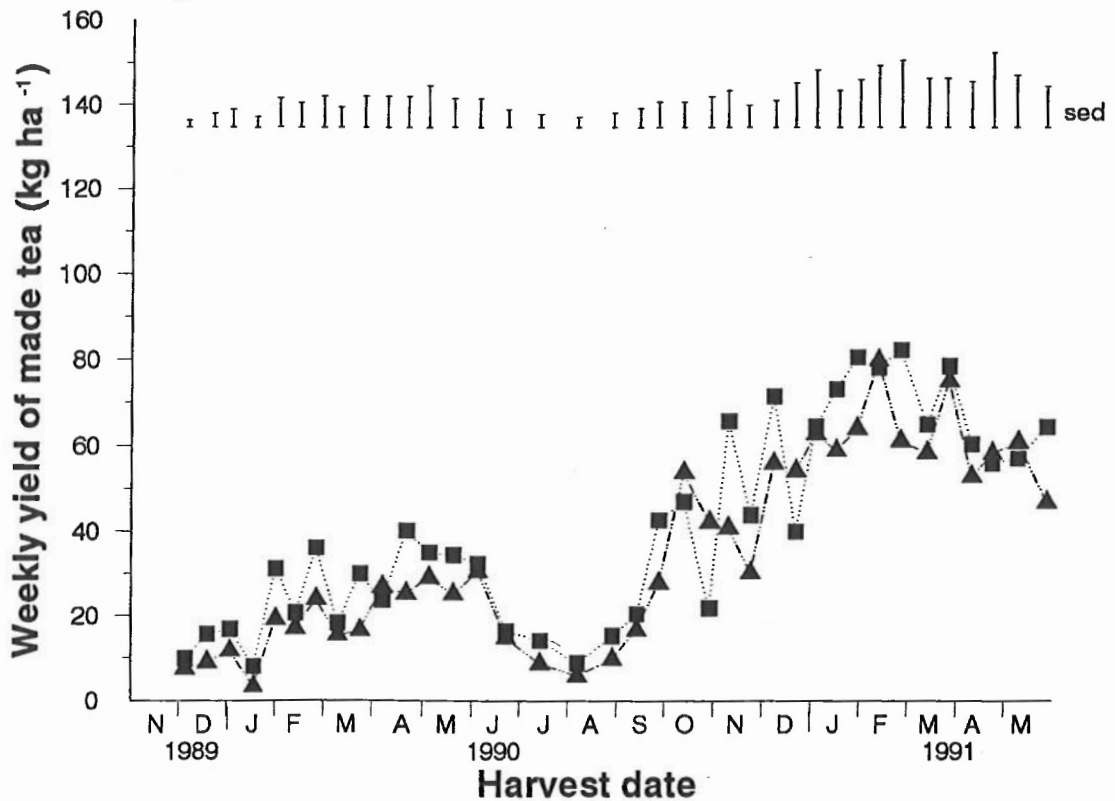


Figure 5.3. Seasonal distribution of the weekly yields of made tea from fully irrigated (I_4) clones 207: $\blacksquare--$, and K35: $\blacktriangle--$.

Responses to drought

Plant survival

There were no significant effects of the drought treatments imposed in 1989 on plant survival. However during the following year there were more ($P \leq 0.01$) plant deaths in the two unirrigated (I_0 and I_1) treatments than in the fully irrigated (I_4 and I_5) sub-plots. At the end of the dry season in 1990 this effect was assumed to be quite small. Although many of the unirrigated (I_0 and I_1) plants had abscised their mature leaves, only five (3.5%) plants of clone 207 and one plant (<1%) of clone K35 out of a total of 144 for each clone were completely defoliated. The dead plants of clone 207 were uprooted and examined. Although they showed strong structural rooting, it appeared that their roots had tended to spread horizontally rather than vertically through the soil.

In June 1991, seven months after the end of the 1990 dry season, the effects of drought on plant survival were more stark (Table 5.4). Many of the plants still living in December 1990 had died with stem canker caused by the fungus *Phomopsis theae* (Petch) (Congdon, personal communication). The number of clone 207 plants that died within the unirrigated I_0 and I_1 sub-plots (19%) was higher ($P \leq 0.01$) than for the other clones (range: 1-6%).

Table 5.4. Effects of drought on the proportion of the established plants that died between August 1990 and June 1991 for each of six clones.

		Plant deaths (%)		
		Fully irrigated I_5 and I_4	Partially irrigated I_3 and I_2	Unirrigated I_1 and I_0
Clone	1	0 a	0 a	1 a
	6/8	1 a	1 a	3 a
	SFS150	0 a	1 a	1 a
	S15/10	0 a	0 a	6
	207	0 a	1 a	19 z
	K35	0 a	1 a	5
sed = 1.9, n=8				

Seasonal yield distribution

The effects of drought on the seasonal distribution of yield are illustrated by the yields from the fully irrigated (I_4) and unirrigated (I_0) treatments of clone S15/10 (Figure 5.4). Although the drought treatments in 1989 did not significantly affect plant survival, the yields during the subsequent wet season were lower ($P \leq 0.001$) in the unirrigated I_0 and I_1 sub-plots than in the fully irrigated treatments.

Drought treatments were imposed again in 1990 from 27 July. After the cool season, yields started to increase again in the fully irrigated treatment in September as air temperatures rose. However yields in the unirrigated treatments continued to decline reaching zero by October. Views across a representative fully irrigated (I_5) and unirrigated sub-plot of clone S15/10 at the beginning of November are shown in Plates 5.1 and 5.2. Yields in the unirrigated sub-plots only started to increase about six weeks after the experiment was uniformly irrigated on 15 November culminating in a first production peak on 3 January. Although the soil within the unirrigated sub-plots had then reached field capacity the weekly yield of made tea declined to zero again at the end of January before peaking for a second time on 26 February, and for a third time on 27 May. Despite these peaks, the yields from the unirrigated treatments remained below those of the fully irrigated sub-plots at all times during the wet season. The responses of clones in the partially irrigated I_2 and I_3 treatments fell between those of the extreme I_0 and I_4 treatments (Figure 5.4b).

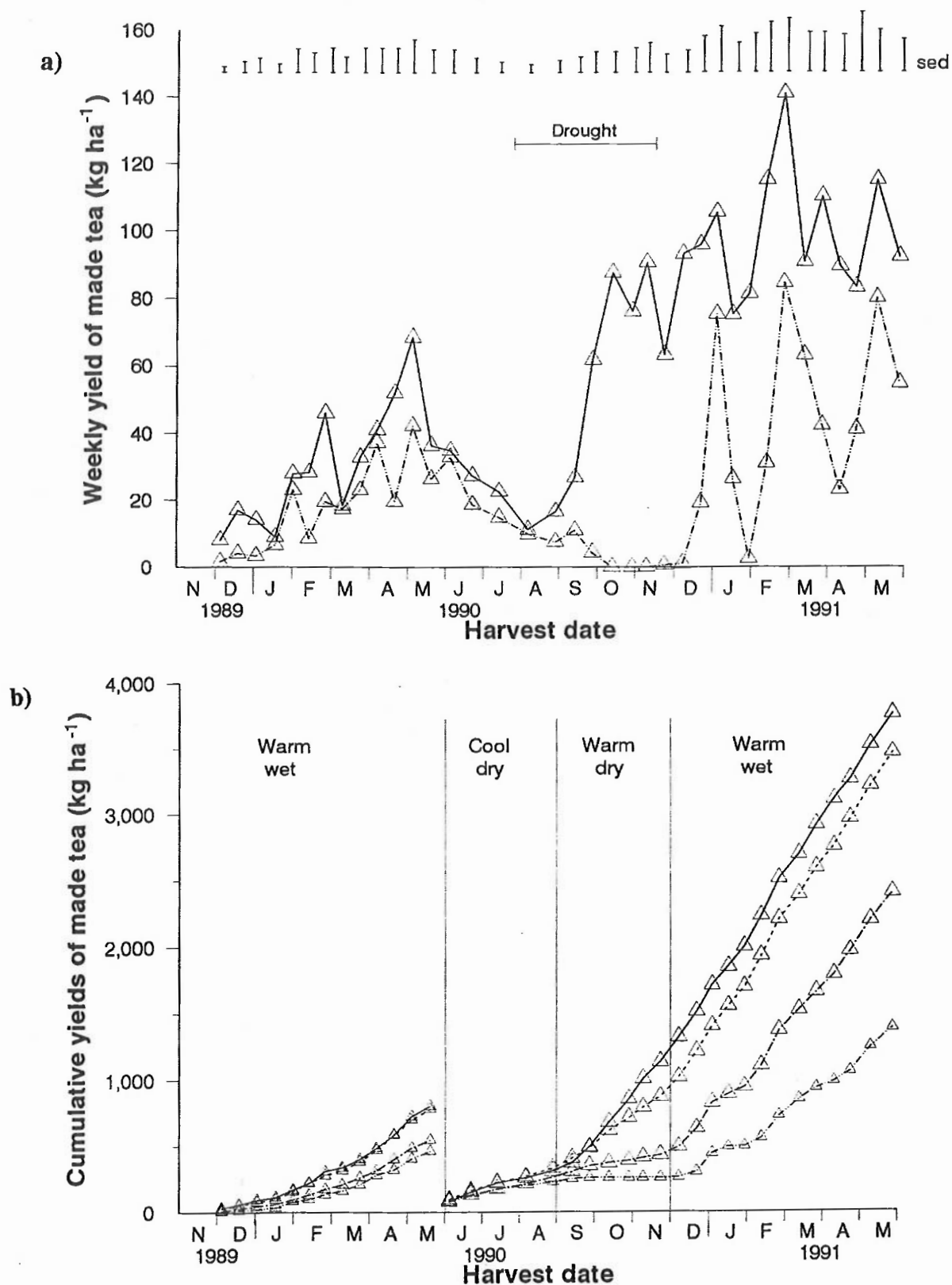


Figure 5.4. Seasonal distribution of a) the weekly yields of made tea from fully irrigated (I_4): $\triangle$, and unirrigated (I_0): $\triangle$ clone S15/10, and b) the corresponding cumulative yields with each of four drought treatments. Fully irrigated (I_4): $\triangle$, partially irrigated (I_3): $\triangle$, (I_2): $\triangle$, and unirrigated (I_0): $\triangle$.



Plate 5.1. View showing a sub-plot of fully irrigated (I_5) clone S15/10 on 1 November 1990



Plate 5.2. View showing a sub-plot of unirrigated (I_1) clone S15/10 on 1 November 1990.

Yield responses to drought

During the six months of the 1989/90 wet season, all the clones showed similar response to the drought treatments imposed during the preceding dry season (Figure 5.5). Yields were reduced ($P \leq 0.05$) in those sub-plots where the mean SWD during the 1989 dry season exceeded 27 mm. When fully irrigated, clone S15/10 was higher yielding ($P \leq 0.05$) than clones 1, 6/8, SFS150 and K35. Clone S15/10 also had the highest yield when unirrigated, but this was not significantly higher than the other clones.

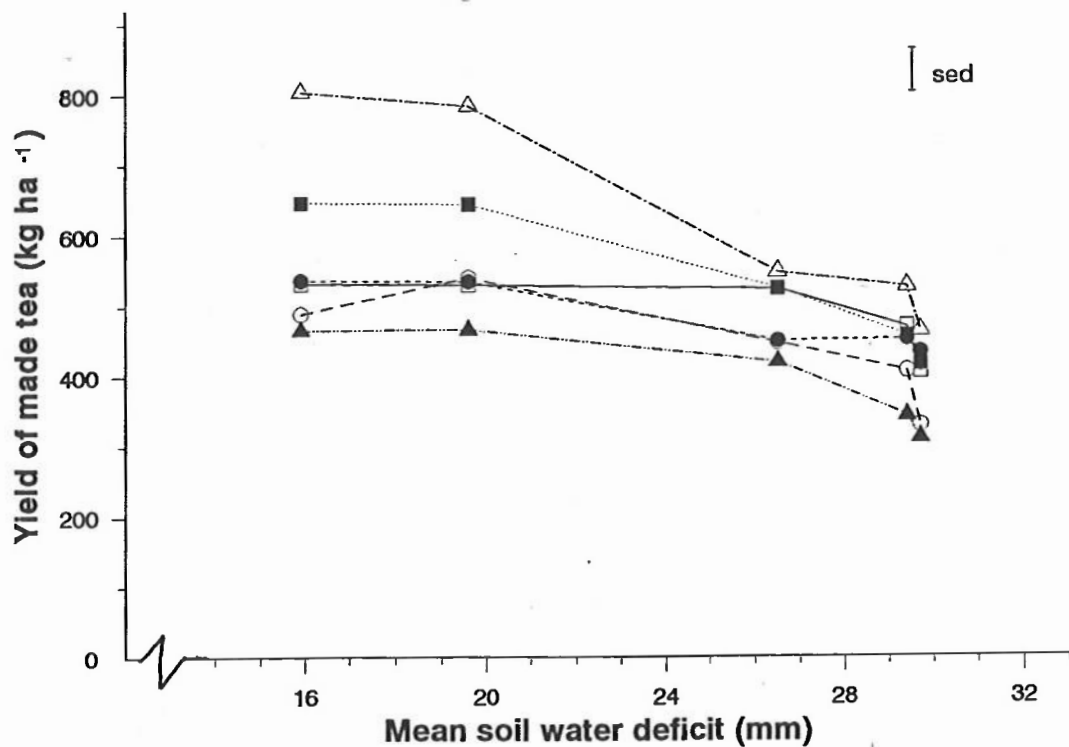


Figure 5.5. Yield responses during the wet season, December 1989 to May 1990, for each of six clones to the mean soil water deficit during the preceding 1989 dry season. Clones 1: —□—, 6/8: --○--, SFS150: ---●---, S15/10: —△—, 207: —■—, K35: —▲—.

In the following year differential drought treatments were imposed from 27 July to mid-November, and the mean SWD between 1 June and 30 November ranged from about 20 mm in the fully irrigated I_5 and I_4 treatments to about 74 mm in the unirrigated I_1 and I_0 treatments. Over the twelve months from 1 June 1990 to 30 May 1991 there were significant ($P \leq 0.001$) clone $\times$ drought interactions on annual yield (Figure 5.6). For example although the maximum yield of clone S15/10 was larger ($P \leq 0.01$) than for each of the other clones, it was not significantly different from clones 1, 6/8 and SFS150 when unirrigated.

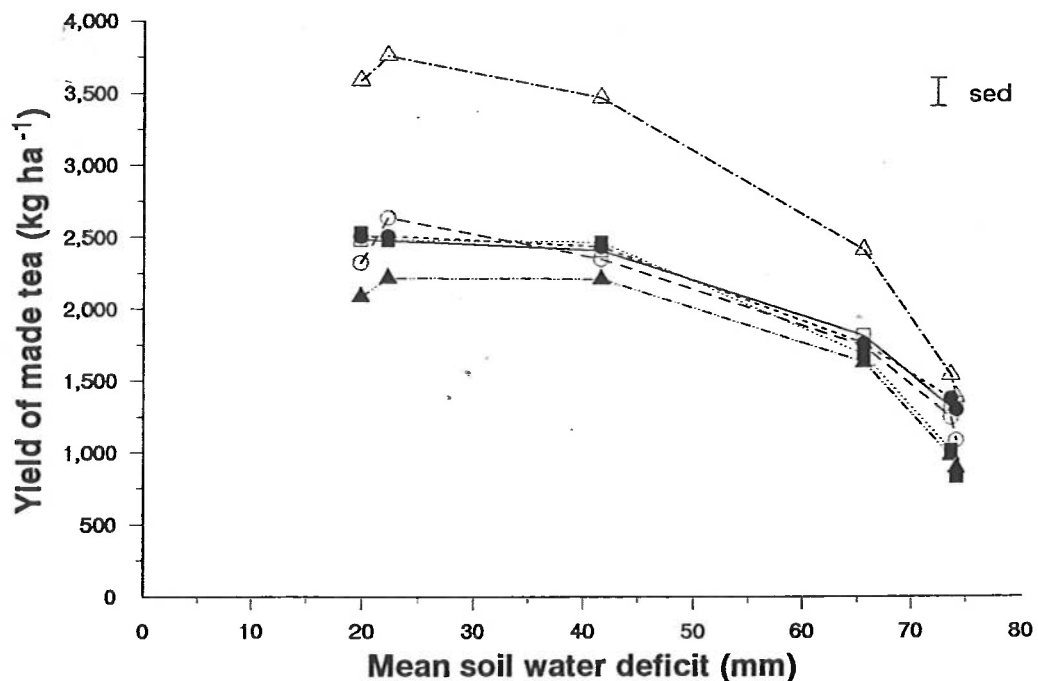


Figure 5.6. Yield responses for the year, June 1990 to May 1991, for each of six clones to the mean soil water deficit in the 1990 dry season. Clones 1: —□—, 6/8: --○--, SFS150: ---●---, S15/10: —△—, 207: —■—, K35: —▲—.

Because the relationships between annual yield and SWD were not linear, the 'drought stress' in each drought treatment was quantified as the mean yield reduction below the maximum yield Y_m . This ranged from zero in the I_4 sub-plots to 1545 kg ha⁻¹ in the I_0 treatments. A linear regression of the ratio of the actual to the maximum yield (Y_a/Y_m) against this measure of drought stress showed that there were clonal differences in drought response (Figure 5.7). Clones 1 and SFS150 had less negative values ($P \leq 0.05$) for K_y (ie, their annual yields were more stable) than clones 207 and S15/10. The responses of clones 6/8 and K35 were intermediate (Table 5.5).

Table 5.5. Maximum yields of made tea (Y_m) and the relative yield response to drought (K_y) for each of six clones from June 1990 to May 1991 inclusive. The yield of made tea from each clone in the unirrigated (I_0) sub-plot is presented for comparison.

June 1990 to May 1991		Maximum yield (Y_m) (kg ha ⁻¹)	Relative yield response to drought (K_y) (t ⁻¹ ha)			Yield in the I_0 sub- plot (kg ha ⁻¹)	
Clone	1	2480	z	-0.313	a	1336	a
	6/8	2636	z	-0.383	az	1083	az
	SFS150	2510	z	-0.320	a	1296	a
	S15/10	3761	a	-0.414	z	1385	a
	207	2485	z	-0.416	z	828	z
	K35	2216	z	-0.379	az	889	z
sed		166		0.039		166	
n		4		137		4	
r ²				81%			

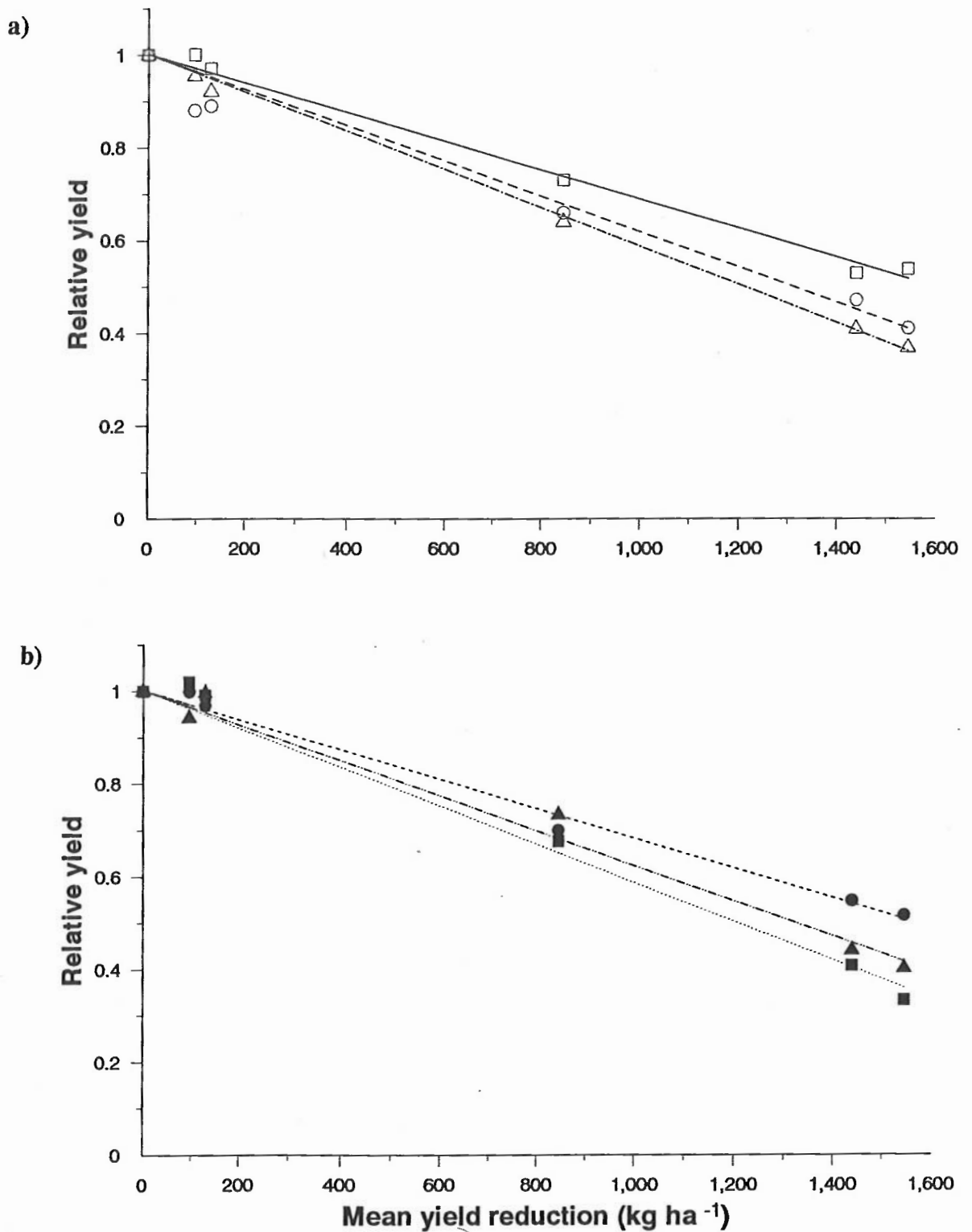


Figure 5.7. Relative yield responses for each of six clones to drought for the year June 1990 to May 1991. Drought stress was quantified as the mean reduction in the yield of the six clones below the mean maximum yield. a) Clones 1: —□—, 6/8: —○—, S15/10: —△—, b) SFS150: —●—, 207: —■—, and K35: —▲—.

The responses of the clones to drought between June 1990 and May 1991 were also examined separately for the dry and wet seasons. During the dry season there were significant ($P \leq 0.001$) clone $\times$ drought interactions in yield (Figure 5.8). Where fully irrigated clone S15/10 again had the highest yield ($P \leq 0.05$), but within the unirrigated I_0 sub-plots it produced less ($P \leq 0.05$) than clone SFS150.

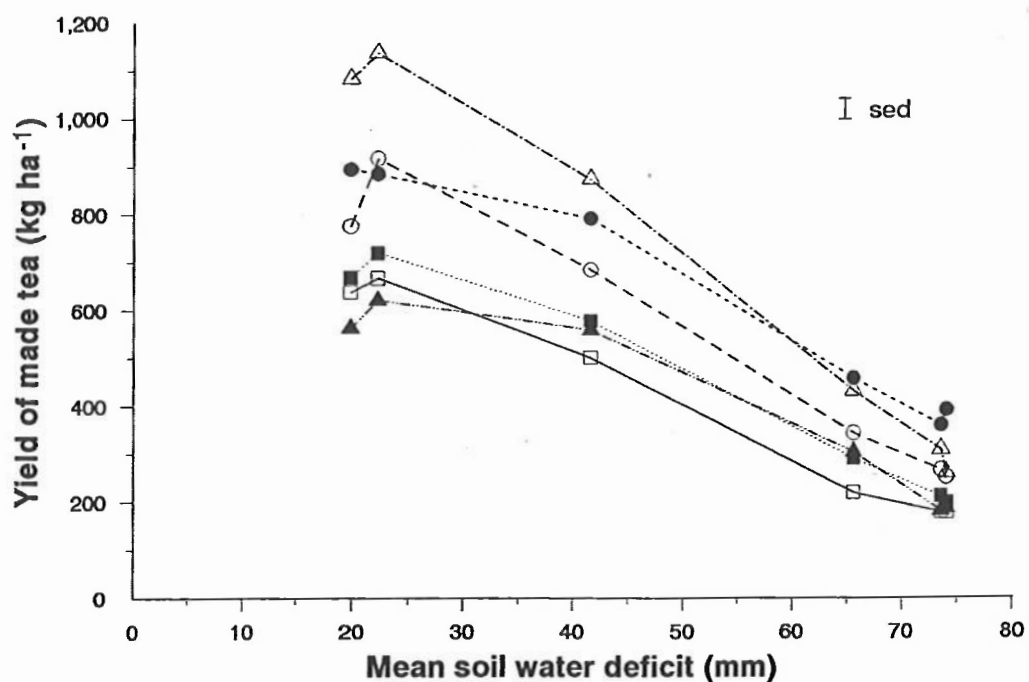


Figure 5.8. Yield responses during the 1990 dry season for each of six clones to the corresponding mean soil water deficit. Clones 1: —□—, 6/8: —○—, SFS150: —●—, S15/10: —△—, 207: —■—, K35: —▲—.

For each of the clones there was an almost linear decrease in dry season yield as the mean SWD increased above 20 mm. The responses of each clone to drought could therefore be examined in terms of a maximum yield (Y_m) and a relative yield response (K_y) to increases in SWD above 20 mm. The value of K_y was less negative ($P \leq 0.05$) for clone SFS150 than for each of the other clones with the exception of clone K35 (Table 5.6). Unlike the analysis for the complete year, the yields for the dry season did not identify clone 1 as drought resistant.

Table 5.6. Maximum yields of made tea (Y_m) and the relative yield response (K_y) to increases in SWD above 20 mm for each of six clones during the 1990 dry season.

June to November 1990		Maximum yield (Y_m) (kg ha ⁻¹)		Relative yield response to drought (K_y) (kg kg ⁻¹ mm ⁻¹)	
Clone	1	667	z	-0.0133	z
	6/8	917	z	-0.0131	z
	SFS150	885		-0.0109	a
	S15/10	1137	a	-0.0132	z
	207	720		-0.0128	z
	K35	621	z	-0.0122	az
sed		44		0.00072	
n		4		137	
r ²				90%	

There were also clone x drought interactions ($P \leq 0.001$) for yields recorded during the wet season from December 1990 to May 1991 (Figure 5.9). However unlike the results for the dry season, these yields were not linearly related to the SWD. Whereas during the dry season the yields from the I_3 treatments were lower ($P \leq 0.05$) than those from the I_4 sub-plots, during the wet season (although not significant) the yields of four clones (1, SFS150, 207 and K35) were higher from the I_3 than the I_4 sub-plots. This yield compensation was only apparent in the I_3 treatments, as in the more severely drought stressed sub-plots wet season yields remained below ($P \leq 0.001$) those which had been fully irrigated.

Because the yields during the rains were not linearly related to the SWD during the preceding dry season (Figure 5.9), the 'drought stress' was again defined as the mean yield reduction below the mean maximum yield (Y_m) determined from the fully irrigated I_4 treatment. Using this definition the relative yield responses to drought (K_y) were less negative ($P \leq 0.05$) for clone 1 than for clones S15/10, 207 and K35. The values of K_y were similar for clones 1, 6/8 and SFS150 (Table 5.7).

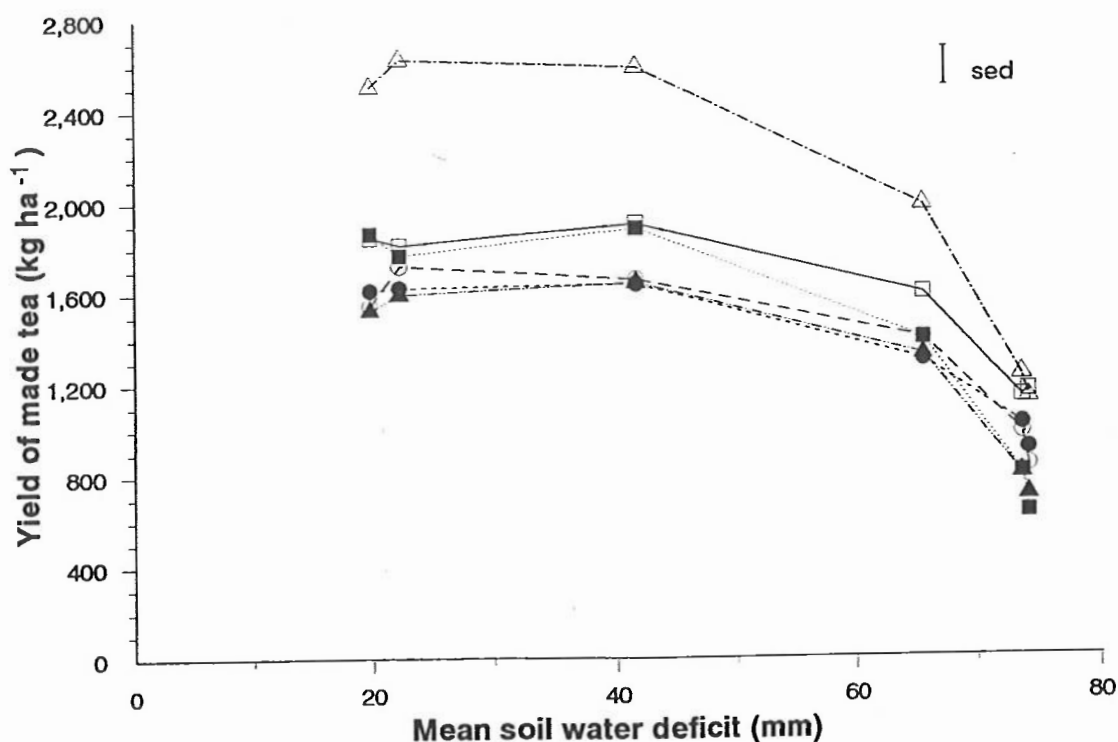


Figure 5.9. Yield responses during the 1990/91 wet season, December to May, for each of six clones to the mean soil water deficit during the preceding dry season. Clones 1:—□—, 6/8:---○---, SFS150: ---●---, S15/10: —△—, 207: —■—, K35: —▲—.

Table 5.7. Maximum yields (Y_m) and the relative yield responses to drought stress (K_y) for each of six clones during the wet season from December 1990 to May 1991.

December 1990 to May 1991		Maximum yield (Y_m) (kg ha ⁻¹)		Relative yield response to drought (K_y) (t ⁻¹ ha)	
Clone	1	1812	z	-0.397	a
	6/8	1719	z	-0.521	az
	SFS150	1625	z	-0.458	a
	S15/10	2624	a	-0.610	z
	207	1765	z	-0.647	
	K35	1595	z	-0.575	
sed		137		0.080	
n		4		137	
r ²				81%	

DISCUSSION

Yields from fully irrigated clones

During the third full year after planting out in the field, a mean annual yield of made tea of 2680 kg ha⁻¹ was achieved from six fully irrigated clones. These yields are comparable to yields of about 3000 kg ha⁻¹ obtained on the best commercial estates in Southern Tanzania from partially irrigated mature seedling tea with full ground cover. The large yields obtained in this experiment at commercial plant spacings were possible through rapid establishment of ground cover by pegging, prevention of drought stress by irrigation and removal of a high proportion of harvestable shoots by tightly controlled plucking. The possibility of achieving such yields within three years has major implications for the cash flow and return from capital for new plantings, as well as requirements for labour.

During this period fully irrigated clone S15/10 yielded 1100 kg ha⁻¹ more than any of the other clones. The reasons for this are examined elsewhere in this thesis, but include larger ground cover (cf Chapter 6) and a greater partitioning of dry matter to stem and shoots (cf Chapter 8) than the other clones.

Although not significantly different, the yields from the fully irrigated I₄ subplots were consistently higher than those from the I₅ treatments. The most probable reason for this difference is that the fully irrigated I₅ treatments (along with the unirrigated I₀ treatments) were the foci of most of the crop measurements taken within the experiment, including ground cover, shoot population density, shoot extension and stomatal conductance. The increased disturbance of these bushes and possible effects of soil compaction due to increased trampling could have caused these reductions in yield.

Yield distribution

There were clonal differences in the seasonal distribution of yield with clones 1 and SFS150 representing extremes. Clone SFS150, which had the lowest base temperature and lowest thermal extension rate (cf Chapter 9), was able to produce the largest yield of tea during the cool season. In contrast clone 1, which has a high base temperature for shoot extension and a high thermal extension rate, whilst producing little yield through the cool season, produced more yield than clone SFS150 after air temperatures increased.

These clonal differences in seasonal yield distribution have implications for quality, labour and factory requirements. Tea produced from shoots harvested during the cool season is generally considered to be of higher quality than that in the wet season. Therefore the total economic value of the made tea may increase if a clone produces a high proportion of its crop during the cool season. In addition if a clone can maintain shoot production through the cool season, not only does this smooth the seasonal distribution of yield, but it also tends to dampen the large peaks and deep troughs of yield found at the end of a period during which growth was inhibited (Fordham and Palmer-Jones, 1977). By creating a more even distribution of yield, people involved in harvesting can be more regularly employed than if the yield is concentrated in the wet season. A more even distribution of yield also enables more effective use of factory and transport capacity.

Effects of drought on plant survival

Over 85% of the plant deaths that occurred between August 1990 and June 1991 occurred within the I_0 and I_1 unirrigated treatments. Very few of these deaths were apparent immediately after the end of the dry season in December 1990, but they occurred over the following seven months and were associated with *Phomopsis theae* which establishes rapidly in drought stressed plants (Rattan, 1986). In this experiment the susceptibility of plants to *Phomopsis theae* was also increased by bringing the plants into bearing by pegging rather than pruning (Rattan, 1981).

The plant deaths in the unirrigated treatments were not evenly distributed between the clones, with fewer plants of clones 1 and SFS150 dying than the other clones. Whilst it is difficult to separate clonal differences in resistance to drought from resistance to *Phomopsis theae* in this experiment, it is clear that there are the substantial clonal differences in plant survival when drought stressed. Clone 207 was particularly susceptible to drought and/or *Phomopsis theae*.

Yield responses to drought

Yield responses to drought were examined for the twelve months from June 1990 to May 1991 in terms of the maximum yield under well watered conditions

and a relative yield response to drought. This procedure allowed the effects of drought resistance to be studied independently from maximum yield.

Over the complete year the relative yield responses to drought were less negative for clones 1 and SFS150 than clones 207 and S15/10. In determining the reasons for the greater drought resistance of clones 1 and SFS150 it is important to separate causes of drought resistance from visible expressions of drought resistance. Both clones 1 and SFS150 showed various expressions of drought resistance which were measurable. They were both able to maintain relatively high xylem water potentials and relatively open stomata in the unirrigated treatments (Tables 12.5 and 12.8). Probably associated with this, both clones were also able to retain their leaves when the SWD was large and thereby maintain ground cover into the wet season (cf Table 6.1).

Among the possible mechanisms inferring drought resistance on clones 1 and SFS150, it is clear that there is no simple link between the base temperatures for shoot extension (cf Chapter 9) and drought resistance. The base temperature for extension was high for clone 1, but low for clone SFS150. There were also no simple effects of ground cover (these clones had neither the largest nor the smallest ground cover; cf Chapter 6) or stomatal conductance (this was generally low for clone 1 and intermediate for clone SFS150; cf Chapter 12).

One possible trait conferring drought resistance is a higher transpiration efficiency. As discussed in Chapter 7, measurements on experiment N10 showed that the leaves of clones 1 and SFS150 had a higher ratio of CO₂ uptake to H₂O loss than the other clones (Smith, 1991a). Whilst clone SFS150 had a higher proportion of thin roots at depth in the soil than clones 6/8 and S15/10, this trait did not distinguish the drought resistance of clone 1 (cf Chapter 8).

Effects of seasonal yield distribution

The analysis of the dry season yields alone did not indicate that clone 1 was relatively drought resistant or that clone 207 was particularly sensitive to drought. Both of these clones have a high base temperature for shoot extension and therefore yields during the cool season and even the early part of the warm dry season are to some extent 'repressed'. It is only during the wet season that the full yield potentials of these clones are expressed. Therefore unirrigated clone 1, which was able to maintain its ground cover (cf Chapter 6) and shoot population density (cf Chapter 10) during the dry season, was able to capitalise on the improvement in environmental conditions during the wet season. By

contrast unirrigated clone 207 was unable to fully benefit from the improved growing conditions, because of the greater number of dead plants and the abscission of mature leaves which had led to reduced ground cover on the remaining bushes. The difference in seasonal yield distribution of clones 1 and 207, in contrast to clone SFS150, means that it is necessary to determine the drought resistances of the clones over a period of at least one complete year.

This need to consider yields over the whole year also applies to the determination of critical soil deficits. The changes in the critical SWD beyond which the yield of mature clone 6/8 is reduced within the dry season have been reported by Stephens and Carr (1989). The compensation of yield in the partially irrigated (I_3) treatments during the wet season suggests that if irrigation policy was based on annual rather than dry season yields then a slightly larger critical deficit for yield loss would be determined. It is possible that this effect is greatest for clones with a high, rather than a low base temperature for shoot extension. These differences are worthy of further study as the clones mature.

Selecting clones for Southern Tanzania

By separating responses in terms of a maximum yield and a relative yield response to drought, it is possible to start identifying those clones which will give the highest yield under different drought regimes. In areas where there is little or no drought stress then clone S15/10 which had the highest maximum yield (Y_m) will obviously provide the largest yield.

During the dry season in Southern Tanzania the monthly maximum air temperatures are about 18-24°C and the afternoon VPD rarely exceeds 2.3 kPa. These are below the levels that are considered to cause heat or atmospheric drought stress (Tanton, 1982b; Carr and Stephens, 1992). However the SWD below mature tea can exceed 300 mm. Therefore in these conditions the yield of a clone also depends upon the response to SWD. If there are two clones with similar relative yield responses to drought, then the clone with the highest maximum yield will consistently give the largest yield. If there are clones with different values of Y_m and K_y , then the highest yielding clone depends upon the anticipated level of drought stress. In this experiment, although the value of K_y was more negative for clone S15/10 than clones 1 and SFS150, the yield of clone S15/10 in the unirrigated treatments was still the highest (although not significantly) because it had a higher value of Y_m . If a greater drought stress is

envisaged than that examined in this experiment then the highest yields may be obtained from clones 1 and SFS150.

CONCLUSIONS

The annual yields of six contrasting clones were examined, in terms of clonal differences in maximum yield (ie, yield under well watered conditions) and a relative yield response to drought. Clone S15/10 had the highest maximum yield, whilst clones 1 and SFS150 were the most drought resistant. If a clone is to be grown under well watered conditions then a high yield potential should be sought. If the clone is to be grown under conditions of drought stress then both the maximum yield and the relative yield response to drought need to be considered. Those factors determining maximum yields and relative yield responses to drought were discussed briefly, and are examined in greater detail through the remainder of the thesis.

There were important clonal differences in the seasonal distribution of yield. By selecting clones able to produce a more even seasonal output of yield, the grower may improve the quality of made tea, maintain a more permanent work force and make more effective use of capital equipment. Clonal differences in seasonal yield distribution also means that it is important to consider carefully the time period over which a response is studied. For a crop such as tea which is frequently harvested, yield responses should ideally be determined over at least one complete year.

CHAPTER 6

LIGHT INTERCEPTION AND DRY MATTER PRODUCTION

INTRODUCTION

The rate of dry matter production (DM; g m⁻² d⁻¹) by tea or any crop (Squire, 1985) can be expressed as:

$$DM = S \cdot f_s \cdot \epsilon_s \quad 6.1$$

where:

S is the incident solar radiation (MJ m⁻² d⁻¹),

f_s is the proportion of solar radiation intercepted by the crop canopy, and

ϵ_s is the net dry matter/light conversion ratio or the conversion efficiency (g MJ⁻¹).

Total light interception ($S \cdot f_s$) for a continuous canopy can be calculated using Equation 6.2 (Charles Edwards, 1982):

$$S \cdot f_s = S \cdot (1 - e^{-k \text{ LAI}}) \quad 6.2$$

where k is a canopy light extinction coefficient and LAI is the leaf area index. However young tea does not form a continuous canopy, but comprises bushes where the leaves are densely grouped and areas between the bushes where there are no leaves at all. In such situations it is advantageous to consider the incident light as consisting of two components (Jackson and Palmer, 1979). There is light which falls directly on the spaces between the bushes, and light that falls within the area of the bush canopy which can be intercepted. The proportion of ground covered by the crop is often termed the ground cover (GC). Therefore the interception of solar radiation by a discontinuous canopy can be expressed as:

$$S \cdot f_s = S \cdot GC \cdot (1 - e^{-k \text{ LAI}'}) \quad 6.3$$

where k is the light extinction coefficient within the bush canopy and LAI is the leaf area per unit area of ground covered by the crop. At complete ground cover ($GC = 1$), Equation 6.3 is identical to Equation 6.2.

Magambo and Cannell (1981) reported that the annual dry matter production of harvested clone 6/8 with complete ground cover at an altitude of 2178 m in Kenya was 16.9 t ha^{-1} . Assuming total interception of the annual receipt of total solar radiation of $6500\text{--}7500 \text{ MJ m}^{-2}$, this is equivalent to a value for ϵ_s of about 0.25 g MJ^{-1} . In comparison the maximum annual dry matter production for tropical plantation crops such as cocoa, oil palm, coconut and rubber is between 30 and 42 t ha^{-1} (Corley, 1983). Assuming a similar radiation receipt ($6000\text{--}7500 \text{ MJ m}^{-2} \text{ y}^{-1}$), this is equivalent to a value for ϵ_s of $0.40\text{--}0.68 \text{ g MJ}^{-1}$. This in turn is less than the value of 1.4 g MJ^{-1} reported for field crops in the U.K (Monteith, 1977).

The dry matter production reported by Magambo and Cannell (1981) were from measurements of one clone at high altitude close to the equator with relatively low mean monthly temperatures (range: $14\text{--}17^\circ\text{C}$) (Stephens *et al.*, 1992). This Chapter reports measurements made at Ngwazi Tea Research Unit to compare the effects of season and drought on the light interception, dry matter production and value of ϵ_s for six clones.

METHODOLOGY

Solar radiation

The radiation received at the atmosphere's surface above Ngwazi Tea Research Unit ($8^\circ 32'S$, $35^\circ 10'E$, altitude 1840 m) remains relatively constant from November to March and descends to a minimum at the end of June in the middle of 'winter' (McCulloch, 1965; Figure 6.1). Measurements made with a Gunn Bellani pyranometer (calibrated against a Kipp Pyranometer) showed that the actual radiation received on site at Ngwazi followed a different seasonal pattern. Maximum values ($23 \text{ MJ m}^{-2} \text{ d}^{-1}$) occurred in October when high atmospheric radiation coincided with little cloud. During the rainy season from November to May, when there was greater cloud cover, incident radiation fell to a mean of $15 \text{ MJ m}^{-2} \text{ d}^{-1}$, before rising again during the dry season.

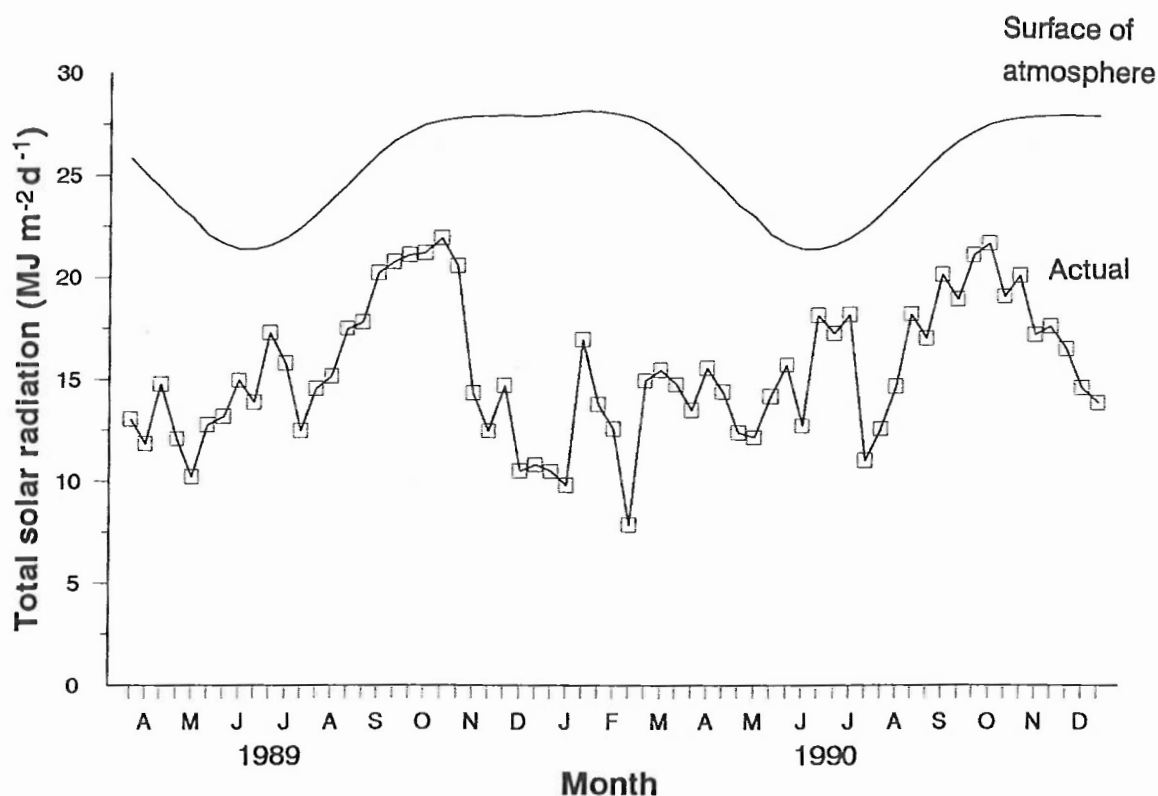


Figure 6.1. Total solar radiation at the surface of the atmosphere and the actual measured total solar radiation at Ngwazi Tea Research Unit from August 1988 to May 1991.

Ground cover

Field measurements of ground cover were taken within the main clone x drought experiment described in Chapter 3. In relation to light interception two points need emphasising: the six clones were planted in August 1988 at a spacing of 1.2 x 0.8 m, and they were pegged between April and October 1989. The effect of pegging was to accelerate the development of ground cover.

Ground cover was measured using a frame of dimensions 1.2 x 0.8 m (identical to the plant spacing) containing a grid of 96 x 0.01 m² squares. This was held in a fixed position immediately above a bush and each square was examined individually from overhead. Ground cover was then estimated as follows: if leaves covered less than 25% of the area of a square there was no count, 25-75% corresponded to one count and over 75% corresponded to two counts. The total count for the whole grid was divided by the maximum total of 186 and the answer was expressed as a percentage.

The ground cover of selected bushes was measured at monthly intervals from September 1989 to June 1991. Initially three bushes were measured in each of the four replicates of the fully irrigated (I_5), partially irrigated (I_2) and unirrigated (I_0) sub-plots for each of the six clones. After April 1990 the number of bushes examined per sub-plot was reduced to two. On three occasions between September and December 1990 ground cover was also measured in the I_4 , I_3 and I_1 drought treatments. It was necessary to perform an arc-sine transformation on those measurements made before March 1990, when the mean ground cover was below 30%, prior to statistical analysis. After this date the data were judged to be normally distributed and a transformation was not required.

Whole plant harvests

Light interception and dry matter production were determined from harvests of whole plants, including roots, taken from the observation block at the lower end of the main clone x drought experiment. This block received the same uniform and differential drought treatments as the main experiment.

The first plants were harvested at the end of the wet season in April 1989 eight months after planting. To determine the effects of season on light interception and dry matter production subsequent samples were taken at the end of the cool season in August and at the end of the warm dry season in December 1989. The same procedure was repeated during 1990 in early May after the wet season, in mid-August and late November.

For each of the four harvests from April 1989 to May 1990 inclusive one plant of clones 1, 6/8, SFS150, S15/10, 207 and K35 was selected from a fully irrigated (I_5 or I_4), intermediate (I_3 or I_2) and unirrigated (I_1 or I_0) sub-plot. In August 1990 only four clones: 1, 6/8, SFS150 and S15/10 were sampled due to the excessive labour requirements for harvesting roots. Clone S15/10 was chosen because it partitioned a higher proportion of dry mass to leaves than the other clones (cf Chapter 8) and clone 6/8 was selected to allow comparison with other measurements on the same clone (Magambo and Cannell, 1981). Clones 1 and SFS150 were chosen on the basis of respectively having high (Stephens and Carr, 1990) and low base temperatures for shoot extension (Cannell *et al.*, 1990). Because only one plant was selected from each treatment it was not possible to test for clone x drought interactions. In November 1990, at the end of the dry season, clones 1, 6/8, SFS150 and S15/10 were sampled again but this time three

plants were selected from within each fully irrigated (I_5 - I_4) and each unirrigated (I_1 - I_0) sub-plot so that clone x drought interactions could be statistically tested.

From December 1989 each harvested plant was selected on the basis of having the median ground cover of a pre-determined group of ten plants. The chosen plants were always surrounded on each side by bushes of the same clone and age.

Light interception

The selected plants were cut at ground level and the canopy was removed and separated into stem and leaves. The total leaf area was determined using a calibrated card to measure the area of each individual leaf (Pethiyagoda and Ragendram, 1965). For the final two harvests total leaf areas were calculated from the total fresh mass of leaf and measurement of leaf area for three randomly selected 100 g samples.

The total light intercepted by each selected clone x drought treatment combination during each season from December 1989 to November 1990 was calculated using Equation 6.3. This required knowledge of the incoming total solar radiation, the mean of the initial and final ground cover, and values for LAI' and k . A constant value for k of 0.6 was assumed for each clone. This is a similar value to apple trees (Jackson and Palmer, 1979) and about mid-way between values of 0.35 for ryegrass and 0.90 for clover (Jarvis, 1981).

Dry matter production

The fresh mass of stems and leaves were measured from each harvested canopy. To determine the root mass an area centred on the base of the plant corresponding to the plant spacing (0.8 x 1.2 m) was excavated beyond the maximum rooting depth of the crop (Plate 6.1). This ranged from 0.4 m in April 1989 to about 2.0 m in November 1990. The excavated soil was sieved through a 10 mm² wire mesh and the soil not passing through the sieve was placed in sacks. It was very rare to find any tea roots passing through the sieve. The soil in the sacks was then washed over another sieve and the tea roots removed by hand (Plate 6.2).



Plate 6.1. Excavation of roots



Plate 6.2. Separation of roots from soil by sieving

The roots, stems and leaves of each plant were oven dried at 85-90°C for 48 hours or until there was no further loss in mass. In the later harvests, when the volume of plant material was too large for the oven, the dry mass of each component was estimated from the total fresh mass and the dry mass/fresh mass ratio of two to four samples selected at random (range: 30 - 240 g).

After December 1989 some of the dry matter produced by each bush was removed as harvested shoots. This mass was estimated for each individual bush from a count of the stumps that remain when a shoot is harvested and the recorded mean shoot dry mass for the corresponding clone x drought treatment within the main experiment. For the final harvest, in November 1990, the dry mass of abscised leaves at the base of each plant was also included in the total dry mass.

Based on the measurements of cumulative dry mass it was possible to estimate the incremental increase in dry mass during each season. For the final three seasons from December 1989 to November 1990 when ground cover measurements were taken it was also possible to estimate light interception and values of ϵ_s .

RESULTS

Ground cover

The mean ground cover of the plants in the fully irrigated (I_5) sub-plots increased from 13% in September 1989, 13 months after planting, to 87% by May 1991. This steady increase was interrupted during the cool season from June to August, when ground cover development effectively stopped (Figure 6.2). It only started again as temperatures rose in September.

There were clonal differences ($P \leq 0.001$) in ground cover, which changed as the plants grew. Within the fully irrigated treatments the ground cover of clone 207 (19%) was higher ($P \leq 0.05$) than that of clones 6/8, S15/10 and K35 (9-12%) for the first set of measurements in September 1989. However by July 1990 the ground cover of fully irrigated clones 1 (64%) and S15/10 (60%) were greater ($P \leq 0.05$) than each of the other clones (37-50%), including clone 207. The ground cover of clone 6/8 was lower ($P \leq 0.05$) than each of the other clones with the exception of clone K35 at this time.

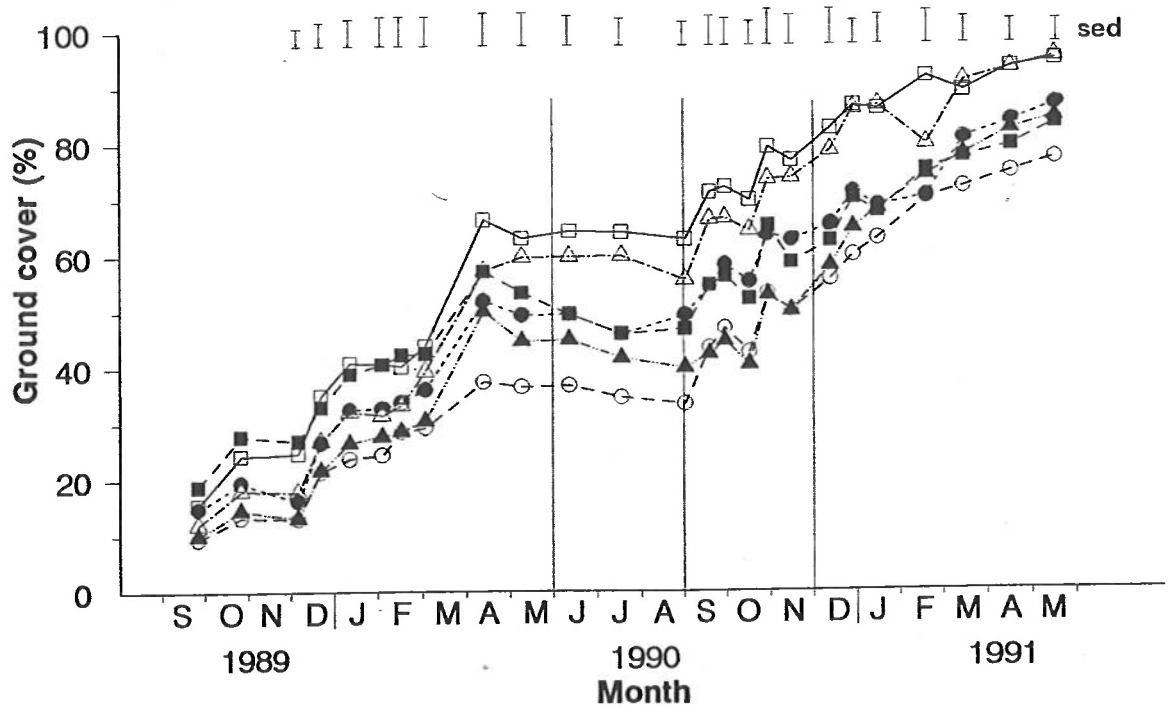


Figure 6.2. Changes in ground cover for each of six fully irrigated clones from September 1989 to May 1991. Clones 1: —□—, 6/8: ---○---, SFS150:●....., S15/10: —△—, 207: —■—, and K35: —▲—.

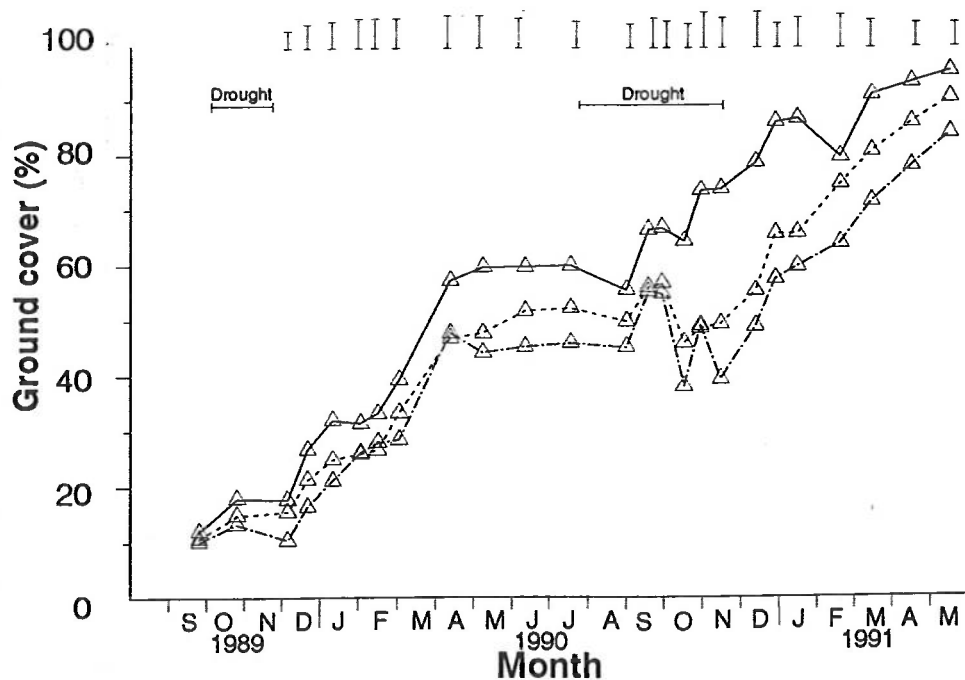


Figure 6.3. Changes in ground cover for clone S15/10 within each of three drought treatments from September 1989 to May 1991. Fully irrigated (I_5): —△—, partially irrigated (I_2): -△--, and unirrigated (I_0):△.....

By May 1991 the ground cover was still higher ($P \leq 0.05$) for clones 1 and S15/10 (95%) than for clones 6/8, 207 and K35 (77-84%).

Effects of drought

The effects of drought on the development of ground cover by clone S15/10 within three treatments are shown in Figure 6.3. Following the imposition of drought treatments between October and November 1989, the ground cover of clone S15/10 in the fully irrigated sub-plots (18%) in early December was greater ($P \leq 0.05$) than that in the unirrigated (I_0) treatments. Although ground cover increased in each treatment after the start of rains, the ground cover of clone S15/10 was still greater ($P \leq 0.05$) in the I_5 (60%) than in the I_0 (46%) sub-plots in early July, prior to the imposition of differential drought treatments in 1990. The ground cover in the I_2 sub-plots was intermediate (52%). Following the cool season ground cover in the fully irrigated sub-plots started to rise again in September. In the unirrigated treatments ground cover only started to increase at the end of November after the start of the rains. By May 1991 the ground cover of S15/10 in the fully irrigated sub-plots (95%) was still higher ($P \leq 0.05$) than that in the unirrigated treatments (84%).

Clone x drought interactions

At the end of the dry season in 1990 for most clones there were no significant differences between the ground cover in the I_0 , I_1 and I_2 irrigation sub-plots receiving little or no irrigation, or between the wetter I_3 , I_4 and I_5 sub-plots (Figure 6.4). If the irrigation treatments were examined as two blocks: (I_0, I_1, I_2) and (I_3, I_4, I_5) then on each of the three occasions when measurements were taken in all drought treatments there were clone x drought interactions ($P \leq 0.05$). Whilst the ground cover for clones S15/10 and 1 were higher ($P \leq 0.001$) than that for clone SFS150 in the well irrigated treatments, in the drier sub-plots the ground cover of clone SFS150 was similar to clones 1 and S15/10 (Table 6.1). Clone 1 had the greatest ground cover within these drier treatments and this was larger ($P \leq 0.05$) than that for clone S15/10. The ground cover of clones 6/8 and 207 which were greater ($P \leq 0.05$) than that for clone K35 in the well irrigated treatments, were similar in the drier sub-plots.

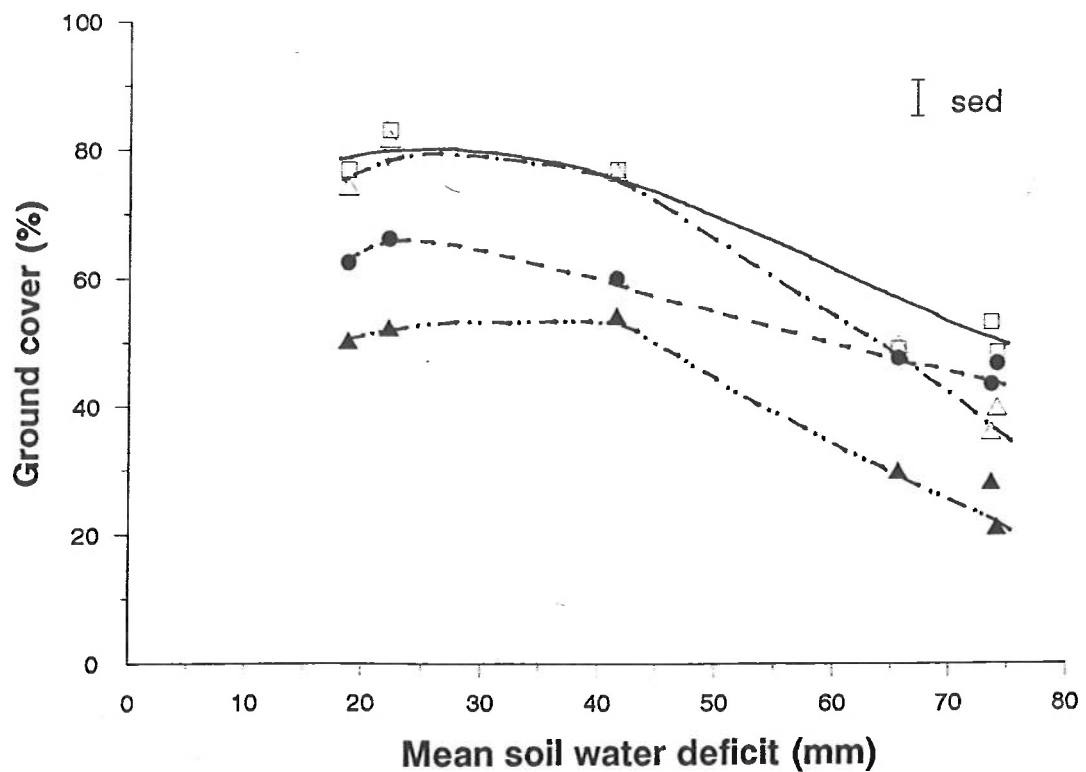


Figure 6.4. Responses of ground cover, measured at the end of the 1990 dry season on 15 November, for each of four clones to the mean soil water deficit during the 1990 dry season. Clones 1: —□—, SFS150: —●—, S15/10: —△—, K35: —▲—. Lines drawn by eye,

Table 6.1. Effects of drought on ground cover for each of six clones at the end of the 1990 dry season on 15 November

		Ground cover (%)	
		well irrigated (I ₅ , I ₄ , I ₃)	droughted (I ₂ , I ₁ , I ₀)
Clone	1	79 a	50 a
	6/8	60	32 z
	SFS150	63	46 a
	S15/10	77 a	41
	207	61	30 z
	K35	52 z	26 z
sed = 3.2, n=24			

Light interception

Light interception measurements were based on measurements of GC and LAI for each the four clones harvested from the observation block. The mean total solar radiation intercepted by clones 1, 6/8, SFS150 and S15/10 increased from 3.7 MJ m⁻² d⁻¹ (between December 1989 and May 1990) to 6.0 MJ m⁻² d⁻¹ (from May to August), and to 10.0 MJ m⁻² d⁻¹ from August to November 1990 (Figure 6.5). These increases were the result of a seasonal rise in solar radiation receipt from 14.9 to 20.7 MJ m⁻² d⁻¹ and an increase in the proportion of intercepted radiation from a mean of 25% between December 1989 and May 1990 to 48% between August and November 1990.

There were clonal differences in light interception during the cool dry season ($P \leq 0.05$) and the warm dry season ($P \leq 0.001$). During these seasons clones 1 and S15/10 intercepted more light ($P \leq 0.05$) than clone 6/8, due to their greater ground cover. This agrees with the measurements taken within the main experiment. There were no significant differences between clones in the value of LAI although this was consistently highest in clone 6/8 (range: 4.7-6.4) and lowest in clone S15/10 (range: 3.7-4.5). This corresponded to visual observations of clone 6/8 having a more 'clumped' and less spreading habit than clone S15/10.

Effects of drought

Following the imposition of differential drought treatments in 1989, although not significant, there was a trend ($P \leq 0.2$) for light interception to be greater in the fully irrigated (I_s) than the unirrigated (I_0) sub-plots during the subsequent wet and cool dry seasons. However the most pronounced effects of drought ($P < 0.001$) were established during the warm dry season in 1990. During this time mean light interception was 10.0 MJ m⁻² d⁻¹ in the fully irrigated treatments compared to 7.4 MJ m⁻² d⁻¹ in the unirrigated sub-plots. There were no significant clone x drought interactions.

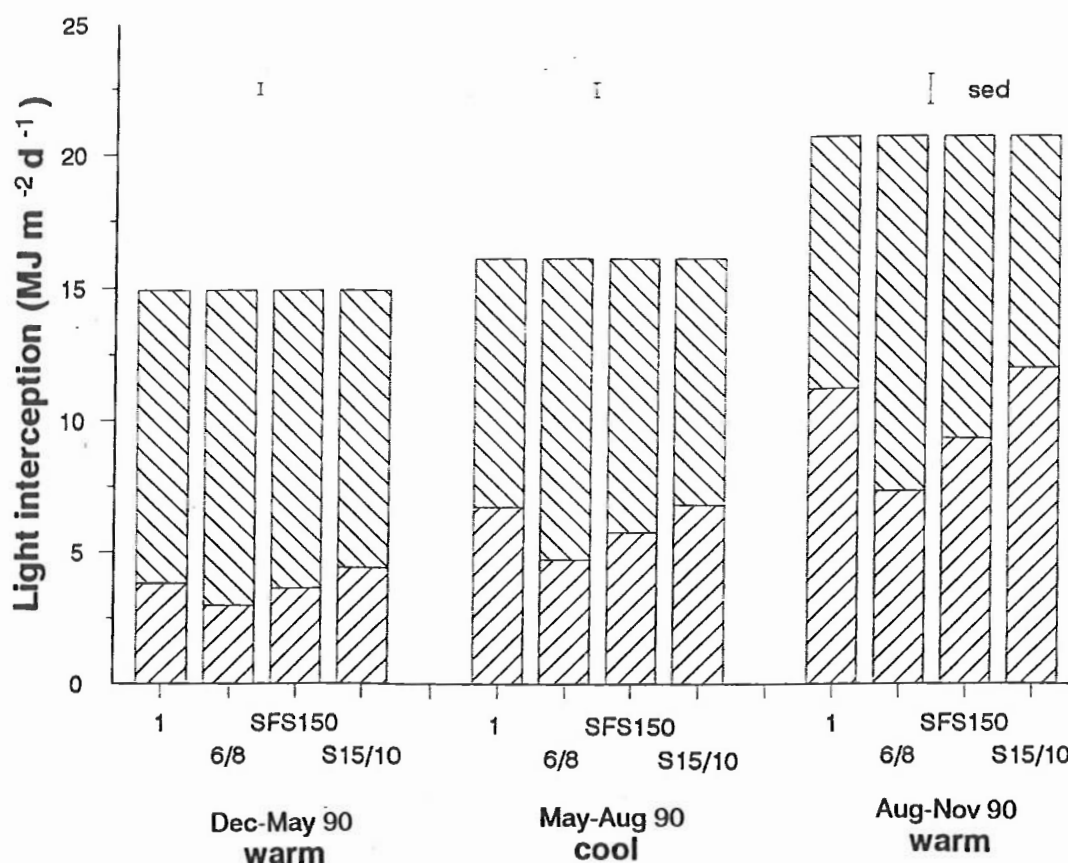


Figure 6.5. Seasonal changes in the daily incident total solar radiation:  and light interception:  for each of four clones.

Dry matter production

The mean dry mass of the tea plants, including harvested shoots, increased from 36 ± 7 g in April 1989, eight months after planting, to 1100 ± 84 g in the fully irrigated treatments by November 1989. The rate of net dry matter production increased from 0.5 (April to August 1989) to $3.3 \text{ g m}^{-2} \text{ d}^{-1}$ (August to November 1990) as the plants grew and intercepted more radiation (Figure 6.6). Over individual seasons there were clonal differences ($P \leq 0.05$) in dry matter production, but these were not consistent.

Effects of drought

Although not statistically significant, drought reduced ($P \leq 0.5$) the rate of dry matter production during the warm dry season from August to November 1989 from 0.81 to $0.55 \text{ g m}^{-2} \text{ d}^{-1}$. The effects of the drought treatments continued in the following wet season, when the mean rate of total dry matter production was

higher ($P \leq 0.05$) in those sub-plots which had been fully irrigated ($2.3 \text{ g m}^{-2} \text{ d}^{-1}$) than those which were unirrigated ($1.1 \text{ g m}^{-2} \text{ d}^{-1}$). The rate of dry matter production in the partially irrigated sub-plots were intermediate ($1.9 \text{ g m}^{-2} \text{ d}^{-1}$). These variations were probably the result of differences in ground cover.

During the 1990 warm dry season the effects of drought were even more marked ($P \leq 0.05$) as the rate of dry matter production ranged from $3.3 \text{ g m}^{-2} \text{ d}^{-1}$ in the fully irrigated treatments to $0.85 \text{ g m}^{-2} \text{ d}^{-1}$ in the dry sub-plots. There was no evidence of significant clone $\times$ drought interactions.

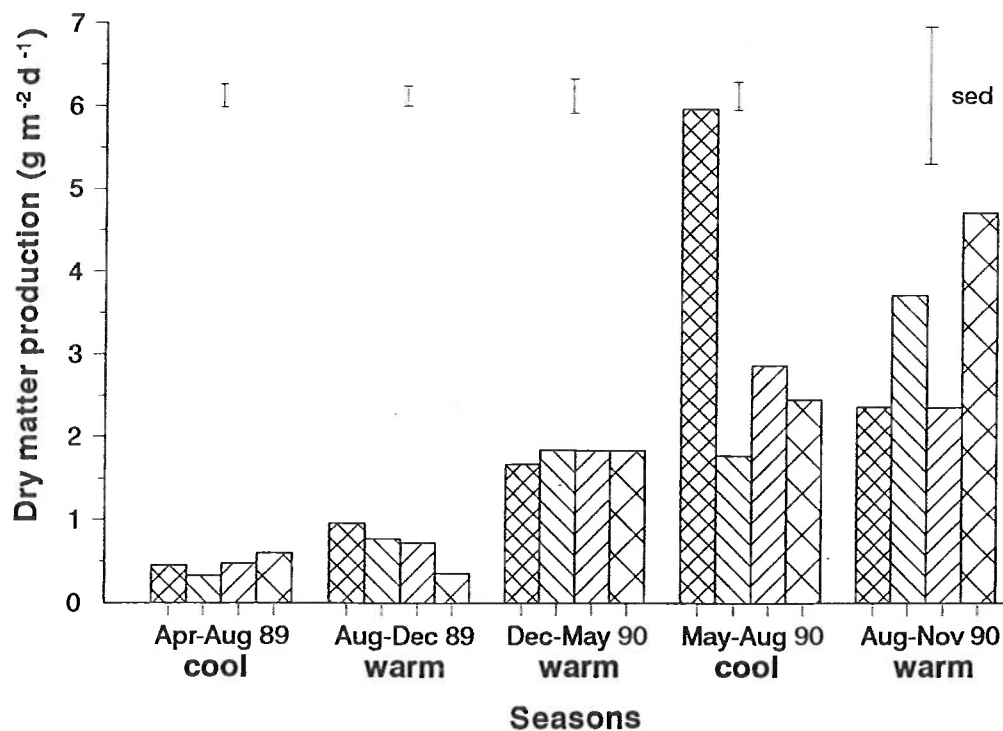


Figure 6.6. Rates of dry matter production for each of four clones during successive seasons from April 1989 to November 1990. The values are the mean of plants from fully irrigated and unirrigated sub-plots, except for the warm dry season 1990, where only values from the fully irrigated sub-plots are presented. Clones 1: , 6/8: , SFS150: , and S15/10: .

Conversion efficiency

The mean conversion efficiency (ϵ_s) during the wet season from December 1989 to May 1990 for the four clones was $0.49 \pm 0.04 \text{ g MJ}^{-1}$ ($n=12$). The mean value of ϵ_s during the cool season from May to August 1990 was similar at $0.55 \pm 0.09 \text{ g MJ}^{-1}$ ($n=12$). During the warm dry season from August to November 1990 the

ϵ_s for the fully irrigated tea surprisingly declined to 0.33 ± 0.06 g MJ⁻¹ (n=12). These values are higher than an estimated value for ϵ_s of 0.25 g MJ⁻¹ derived from dry matter production data for mature harvested tea in Kenya reported by Magambo and Cannell (1981). During the cool season a particularly high value of ϵ_s of 0.92 ± 0.20 (n=3) was calculated for clone 1 but this may have been the result of using a small sample. There were no significant clonal differences in ϵ_s during the wet or warm dry seasons.

Drought reduced ($P \leq 0.05$) the value of ϵ_s from 0.33 to 0.09 g MJ⁻¹ during the 1990 warm dry season. However there were also clone x drought interactions ($P \leq 0.05$). Clones 6/8 and S15/10 appeared to be the most sensitive to drought whilst clones 1 and SFS150 appeared the more drought resistant (Table 6.2). Although these results should be treated with caution because of the limited sample size, the greater drought resistance of clones SFS150 and 1 was also established in the yield measurements described in Chapter 5.

Table 6.2. Effects of drought on the conversion efficiencies (ϵ_s) for each of four clones during the 1990 warm dry season.

		Conversion efficiency ϵ_s (g MJ ⁻¹)	
		fully irrigated (I ₅ and I ₄)	unirrigated (I ₁ and I ₀)
Clone	1	0.18	0.11
	6/8	0.50	-0.13
	SFS150	0.25	0.38
	S15/10	0.36	-0.02
Mean		0.33	0.09

sed between drought treatments = 0.084 (n=12)

sed between clone x drought treatments = 0.168 (n=3).

DISCUSSION

Light interception

Jackson and Palmer's (1979) model for light interception in a discontinuous canopy allowed the effects of ground cover to be separated from those of leaf area and the extinction coefficient. The most important factor determining light interception in this young tea was ground cover. This is because the leaf area per unit area of ground cover (LAI') was similar for each clone. In addition because

LAI' was consistently high (range: 3.7-6.3) light interception was relatively insensitive to changes in k . If the value of k , which was assumed to be 0.6, was reduced to 0.3 then the estimated light interception would only fall by 18% (Table 6.3).

Table 6.3. Effects of changes in ground cover (GC), leaf area per unit area of ground cover (LAI') and extinction coefficient (k) on the proportion of light that is intercepted (f_s): $f_s = GC (1 - e^{-k LAI'})$.

GC	LAI'	k	Proportion of light intercepted f_s
50%	5.0	0.6	0.47
25%-75%	5.0	0.6	0.24-0.71
50%	2.5-7.5	0.6	0.39-0.49
50%	5.0	0.3-0.9	0.39-0.49

Ground cover

Two major factors determining ground cover development which were not specifically studied are plant spacing and the method of bringing tea plants into bearing. The plant spacing of 0.8 x 1.2 m was the same as current commercial practice in Southern Tanzania. If the plants were spaced more closely together then obviously full ground cover can be achieved more rapidly. The plants in this experiment were brought into bearing by pegging. This would have led to a more rapid ground cover development than if the plants had been brought into bearing by pruning.

There were changes in the ranking of the ground cover of the clones between September 1989, thirteen months after planting, and May 1991. Initially fully irrigated clone S15/10 ranked fourth, but by May 1991 it had the greatest ground cover. This change was probably a result of this clone partitioning a higher proportion of dry matter to leaf than the others (cf Chapter 8). This attribute would start a positive feedback: because this clone produces more leaf it can intercept more radiation, increase dry matter production and thereby increase leaf production still further.

The development of ground cover was slowest during the cool season when low temperatures are known to limit shoot extension (Stephens and Carr, 1990). Although the shoots of clones with a low base temperature for extension such as SFS150 continued to grow during this season (cf Chapter 9) this growth did not appear to result in greater ground cover. This suggests that continued extension of shoots released from apical dominance at the surface of the bush did not contribute to greater ground cover. Instead development of ground cover is perhaps primarily caused by the growth of side shoots from lower in the canopy. The thermal responses of these shoots may be different from those in the centre of the bush.

Ground cover was reduced by drought, but the response varied between clones. When drought stressed, clones 1 and SFS150 were able to maintain a greater ground cover than the other clones. This was principally a result of these two clones retaining their leaves, whilst other clones tended to prematurely abscise their leaves. This effect appeared to be more important than clonal differences in the responses of shoot extension rate to drought. In fact the shoot extension rate of clone 1 was more susceptible to drought than most clones (cf Chapter 9).

Conversion efficiency

The mean ϵ_s averaged 0.49-0.55 g MJ⁻¹ during the wet season (December to April) and cool season (May to September), declining to 0.33 g MJ⁻¹ for irrigated plants during the warm dry season (September to November). These values are higher than the 0.25 g MJ⁻¹ for mature harvested clone 6/8 at high altitude at TRFK, Kenya inferred from data presented by Magambo and Cannell (1981). A possible reason for this is that the mean air temperatures at Ngwazi are slightly higher (13.5-18.5°C) than those at TRFK, Kenya (14.0-17°C). Photosynthesis is known to be reduced by low temperatures (Smith *et al.*, 1991) and this could reduce the value of ϵ_s . The lower values in Kenya may also be the result of the sampled tea bushes being more mature than those sampled at Ngwazi. If the relative level of respiration increases as a plant becomes larger (Charles-Edwards, 1982), then this would also reduce the value of ϵ_s .

The values of ϵ_s reported here are similar to estimates for other tropical perennial crops (range: 0.4-0.7 g MJ⁻¹), but below values of about 0.7 g MJ⁻¹ reported for tropical annual crops (Singh and Sri Rama, 1989; Azam Ali *et al.*, 1989) and substantially below those of 1.4 g MJ⁻¹ for annual crops grown in temperate regions (Monteith, 1977). The value of ϵ_s depends upon the

efficiency with which light is used for photosynthesis and the level of respiration. The reduction in ϵ_s during the warm dry season occurred over a period when it was relatively warm, solar radiation levels were high and harvested yields were increasing (cf Chapter 5). Magambo and Cannell (1981) proposed that the low dry matter production of the tea they examined in Kenya was reduced by harvesting shoots, because this removed sinks for dry matter (Cannell, 1985). This presumably fed back to lower photosynthetic rates (Squire, 1985). However values of ϵ_s are also likely to be reduced at high light intensities. Measurements also taken within experiment N10 reported Smith (1991a) show that the photosynthesis of a single leaf of a well watered plant was light saturated when the light intensity reached about $1200 \mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD. This intensity is equivalent to about 520 W m^{-2} total solar radiation. However over 90% of this photosynthetic response to light intensity was achieved at about 350 W m^{-2} . Therefore during the warm dry season when midday light intensities often reached 900 W m^{-2} , if the light intercepted by a single leaf was not reflected downwards through the canopy then 40 to 60% of the intercepted radiation was not photosynthetically effective. This too would obviously reduce the measured radiation use efficiency.

The point at which radiation becomes saturating for a canopy also depends upon canopy structure, being less for planophile than for erectophile canopies (Russell *et al.*, 1989). The regular harvesting of shoots means that in commercial tea a dense layer of mature leaf is formed at the plucking surface which restricts light penetration into the canopy (Smith *et al.*, 1991). Many of these mature leaves tend to be nearly horizontal. In contrast if tea is left unharvested for many months the result is likely to be a more uneven canopy made up of fewer, but larger individual shoots with erect leaves at the top and horizontal leaves lower in the canopy. Within this canopy light penetration will be deeper and a greater number of leaves will receive light at intensities where photosynthesis per unit of radiation is more efficient. Such a change could explain why Magambo and Cannell (1981) found higher conversion efficiencies in unplucked tea than plucked tea, even though each had complete ground cover.

If the low conversion efficiency of tea is a result of maintaining a dense flat canopy which results in saturation of photosynthesis at relatively low light intensities, then this has important implications for clonal selection and bush management. Hadfield (1974) working in Assam proposed that high yielding clones would have more erect leaves. Whilst this would reduce heat stress at high temperatures, such as in Assam, this would also allow more even light

distribution. There is also the possibility that management practices that result in a dense canopy of mainly horizontal leaves, rather than erect leaves could reduce dry matter production.

The low conversion efficiency of tea compared to tropical annual species may be caused by high respiration loss from non-photosynthetic roots and stems (Corley, 1983). It has been estimated that from 67% (Tanton, 1979) to 85% (Hadfield, 1974) of the total dry matter produced by photosynthesis in tea is respired. A reduction in relative respiratory losses may be achieved by increasing the proportion of actively photosynthesising tissue.

It was not possible to determine consistent differences between the clones in conversion efficiency. During the warm dry season in 1990 Smith (1991a) measured the uptake of CO₂ by individual leaves of each of the six fully irrigated clones (Table 6.4). This showed that the photosynthetic rates of the four examined clones were similar, but that the corresponding rates for clones 207 and K35 tended to be lower. The ranking of clone 207 in terms of ground cover tended to decrease with time and it is possible that this was linked with the lower photosynthetic rates.

Table 6.4. Photosynthetic rates per unit area of leaf for each of six fully irrigated clones during the 1990 warm dry season (Smith, 1991a).

		Photosynthetic rate (mg CO ₂ m ⁻² s ⁻¹)	
Clone	1	0.176	a
	6/8	0.165	a
	SFS150	0.166	a
	S15/10	0.167	a
	207	0.131	z
	K35	0.154	z

The value of ϵ_s during the warm dry season was reduced by drought from 0.33 to 0.09 g MJ⁻¹. Measurements reported by Smith (1991b) also showed that drought resulted in lower photosynthetic rates and that these were closely correlated with reductions in stomatal conductance. The effects of drought on stomatal conductance are examined in Chapter 12. There were also significant clone x drought interactions in the value of ϵ_s . The efficiency of dry matter production per unit of radiation in the unirrigated treatments appeared to be greater for

clone SFS150, which was drought resistant, than for clone 6/8. This suggests that drought resistance is linked to the capacity to maintain dry matter production under drought stress.

CONCLUSIONS

The major variable determining the light interception of this young tea was ground cover. The development of ground cover was reduced during the cool season. During the period from September 1989 to May 1990 the ranking of clone S15/10 increased in terms of ground cover increased, whilst that of clone 207 declined. The reduced ground cover of 207 could have been caused by a lower photosynthetic rate (Smith, 1991). Drought reduced ground cover primarily by accelerating the abscission of leaves, but this effect was less pronounced in clones 1 and SFS150 than the other clones.

The estimated values of ϵ_s for fully irrigated plants within this experiment ranged from 0.33 to 0.55 g MJ⁻¹. These values are higher than those recorded on mature tea in Kenya, where temperatures were lower. However they are still below those for tropical annual crops, and substantially below those for temperate crops. The low values of ϵ_s for tea are probably linked to the poor distribution of light within the canopy and high respiration. There were significant clone x drought interactions in the value of ϵ_s for four examined clones. Clone SFS150, which is drought resistant, was able to maintain a higher value of ϵ_s when drought stressed than the other clones.

CHAPTER 7

TRANSPIRATION AND DRY MATTER PRODUCTION

INTRODUCTION

The yield (Y_a ; kg ha⁻¹) of tea, or any crop, can be expressed as:

$$Y_a = E_t \cdot \epsilon_w \cdot HI \quad 7.1$$

where:

E_t is the actual transpiration (mm),

ϵ_w is the net dry matter/transpired water ratio (kg ha⁻¹ mm⁻¹) or the transpiration efficiency (Tanner and Sinclair, 1983), and

HI is the harvest index.

The harvest index is defined here as the proportion of the total dry matter harvested as 'economic yield'. The product of ϵ_w and HI gives the yield/transpired water ratio (kg ha⁻¹ mm⁻¹) which is termed here the transpiration ratio for yield.

The relationships between dry matter production and transpiration for a range of irrigation experiments were reviewed by de Wit (1958). He found that the transpiration efficiency (ϵ_w) remained constant where production was only limited by soil water. The physiological basis for this observation at a leaf level is that the influx of the CO₂ into the leaf needed for photosynthesis is controlled by the same stomata that regulate transpiration (Bierhuizen and Slatyer, 1965). At a whole plant level factors such as high temperatures, radiation and leaf area which can increase total photosynthesis also tend to increase transpiration. Two factors which can increase the ratio of CO₂ uptake to transpiration are higher partial pressure gradients of CO₂ and lower water vapour pressure deficits (Bierhuizen and Slatyer, 1965). Changes in the partial pressure gradient for CO₂ are related to the carboxylation pathway, being twice as high for C₄ species such as sorghum than for C₃ species such as tea and groundnut (Roberts and Keys, 1978; Ludlow and Muchow, 1991). A decrease in the VPD from 2.0 kPa to 1.0 kPa was reported to increase the transpiration efficiency of groundnut from 15 kg ha⁻¹ mm⁻¹ to 52 kg ha⁻¹ mm⁻¹ (Squire, 1990).

There has been no reported work on the measurement of ϵ_w for tea in eastern Africa, partly due to the problems of measuring total dry matter production. To measure directly the dry mass of a tea bush in the field requires the destructive harvest of the canopy and the excavation of roots. One non-destructive field technique which has been used to determine the total dry mass of young tea plants is the measurement of stem diameter. Fordham (1971) reported that for young tea plants there was a linear relationship between total dry mass (range: 10-80 g) and stem diameter (range: 6-12 mm). Stem diameter is also used in the forestry industry to estimate the total dry mass of timber trees (Causton, 1985). An easier index to measure is the transpiration ratio for yield. Stephens and Carr (1991b) reported that this ratio varied from 1.8 to 4.0 kg ha⁻¹ mm⁻¹ for well fertilized mature clone 6/8 during the dry season in Southern Tanzania.

In this chapter the dry season yield of six contrasting clones under different drought regimes are examined in terms of the corresponding total transpiration. By estimating the dry matter production of the same plants from stem diameter measurements estimates of ϵ_w and HI are also derived.

METHODOLOGY

A full description of the clone x drought experiment at Ngwazi Tea Research Unit was given in Chapter 3. The tea was planted at a spacing of 1.2 x 0.8 m in August 1988, and was uniformly irrigated during the remainder of the 1988 dry season, from April to September in 1989, and from April to mid-July in 1990. Differential drought treatments were imposed during the final two months of the 1989 dry season (October to November) and from 27 July to mid-November in 1990.

Yield and transpiration

The soil water balance model described in Chapter 4 was used to estimate the total transpiration for each clone x drought treatment during the 1990 dry season from 1 June to 30 November. Clonal differences in ground cover were incorporated in these estimates, but the same canopy conductances (14.5 mm s⁻¹) and rooting depths (1.32 m) were assumed for each clone.

The fresh mass of shoots harvested from each of the four replicates of each clone x drought treatment was recorded during the dry season, as described in Chapter 5. These values were converted to yields of made tea using the dry matter content conversion factor also described in Chapter 5. These measurements of yield of made tea during the dry season were regressed against the corresponding transpiration to determine the transpiration ratio for yield for each clone.

Dry matter production and transpiration

The transpiration ratio for yield is the product of the dry matter production per unit transpiration (transpiration efficiency, ϵ_w) and the harvest index. The dry matter production of plants within the experiment during the dry season was estimated from measurements of stem diameter at the soil surface. The stem diameters of two selected bushes within each of the four replicates of the fully irrigated (I_5), partially irrigated (I_2) and unirrigated sub-plots (I_0) of each clone were measured on 6 June 1990 at the beginning of the dry season. The stem diameters of same bushes at the end of the dry season (30 November) were determined from a linear interpolation of readings taken on 27 October and 19 December 1990.

The relationship between dry mass and stem diameter was established from measurements of the total dry mass (including roots) of 111 plants as described in Chapter 6. The stem diameter of each of these plants was measured prior to harvest. Using the established relationship, the production of dry matter within each clone x selected drought treatment combination was estimated for the dry season. These values were then used to estimate ϵ_w and HI.

RESULTS

Yield and transpiration

There were positive linear relationships between yield and transpiration for each of the clones during the dry season (Figure 7.1). However the relationship varied between clones in the slope of the line ($P \leq 0.001$) and the y-axis intercept ($P \leq 0.001$) (Table 7.1). For each of the clones the y-axis intercept was negative, indicating that for severely drought stressed plants transpiration would occur without any commensurate yield. The maximum amount of transpiration for

which there was no yield (ie, the intercept of the x-axis) ranged from 10 mm for clone SFS150 to about 100 mm for clone 1. Above these thresholds the increase in yields per unit increase in transpiration was higher ($P \leq 0.05$) for clones 6/8 and S15/10 ($2.7\text{--}2.8 \text{ kg ha}^{-1} \text{ mm}^{-1}$) than for clones K35 and 1 ($1.8\text{--}2.0 \text{ kg ha}^{-1} \text{ mm}^{-1}$). The slope for clone SFS150 was similar to that for clones 6/8 and S15/10.

Table 7.1. Linear relationships between dry season yield (Y_a) and the estimated transpiration (Et) for each of six clones. The relationship was of the form: $Y_a = m.Et + c$ ($n=24$)

		Slope m ($\text{kg ha}^{-1} \text{ mm}^{-1}$)	Y-axis intercept c (kg ha^{-1})	r^2 (%)
Clone	1	1.77 ± 0.099 z	-183 ± 34 z	93
	6/8	2.71 ± 0.220 a	-89 ± 55 az	87
	SFS150	2.43 ± 0.149 a	-23 ± 42 a	92
	15/10	2.78 ± 0.146 a	-169 ± 48 z	94
	207	2.29 ± 0.117	-148 ± 32 z	94
	K35	2.04 ± 0.163 z	-49 ± 39 a	87

Relationship between dry matter and stem diameter

The relationship between dry mass (DM; range: 17-1532 g) and stem diameter (d_c ; range: 9-43 mm) was not linear but more closely resembled a power function (Figure 7.2). Such a relationship in tree crops has previously been described using Equation 7.2 where a and b are constants (Causton, 1985).

$$DM = a d_c^b \quad 7.2$$

A multi-variate regression analysis of this relationship which included clone, drought, season and year as variables indicated that the value of 'a' tended to increase and the value of 'b' tended to decrease with time.

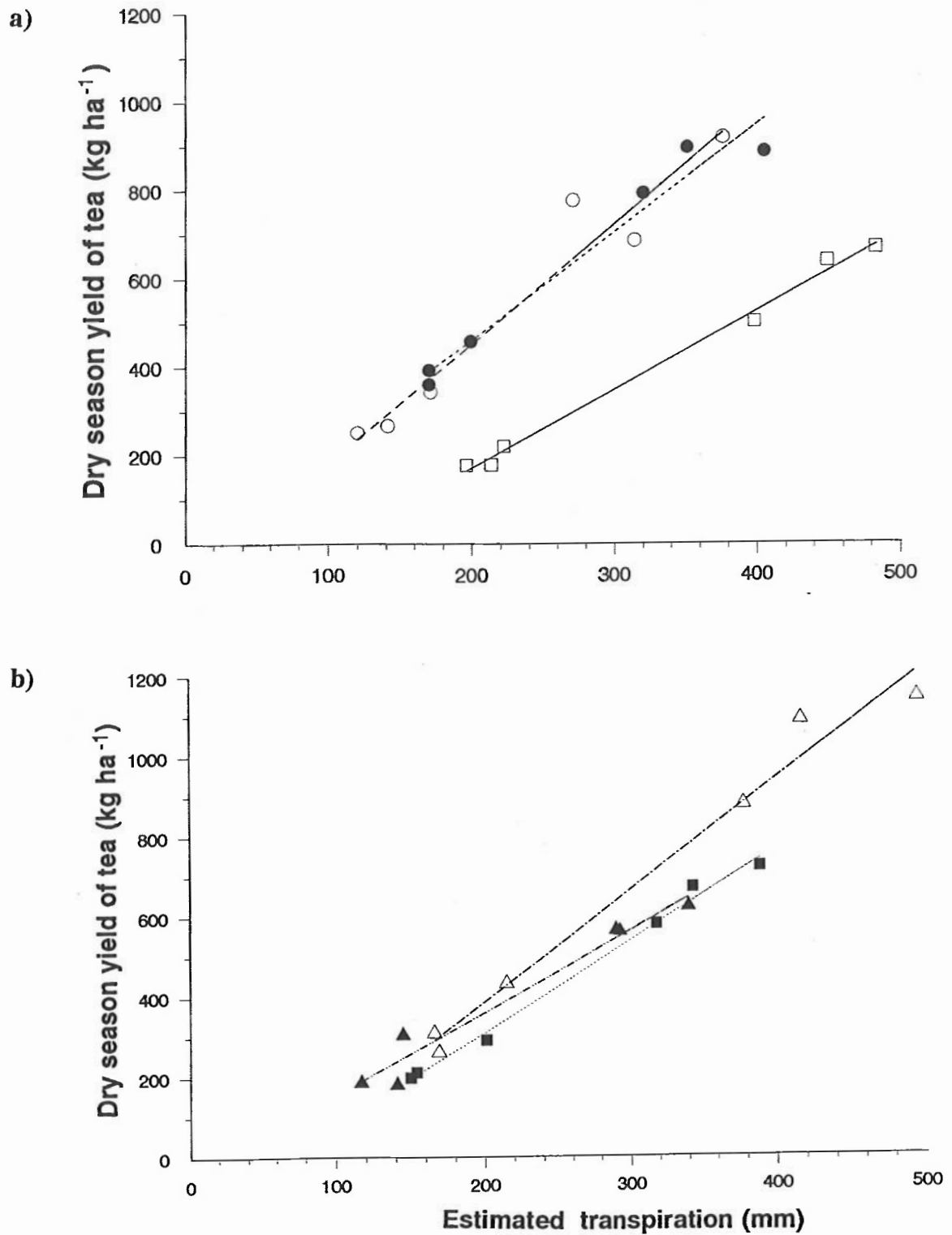


Figure 7.1. Relationships between the yield of made tea and the estimated total transpiration for each of six clones during the 1990 dry season. a) clones 1: —□—, 6/8: --○--, S15/10:●.... . b) clones SFS150: —△—, 207: ■—, K35: —▲—.

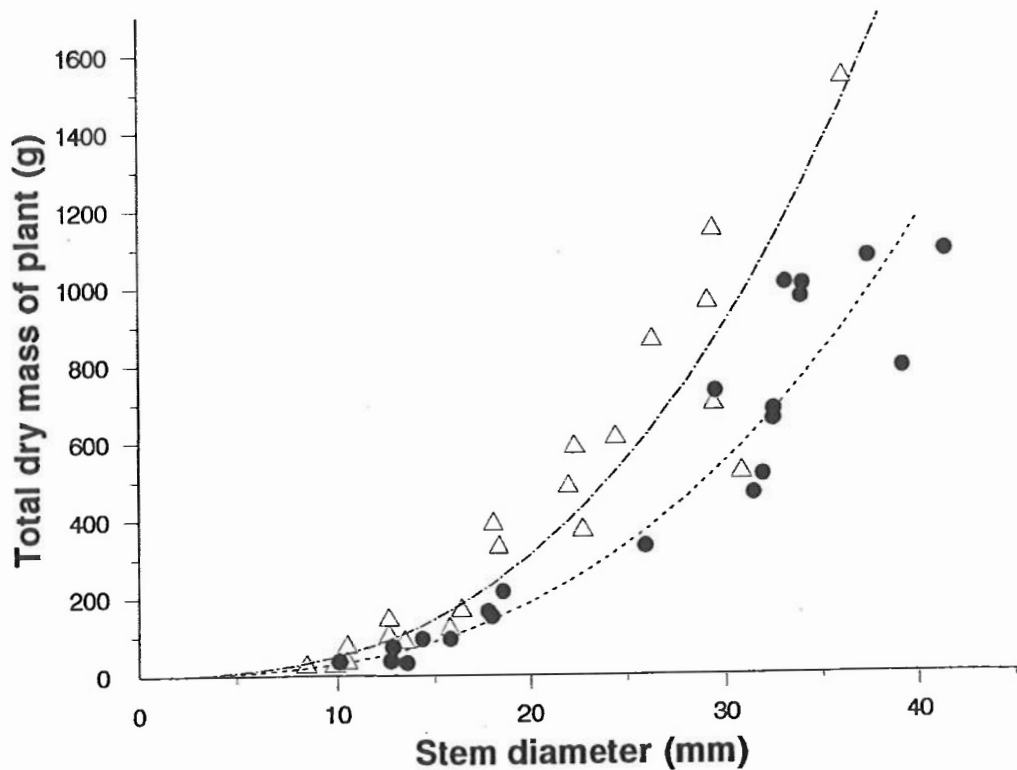


Figure 7.2. Relationships between total dry mass and stem diameter, measured at the soil surface, for plants of clones S15/10: $\triangle$ and SFS150: $\bullet$.

Since a complete set of data for clones 207 and K35 was not collected at the last two harvests, missing values for these clones were calculated using a model which included year and season as variables to avoid bias. Using these estimates the relationships between dry mass and stem diameter were recalculated for each clone $\times$ drought treatment. The relationship was not affected by drought, but the value of 'a' was higher ($P \leq 0.05$) for clone S15/10 than for the others, indicating that for a given stem diameter plants of clone S15/10 had the highest total dry mass. There were no significant differences in the value of 'a' for the other clones. Although there were clonal differences in the value of 'b', these were only just significant at the 5% level ($P = 0.048$) and their inclusion did not substantially improve the model. The best fit value of 'b' was 2.65.

Table 7.2. Best-fit relationships between total dry mass (DM; g) and stem diameter (d_c ; mm) for each of six clones up to twenty seven months after planting. The relationship took the form: $DM = a d_c^{2.65}$ ($n = 111$, $r^2 = 94\%$).

		Value of 'a'	
Clone	1	0.075	$\pm 0.0044 z$
	6/8	0.079	$\pm 0.0074 z$
	SFS150	0.067	$\pm 0.0063 z$
	S15/10	0.111	$\pm 0.0104 a$
	207	0.063	$\pm 0.0060 z$
	K35	0.078	$\pm 0.0072 z$

Dry matter production and transpiration

Using Equation 7.2 and the values presented in Table 7.2 the measured stem diameters within the main experiment were used to estimate the dry matter production of each clone within the fully irrigated (I_5), partially irrigated (I_2) and unirrigated (I_0) drought treatments during the dry season. The dry matter production was greater ($P \leq 0.05$) in the I_5 sub-plots ($0.18\text{--}0.43 \text{ kg ha}^{-2} \text{ d}^{-1}$) than in the I_2 treatments ($0.13\text{--}0.31 \text{ kg ha}^{-2} \text{ d}^{-1}$), which in turn was greater ($P \leq 0.05$) than in the unirrigated (I_0) sub-plots ($0.07\text{--}0.20 \text{ kg ha}^{-2} \text{ d}^{-1}$) (Table 7.3). The estimates of daily dry matter production within the fully irrigated sub-plots are similar to the corresponding estimates of dry matter production ($2.7\text{--}3.3 \text{ g m}^{-2} \text{ d}^{-1}$) from the destructive harvests described in Chapter 6. There were clonal differences with the dry matter production for clone K35 being lower ($P \leq 0.05$) than each of the other clones with the exception of clone 207.

To determine the transpiration efficiency, the total dry matter produced by each selected treatment during the dry season was regressed against the corresponding total transpiration. There were no significant effects of drought on the value of ϵ_w , indicating that the relationship between dry matter production and transpiration could be described using a straight line passing through the origin (Figure 7.3). The resulting best fit relationship indicated that ϵ_w ranged from $12 \text{ kg ha}^{-1} \text{ mm}^{-1}$ for clone K35 to $25 \text{ kg ha}^{-1} \text{ mm}^{-1}$ for clone 6/8 (Table 7.4).

Table 7.3. Effects of drought on the estimated rates of dry matter production for each of six clones during the 1990 dry season (1 June - 30 November).

		Rate of dry matter production ($\text{kg ha}^{-2} \text{d}^{-1}$)							
		Drought treatment							
		Fully irrigated		Partially irrigated		Unirrigated			
		I_5		I_2		I_0		Mean	
Clone	1	43	az	19	az	12	z	25	a
	6/8	34	az	31	a	16	z	27	a
	SFS150	34	az	26	az	20	z	27	a
	S15/10	39	a	25	az	20	z	28	a
	207	32	az	20	az	9	z	20	z
	K35	18	z	13	z	7	z	13	z
Mean		33		20		14			

sed between clones

=3.8(n=48)

sed between drought treatments

=3.8(n=96)

sed between clone x drought treatments

=8.2(n=16)

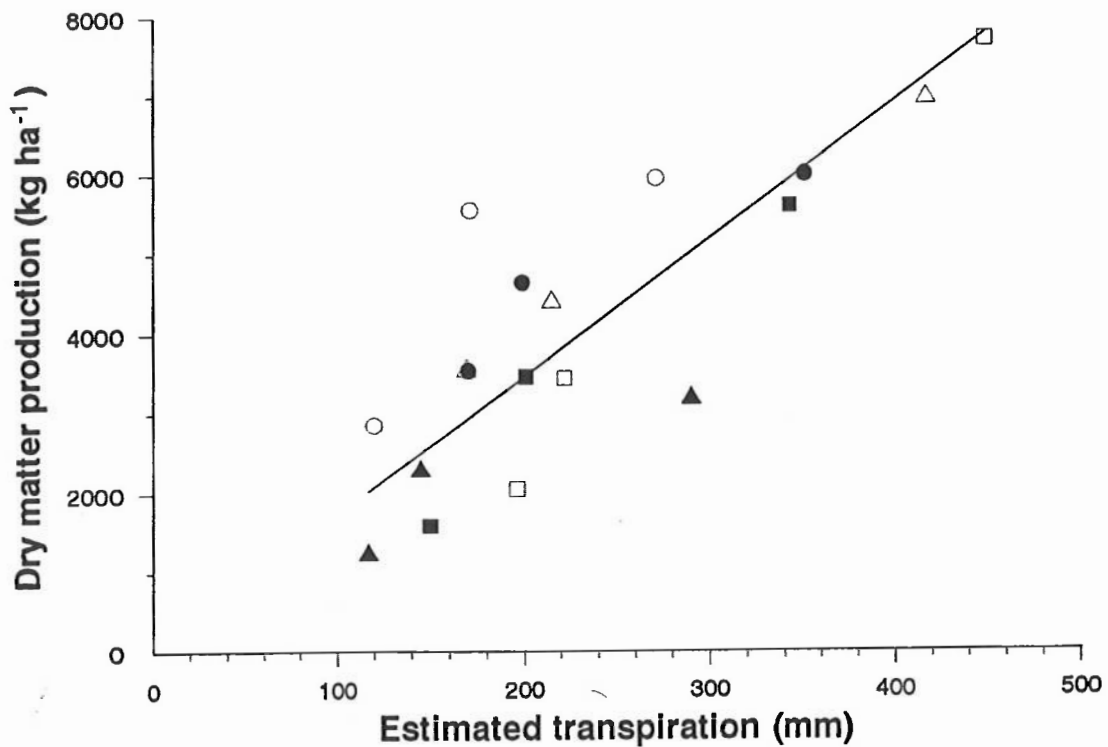


Figure 7.3. Relationships between the estimated dry matter production and total transpiration for each of six clones during the 1990 dry season. Clones: 1: $\square$, 6/8: $\circ$, SFS150: $\bullet$, S15/10: $\triangle$, 207: $\blacksquare$, K35: $\blacktriangle$.

The determination of dry matter production also enabled the harvest index during the dry season to be estimated. A mean value for each treatment was calculated by dividing the mean yield of made tea by the corresponding total dry matter production. The values of harvest index in the fully irrigated (I_5) treatments (13.6%) were higher ($P \leq 0.05$) than those in the partially irrigated (I_2) (9.4%) and the unirrigated (I_0) (10.5%) treatments. There were no significant differences in the mean harvest index of clones 1, 6/8, SFS150, S15/10 and 207 which ranged from 7 to 12%, but the mean value for clone K35 (15%) was higher ($P \leq 0.05$) than those for clones 6/8 and 1.

DISCUSSION

Transpiration ratio for yield

There was a positive linear relationship between total yield and the corresponding total transpiration for each of the clones during the dry season. The slope of this relationship was greatest for clones S15/10, 6/8 and SFS150, which all have low base temperatures (cf Table 9.4). As reported in Chapter 5, clones with low, rather than high, base temperatures for shoot extension produce a higher proportion of the annual yield during the dry season. This is because the initial half of the dry season is cool. It was proposed that measurements of stem diameter could be used to estimate dry matter production. These could then be used to determine whether the high transpiration ratios for yield of clones with a low base temperature were primarily the result of high transpiration efficiencies or high values of harvest index.

Calculation of dry mass from stem diameter

Although a linear relationship can be satisfactory when the diameters are less than 20 mm (Fordham, 1971) over a wider range of stem diameters (range: 10-40 mm) a power function is more appropriate. A power function is analogous to considering that total dry mass as a function of the cross-sectional area of the stem. Because of the power relationship the precision of estimating total dry mass is reduced at large diameters.

The relationship between total dry mass and stem diameter varied with clone. This means that stem diameter should not be used to determine clonal

differences in dry matter production unless the specific relationship for each clone can be substantiated. This variation could have been caused by differences in the proportion of dry matter partitioned to stem, but this was similar for each of the clones (cf Chapter 8). Alternatively the variation could be caused by differences in stem structure and associated secondary thickening. As will be reported in Chapter 8 the stems of the two 'China' type clones and clone SFS150 tended to be more woody than those of the other clones. It was these 'woody' clones that tended to have the greatest diameter of stem for a given total dry mass.

Transpiration efficiency and drought

There were no significant effects of drought on transpiration efficiency. This suggests that the relationship between dry matter production and transpiration could be described by a linear relationship passing through the origin. This linear relationship has been described before for groundnut (Azam-Ali *et al.*, 1989), barley (Monteith, 1986) and corresponds to the link between CO₂ uptake and transpiration described by Bierhuizen and Slatyer (1965). By contrast the relationship between yield and transpiration during the dry season did not pass through the origin. This suggests that the harvest index was reduced by drought. Although this is in apparent contrast to Othieno (1982b), who reported no consistent effect of drought on the harvest index of five clones over a period of about three years, the reduction in harvest index with drought reported here is emphasised by considering only yield during the dry season. Some of the shoots, which had reduced extension rates because of drought, will contribute to yield during the wet season. This would tend to increase the harvest index.

The estimated ϵ_w values of 12 to 25 kg ha mm⁻¹ are sensible. The transpiration ratio for yield of fully irrigated and well fertilized mature clone 6/8 at an adjacent site and therefore under similar environmental conditions was reported by Stephens and Carr (1991b) to be 1.8-4.0 kg ha⁻¹ mm⁻¹. Assuming a harvest index of 10 to 15% then the equivalent values of ϵ_w were 12 to 40 kg ha⁻¹ mm⁻¹, similar to those reported here.

Clonal differences in transpiration efficiency

Although higher values of ϵ_w were estimated for those clones with a low base temperature, two of these clones also had high stomatal conductances (cf

Chapter 12) and therefore the transpiration rates could have been underestimated relative to those of the other clones. Likewise the stomatal conductance for clones 1 and 207 tended to be low. Transpiration could therefore have been overestimated, resulting in an underestimation of ϵ_w . Further work is required to determine if low base temperatures are associated with increased dry matter production.

During the warm dry season in 1989 and 1990 the uptake of CO_2 by and the loss of water vapour from individual healthy leaves of each clone were measured using an ADC photosynthesis system comprising a LCA-2 leaf chamber and an infra-red gas analyser. These measurements have been reported by Smith (1991a) and the mean ratios of leaf uptake of CO_2 (A ; $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) to leaf conductance of water vapour (g ; $\text{mmol m}^{-2} \text{ s}^{-1}$) for the leaves of fully irrigated plants during the warm dry season in 1990 are presented in Table 7.4.

Table 7.4. The mean estimated transpiration efficiency (ϵ_w) for each of six clones within three drought treatments over the 1990 dry season, and the assimilation/stomatal conductance ratio (A/g) of individual leaves of the same clones within the fully irrigated sub-plots during the 1990 warm dry season (Smith, 1991a).

		ϵ_w		A/g	
		(kg ha ⁻¹ mm ⁻¹)		(μmol mmol ⁻¹)	
Clone	1	16.0	z	168	a
	6/8	24.9	a	148	
	SFS150	19.0	a	154	a
	S15/10	17.9		142	z
	207	15.8	z	128	z
	K35	11.8	z	148	

There is little apparent relationship between the estimated values of ϵ_w and the measured values of A/g . As already explained this may be the result of not incorporating clonal differences in canopy conductance into the model used to estimate transpiration. This could have caused the values of ϵ_w for clones S15/10 and 6/8 to be overestimated and that for clone 1 to be underestimated. The results in Table 7.4 also relate to different periods: the values of A/g relate

only to the warm dry season, whilst those for ϵ_w relate to the complete dry season. An analysis of how the values of A/g change with temperature for each clone could indicate whether this was significant.

The values of A/g determined by Smith (1991a) show a similar clonal ranking to the relative yield responses to drought for the year June 1990 to May 1991 (cf Chapter 5). Clones 1 and SFS150 which had high values of A/g were the most drought resistant, and clones 207 and S15/10 which had low values were the most drought susceptible. Passioura (1983) proposed that increases in any component of Equation 7.1: transpiration, transpiration efficiency or harvest index could increase drought resistance. This correlation between the clonal values of A/g and drought resistance suggests that measurement of A/g could provide a means of screening clones for drought resistance.

CONCLUSIONS

There were positive linear relationships between total yield and total transpiration during the dry season. The slopes of these relationships were steepest for those clones with low base temperatures for shoot extension. Such clones produce a higher proportion of their annual yield during the cool season, at the start of the dry season, than those with high base temperatures.

There were no significant effects of drought on the value of ϵ_w , indicating that the relationships between dry matter and transpiration could be described by straight lines passing through the origin. This indicated that the positive x-axis intercept of the yield/transpiration relationships were a result of harvest index being reduced by drought.

Although the values of ϵ_w tended to higher for those clones with a low base temperature for shoot extension, this could have been a result of these clones also having high stomatal conductances. Measurement of differences in the value of A/g with changes in temperature may indicate whether clonal differences in base temperature are related primarily to dry matter production or harvest index.

On the same site instantaneous measures of the ratio of CO_2 uptake to leaf conductance of water vapour, reported by Smith (1991a), gave a similar ranking

of clones as the annual estimates of drought resistance. Measurement of A/g may therefore be a possible method of determining drought resistance.

CHAPTER 8

DRY MATTER PARTITIONING

INTRODUCTION

Although the efficiency of conversion of intercepted radiation to dry matter is low for tea, the crop's productivity is also limited by the small proportion of dry matter that is harvested as 'economic' yield (Squire, 1985). The 'economic' yield of tea consists of shoots with a apical bud and up to three expanded tender leaves. The dry mass of these shoots comprises about 25% green stem and 75% leaf (Clowes, 1989). Although yield may be increased by harvesting shoots with more leaves the quality of the tea is reduced (Cloughley *et al.*, 1983).

The proportion of the total dry matter (including roots) that forms the economic yield is termed the harvest index. For tea this harvest index has been reported to range from 7 to 16% (Murty and Sharma, 1986). This is a similar range to other tropical perennial crops (Corley, 1983), but is substantially lower than for annual crops such as barley (Wahbi and Gregory, 1989) and soyabean (Huck *et al.*, 1986). The maximum harvest index reported by El-Sharkawy *et al.* (1990) for ten month old cassava was 81%.

There is potential to increase the harvest index of tea through clonal selection. The harvest index of five clones examined by Othieno (1982b) in Kenya ranged from 8% for clone 6/8 to 13% for clone 31/8. The difference from 7 to 16% reported by Murty and Sharma (1986) was for two clones in Southern India. In each of these studies a high harvest index was positively related to an increase in the ratio of shoot to root partitioning.

This chapter reports the partitioning of dry matter by six contrasting clones at Ngwazi within three distinct seasons and under different levels of drought stress.

METHODOLOGY

The climate at Ngwazi Tea Research Unit (8°32'S, 35°10'E, altitude 1840 m) can be split into three seasons. There is a wet season from the end of November to April when mean temperatures range from 17.5 to 18.5°C. This is followed by a cool dry season from about May until August when mean air temperature range

from 13.5 to 16.5°C. From September to the beginning of the rains at the end of mean temperatures are higher (15.5-18.5°C) and this has been termed the warm dry season (Stephens and Carr, 1990).

Whole plant harvests

Measurements of dry matter partitioning were made from harvests of complete plants from an observation block at the end of the main clone x drought experiment. This block was subjected to the same drought treatments and management regime as the main experiment (cf Chapter 3).

The first plants were harvested at the end of the wet season in April 1989, eight months after planting. To determine the seasonal effects on partitioning subsequent harvests were taken at the end of the cool season in August, and after the end of the warm dry season in December 1989. The same procedure was repeated the following year in early May, after the end of the 1990 wet season, and in August and in late November. The selection of plants is described in Chapter 6, but is repeated here for convenience.

For each harvest, except in November 1990, a single plant of clones 1, 6/8, SFS150 and S15/10 was selected from a fully irrigated (I_5 or I_4), partially irrigated (I_3 or I_2) and unirrigated (I_1 or I_0) sub-plot. In November 1990 no plants were harvested from the partially irrigated sub-plot, but three plants of each clone were selected from the fully irrigated and the unirrigated sub-plot to allow statistical analysis of clone x drought interactions. For the first four harvests clones 207 and K35 were also examined.

Once a plant was selected it was cut at ground level and the canopy was removed and separated into woody stem, green stem and leaves. To determine the root mass an area centred on the base of each plant corresponding to the plant spacing (0.8 x 1.2 m) was excavated beyond the maximum depth of rooting. The excavated soil was sieved through 10 mm² wire mesh. The soil not passing through this sieve was washed over a second sieve and the roots were removed by hand.

The roots, stems and leaves of each plant were oven dried at 85-90°C for 48 hours or until there was no further loss in mass. In the later harvests, when the volume was too large for the oven the dry mass of each component was

estimated from the total fresh mass and the dry mass/fresh mass ratio of two to four randomly selected samples (range: 30 - 240 g).

After December 1989 some of the dry matter produced by each bush was removed as harvested shoots. This mass was estimated for individual bushes from a count of the plucked stumps and the recorded mean shoot dry mass for the corresponding clone x drought treatment within the main experiment. For the last harvest in November 1990 the mass of abscised leaves at the base of each plant was also included within the total mass of leaf.

The rates of total dry matter production ($\text{g m}^{-2} \text{d}^{-1}$) for each clone x drought treatment between each harvest were calculated, and these were described in Chapter 6. The rate of dry matter partitioning to harvested shoots, leaves, woody and green stems and roots were also calculated individually. This was determined in absolute terms ($\text{g m}^{-2} \text{d}^{-1}$) and as a proportion of the total rate of dry matter production.

Root depth and distribution

Maximum root depths for the selected clone x drought treatments were recorded during the whole plant harvests in April and August 1989 and November 1990. For the final harvest in November 1990 the maximum rooting depth of three plants of clone 207 within the unirrigated treatments was also determined. In this last harvest the distribution of the roots was also examined by excavating the soil in 0.4 m layers. Within each layer roots were divided into thin roots (less than 1 mm diameter) and thick roots (greater than 1 mm). A similar division was used by Magambo and Cannell (1981).

RESULTS

Harvest index

The mean total dry matter production in the fully irrigated sub-plots for clones 1, 6/8, SFS150 and S15/10 increased as the plants grew in size. It rose from $0.5 \text{ g m}^{-2} \text{d}^{-1}$ between April and August 1989, to $2.7 \text{ g m}^{-2} \text{d}^{-1}$ between May and August 1990, and to $3.3 \text{ g m}^{-2} \text{d}^{-1}$ between August and November 1990 (Figure 8.1).

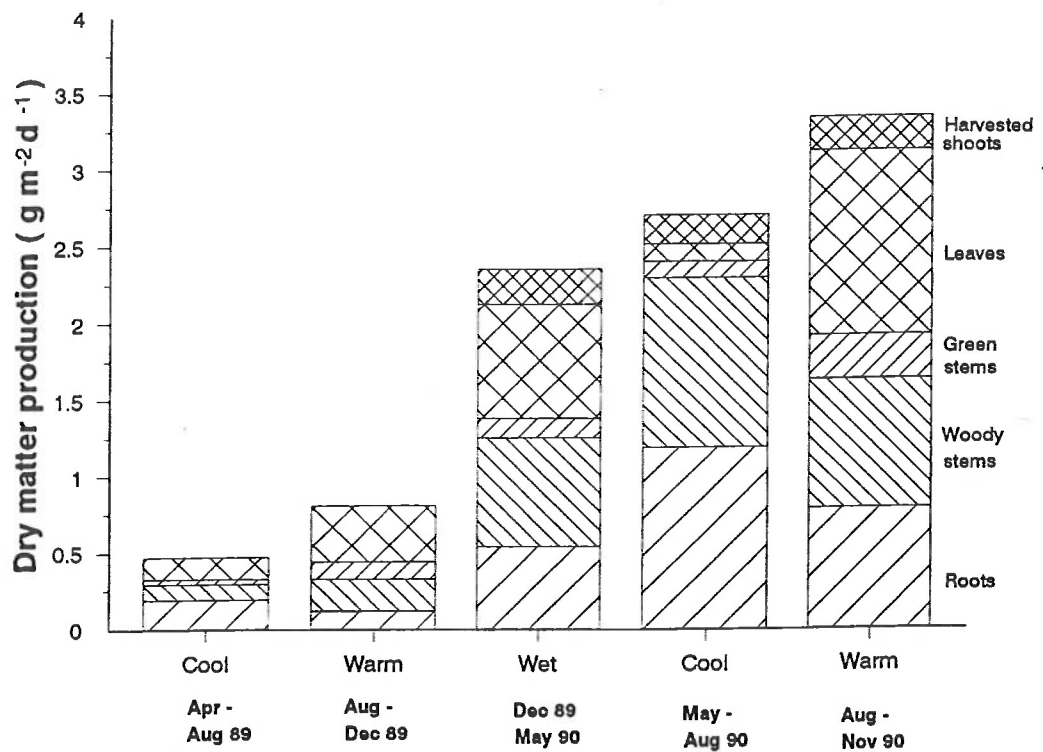


Figure 8.1. Changes in the rate of dry matter production and the partitioning of that dry matter to yield, leaves, green stems, woody stems and roots for four clones (clones 1, 6/8, SFS150 and S15/10) for each of five seasons from April 1989 to November 1990.

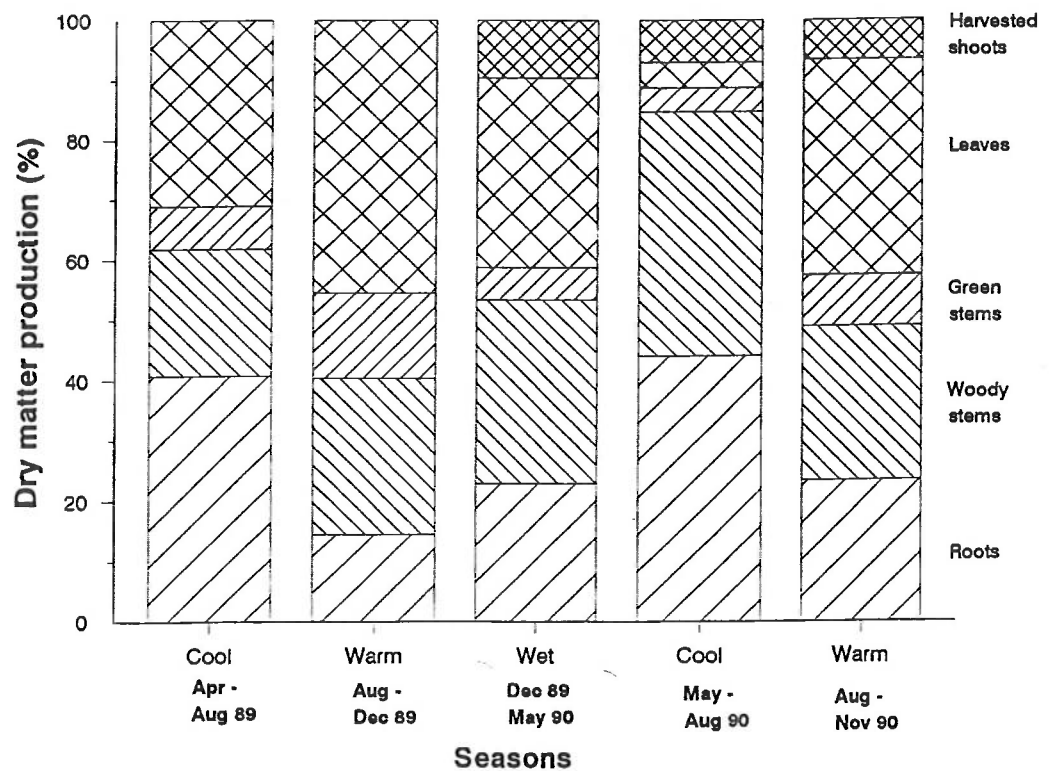


Figure 8.2. Changes in the proportion of dry matter partitioned to yield, leaves, green stems, woody stems and roots for four clones for each of five seasons from April 1989 to November 1990.

The rate of dry matter partitioning to harvested shoots within each of the three seasons in 1990 were similar for each clone, and the mean value ranged from 0.18 to 0.22 g m⁻² d⁻¹. This is equivalent to a mean weekly yield of made tea of about 14 kg ha⁻¹.

If the dry matter data were analysed for the whole year (December 1989 to November 1990) then the estimated harvest index for clone S15/10 (11.5%) was higher ($P \leq 0.05$) than clones 6/8 (7.9%) and SFS150 (7.3%). Clone 1 had the lowest estimated harvest index (4.0%). Although not quite significant ($P = 0.056$), the mean partitioning of dry matter to yield was reduced by drought during the warm dry season from 0.22 g m⁻² d⁻¹ to about zero.

Partitioning to root, leaf and stem

The partitioning of dry matter to the roots decreased from 0.19 g m⁻² d⁻¹ during the cool season in 1989 to 0.12 g m⁻² d⁻¹ during the subsequent warm dry season. In the following year daily partitioning of dry matter to the roots in the cool season had increased to 1.2 g m⁻². In a similar way to the first year, partitioning of dry matter to the roots decreased ($P \leq 0.05$) from the cool season to 0.8 g m⁻² d⁻¹ (where fully irrigated) in the warm dry season. This occurred despite an increase in the daily rate of dry matter production. The proportion of dry matter partitioned to root was therefore higher during the cool season than the warm dry season (Figure 8.2).

The greater partitioning of dry matter to the roots in the cool season was associated with reduced partitioning to leaves. In 1990 partitioning to the leaves (including harvested shoots) decreased from 1.0 g m⁻² d⁻¹ during the wet season to 0.3 g m⁻² d⁻¹ during the cool season. By contrast the proportion of dry matter that was partitioned to stem (range: 26-41%) was similar in each of the seasons.

Clonal differences

At the first harvest in April 1989 clone 207 was heavier ($P \leq 0.05$) than clones 1, 6/8 and S15/10. Therefore clone 207 had the highest leaf, stem and root mass. However clone S15/10 had partitioned a greater proportion ($P \leq 0.05$) of the dry matter to leaves than clones 1, 6/8, SFS150 and 207 (Table 8.1).

Table 8.1. Total dry matter and the proportion of that mass which was partitioned to leaves, stem and roots for each of six clones harvested in April 1989, eight months after planting.

		Total dry mass (g)		Proportion of total dry matter					
				Leaf (%)		Stem (%)		Root (%)	
Clone	1	25	z	40	z	35	z	25	z
	6/8	30	z	40	z	33	z	27	z
	SFS150	35	az	39	z	32	z	29	z
	S15/10	27	z	50	a	29	z	21	z
	207	61	a	41	z	34	z	25	z
	K35	41	az	42	az	33	z	25	z
sed (n=3)		9.2		2.6		1.9		2.7	

The higher proportion ($P \leq 0.05$) of dry matter partitioned to leaf by clone S15/10, compared to other clones, continued throughout the experiment (Figure 8.3). Over the thirteen months from April 1989 to May 1990 clone S15/10 partitioned 51% of its dry matter to leaf and harvested shoots, compared to 34-39% for the other clones. This increase was offset by a reduction in the proportion of dry matter distributed to the roots to 16%, compared to 25-33% for the other clones

There were no significant differences between the clones in the proportion of dry matter was partitioned to stem. However there were clonal differences in the proportion of stem growth that was green. At the first harvest in April 1989 this was lower for clone 207 than clones 6/8 and K35 (Table 8.2). Over the following year, from April 1989 to May 1990, clone S15/10 partitioned a lower ($P \leq 0.05$) proportion of the stem mass to wood than clones 1 and 207. The proportion of stem growth that was woody was similar for clones 1, 207, SFS150 and 6/8.

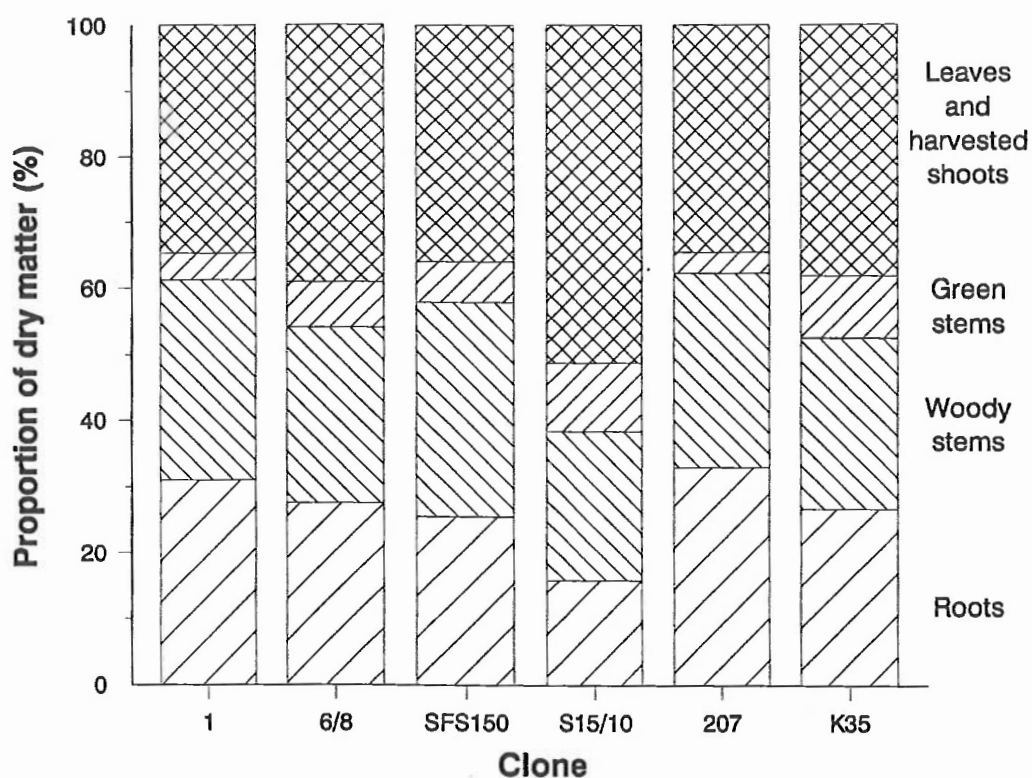


Figure 8.3. Proportions of dry matter partitioned to leaf and harvested shoots, green stems, woody stems and roots for each of six clones from April 1989 to May 1990.

Table 8.2. Proportions of the stem mass in April 1989 and the proportions of the stem growth from April 1989 to May 1990 that was green for each of six clones.

		Proportion of stem that was green		Proportion of stem growth that was green	
		April 89 (%)		April 89 to May 90 (%)	
Clone	1	26	az	12	z
	6/8	37	az	21	az
	SFS150	31	az	16	az
	S15/10	28	az	32	a
	207	20	z	10	z
	K35	41	a	28	a
sed (n=3)		5.5		5.6	

Effects of drought

Drought treatments were imposed for the first time for six weeks during October and November 1990. Drought reduced ($P \leq 0.5$) the rate of dry matter production during the warm dry season from August to November from 0.81 to 0.55 $\text{g m}^{-2} \text{d}^{-1}$, but this was not significant (Figure 8.4). The partitioning of dry matter to leaves was also reduced ($P \leq 0.5$) by the drought, but this again was not significant. However the partitioning of dry matter to green stem was significantly ($P \leq 0.05$) reduced by drought from 0.11 to 0.008 $\text{g m}^{-2} \text{d}^{-1}$.

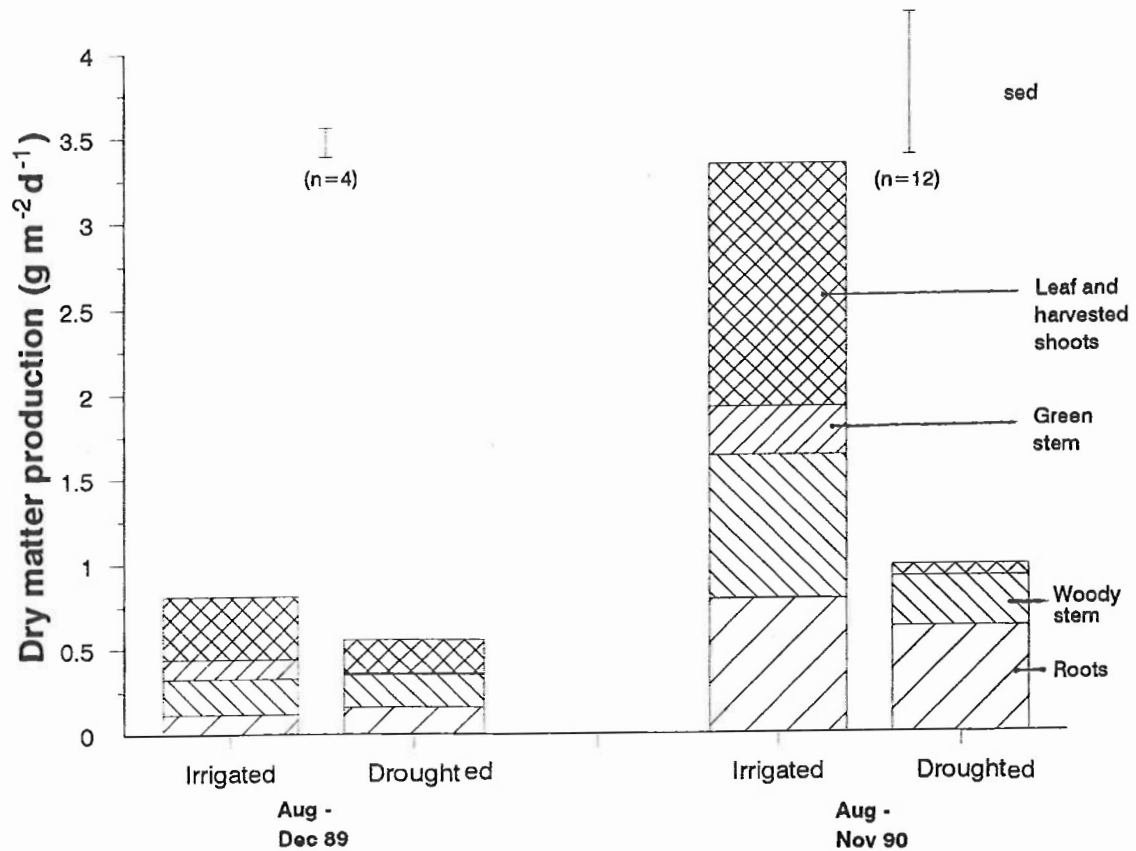


Figure 8.4. Effects of drought on the mean rate of dry matter production and its partitioning by four clones (1, 6/8, SFS150 and S15/10) during the warm dry season in 1989 and in 1990.

More marked effects of drought were found between August and November in the 1990 dry season, when the rate of dry matter production was higher ($P \leq 0.05$) in the fully irrigated treatments ($3.3 \text{ g m}^{-2} \text{d}^{-1}$) than in the unirrigated sub-plots ($0.9 \text{ g m}^{-2} \text{d}^{-1}$). The combined production of green leaf and yield was also higher ($P \leq 0.001$) for the irrigated ($1.4 \text{ g m}^{-2} \text{d}^{-1}$) than for the unirrigated plants (0.05 g

$\text{m}^{-2} \text{d}^{-1}$). The net production of green stem in the fully irrigated treatments was also higher ($P \leq 0.001$) at $0.3 \text{ g m}^{-2} \text{d}^{-1}$, than in the unirrigated treatments where there was a net loss of $0.1 \text{ g m}^{-2} \text{d}^{-1}$. This net loss was probably the result of existing green stem being lignified at a faster rate than new green stem was being produced. There were no significant effects of drought on the production of root or woody stem (Figure 8.4).

Abscised leaf

The loss of dry matter from the plant through leaf abscission was only examined at the last harvest in November 1990 by collecting the leaves around the base of clones 1, 6/8, SFS150 and S15/10. There were no significant effects of drought on the mass of leaf below these clones. However there was more ($P \leq 0.001$) leaf litter below clone S15/10 (80 g m^{-2}) than the other three clones (range: 21-36 g m^{-2}). This was equivalent to about nine percent of the total dry mass for clone S15/10 and between two and four percent for the other clones.

Field observation of the bushes suggested that the greatest abscission of older leaves occurred in the unirrigated plots of clones 207 and K35. However it was apparent that measurement of abscission by collection of leaf litter on the ground was confounded by the effects of ground cover. Leaves that fell from plants with a large ground cover were more likely to be collected as they were sheltered from the wind. Because they were also better protected from solar radiation they dried out and decomposed more slowly than exposed leaves.

Root depth and distribution

Maximum rooting depth

When the tea was transplanted in the field in August 1988 the maximum root depth was limited by the length of the polythene sleeves, which would have been about 0.15 m. The rooting depths of the six clones were still similar eight months later in April 1989 (range: 0.28-0.34 m). The mean rooting depth had increased to 0.55 m in August 1989 and by November 1990 it had reached 1.50 m. For this final set of measurements there were no significant effects of drought (Table 8.3). Therefore the rooting depths from the different drought treatments could be pooled to determine a mean rate of increase. Between August 1989, twelve months after planting, to November 1990 the mean rate of

increase in the maximum depth of rooting was $1.86 \pm 0.082 \text{ mm d}^{-1}$ ($n=53$, $r^2=90\%$) (Figure 8.5).

The ranking of clones according to root depth was not consistent. In August 1989 the maximum root depth of clone 207 (0.80 m) was greater ($P \leq 0.05$) than for clones 6/8, SFS150, S15/10 and K35 (range: 0.43-0.51 m) (Table 8.3). However by November 1990 in the unirrigated treatments the roots of clone SFS150 (1.76 m) went deeper ($P \leq 0.05$) than clones S15/10 (1.48 m), 1 (1.34 m) and 207 (1.06 m) (Table 8.3).

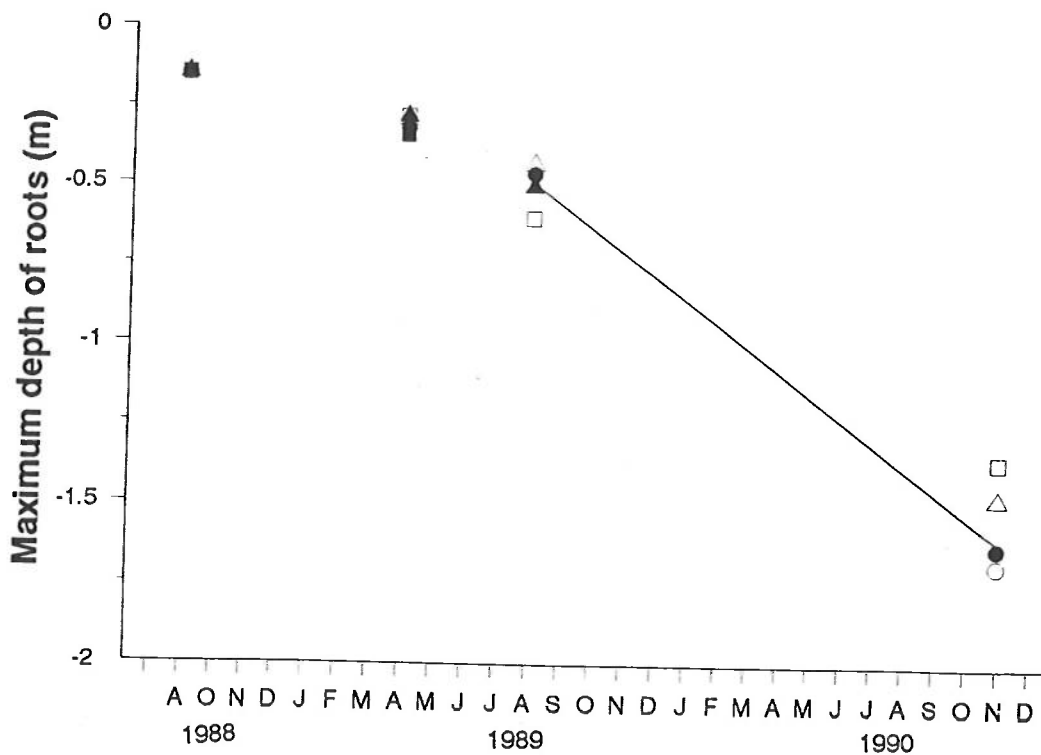


Figure 8.5. Increase in the maximum rooting depth for four clones (1, 6/8, SFS150 and S15/10) from August 1988 to November 1990. (Mean of irrigated and unirrigated plants).

Table 8.3. Maximum rooting depths for each of six clones in August 1989, twelve months after planting, and in November 1990 following differential drought treatments.

		Maximum root depth (m)		
		August 1989 Irrigated	November 1990 Irrigated Droughted	
Clone	1	0.60	1.37	1.34
	6/8	0.46	1.66	1.70
	SFS150	0.46	1.49	1.76
	S15/10	0.43	1.46	1.48
	207	0.80	-	1.06
	K35	0.50	-	-
sed (n=3)		0.078	0.080	

Thick and thin roots

The mean total root mass of the plants sampled in November 1990, twenty seven months after planting, was 305 g m⁻², of which 249 g m⁻² (82%) comprised thick roots. In the fully irrigated treatments clone S15/10 had a smaller ($P \leq 0.05$) mass of thick roots than clones 1 and 6/8 (Table 8.4a). However there were no significant differences in the mass of thin roots between the clones (Table 8.4b). Therefore a higher proportion of the roots of clone S15/10 were thin, in comparison to the roots of the other clones.

The mass of thick root was not significantly affected by drought, only varying from 240 to 260 g m⁻² and there were no significant clone x drought interactions. In contrast the small roots appeared to be more sensitive to drought stress. Although not significant, the mass of small roots in the fully irrigated treatment of each clone was consistently greater ($P \leq 0.1$) than that in the unirrigated sub-plots (Table 8.4b).

Table 8.4. Effects of drought on a) the mass of thick roots and b) the mass of thin roots for each of four clones in November 1990, twenty seven months after planting.

		Mass of thick roots (g m ⁻²)		
		Fully irrigated	Droughted	Mean
Clone	1	368	400	384
	6/8	278	158	218
	SFS150	259	294	277
	S15/10	133	106	120
Mean		240	260	

sed between clones	= 31.8 (n=6)
sed between drought treatments	= 22.5 (n=12)
sed between clone x drought treatments	= 44.9 (n=3)

		Mass of thin roots (g m ⁻²)		
		Fully irrigated	Droughted	Mean
Clone	1	64	48	57
	6/8	44	43	43
	SFS150	63	49	56
	S15/10	92	42	67
Mean		66	45	

sed between clones	= 16.1 (n=6)
sed between drought treatments	= 11.4 (n=12)
sed between clone x drought treatments	= 22.7 (n=3)

Root distribution

Between 90 to 98% of the total mass of thick root was present in the top 0.4 m of soil, compared to 23-61% of the thin root mass. Below 0.4 m thin roots formed the majority of the root mass (range: 66-80%). Although not significantly different, the mass of thin roots was consistently higher in the fully irrigated treatments than in the droughted treatments. Within the top 0.4 m of soil this difference was significant at the 10% level. There were no significant clonal differences in the mass of small roots within any of the soil strata, but clone SFS150 had a higher proportion ($P \leq 0.05$) of thin roots (on a mass basis) below 0.8 m than the other clones (Figure 8.6).

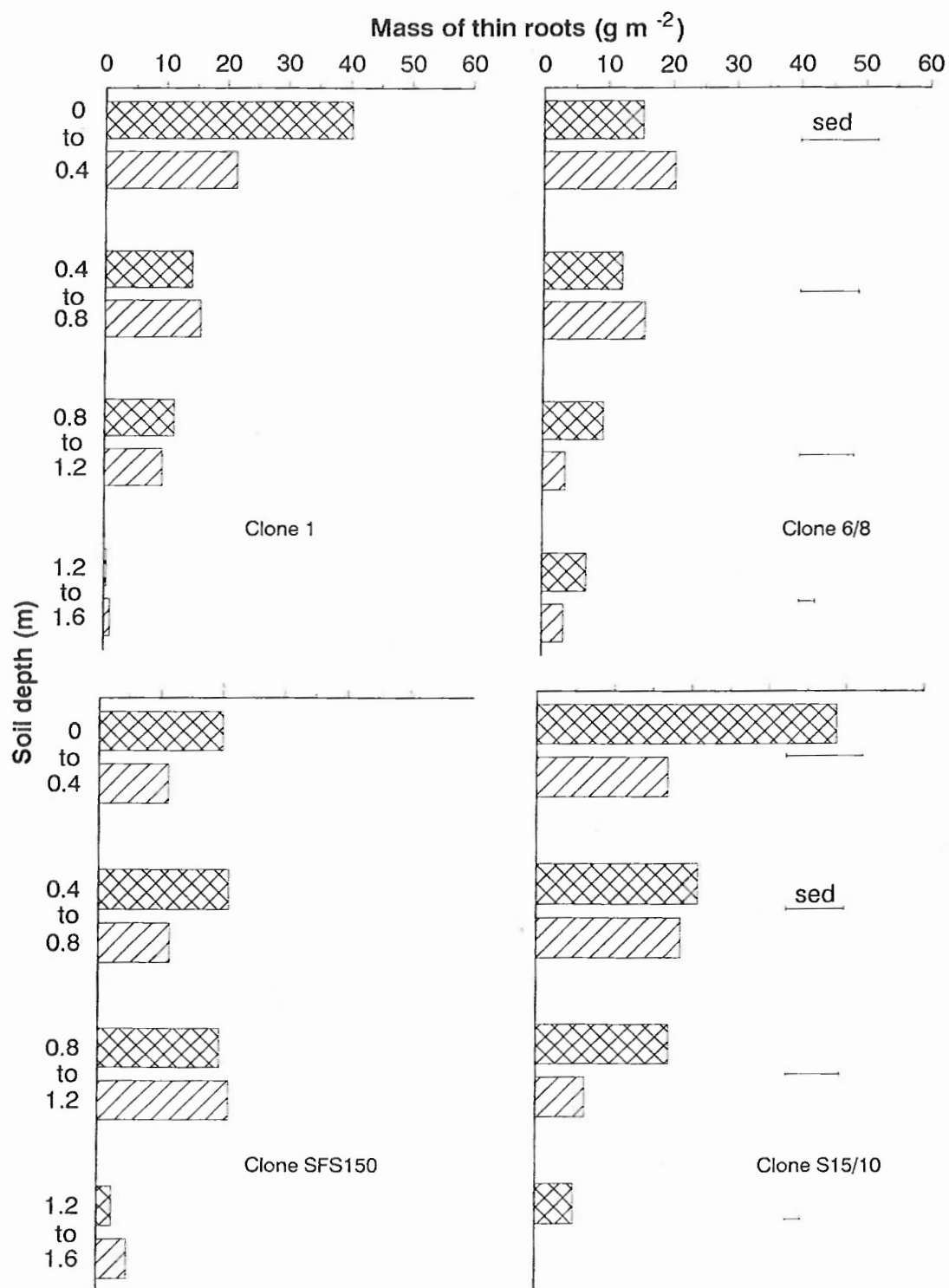


Figure 8.6. Effects of drought on the distribution of thin roots within four incremental depths of soil for each of four clones in November 1990, twenty seven months after planting. Fully irrigated:  , Unirrigated:  .

DISCUSSION

Harvest index

The estimated harvest index during the first year of harvest from December 1989 to November 1990 was higher for clone S15/10 (11.5%) than for clones 6/8 and SFS150 (7-8%) and clone 1 (4.0%). The values for clones 6/8, SFS150 and S15/10 are similar to values between 7 and 16% measured elsewhere for tea (Murty and Sharma, 1986; Othieno, 1982b), but the value for clone 1 is lower. This could be a result of clone 1 producing a smaller proportion of the annual crop during the dry season than the other examined clones (cf Chapter 5). The estimates of harvest index reported here also relates to tea in its first year of harvest, when a substantial proportion of growth was occurring below the level of the plucking surface.

Partitioning to leaves, stems and roots.

Seasonal effects

Partitioning of dry matter to the roots was greatest (both in absolute and relative terms) during the cool season. It was reported in Chapter 6 that the conversion efficiency for light interception was not reduced during the cool season. At this time mean day-time air temperatures range from 12.5-14.5°C at 09.00 h to a maximum of 18.0-20.0°C around midday. Smith *et al.*, (1991) reported no appreciable effect of leaf temperature between 17 and 35°C on leaf photosynthetic rate in a mature stand of clone 6/8 at Ngwazi. Leaf temperature was typically 1.7°C higher than air temperature. Therefore there were probably only marginal reductions in photosynthetic and thereby total dry matter production rate during the cool season.

Whilst photosynthetic rates may have remained relatively stable, shoot extension rates were substantially reduced during the cool season (cf Chapter 9). Under such conditions when the 'demand' for photosynthates by the shoots is low, a higher proportion of photosynthates will be allocated to the roots. The increased movement of photosynthates to the roots during cool weather has been demonstrated for tea in Assam by Manivel and Hussain (1982) with radio-carbon tracing techniques. This increased allocation of dry matter to the roots can be observed visually in the continued extension of roots during the cool season (Carr, 1971b).

After the cool season the proportion of dry matter partitioned to the roots decreased at the same time as shoot extension rates increased (cf Chapter 9). This suggests that after the cool season the 'demand' or 'sink strength' of the shoots for photosynthates increased relative to the 'demand' of the roots. Increased partitioning of dry matter to the canopy after a cool season has also been reported for tea in Malawi (Fordham, 1972 ; Herd and Squire, 1976).

Comparison with other measurements

The proportion of dry matter partitioned to leaves and harvested shoots by irrigated clone 6/8 during the cool season at Ngwazi was lower during the cool season, and higher during the warm dry season, than the annual value reported for mature plants of the same clone at TRFK, Kenya (Magambo and Cannell, 1981) (Table 8.5).

Table 8.5. Comparison of the proportion of the dry matter partitioned to leaf, stem and roots by irrigated clone 6/8 aged 8 to 27 months at Ngwazi Tea Research Unit (8°32'S, 35°10'E; 1840 m) reported here with that of the same clone aged 6 to 7 years at TRFK, Kenya (0°22'S, 35°21'E; 2178 m) (Magambo and Cannell, 1981).

Monthly mean air temperature	Proportion of total dry matter (%)		
	Ngwazi, Tanzania cool season 13.5-15.0°C	warm season 16.0-18.5°C	TRFK, Kenya. annual 14.9-17.0°C
Component			
Leaf and harvested shoots	20-25	29-41	27-31
Stem	22-46	33-38	44-51
Root	34-53	23-33	21-25

The monthly mean air temperature at TRFK, is relatively stable throughout the year only varying from 14.9°C in July to 17.0°C in March (Stephens *et al.*, 1992). The mean air temperature at Ngwazi was 13.5-15°C during the cool season and 16-18.5°C during the warm dry season. Therefore these data again indicate that the partitioning to harvested shoots and leaves is temperature dependent. The measurements also indicate that a lower proportion of dry matter was

partitioned to the stems at Ngwazi than at TRFK. This could be a result of sampling younger plants (between 8 and 27 months) than in Kenya (6 to 7 years).

Clonal differences

Clone S15/10 had the highest harvest index and also partitioned a greater proportion of dry matter to leaf and harvested shoots than the other clones. Othieno (1982b) also reported a positive relationship between the harvest index and the proportion of dry matter partitioned to the canopy. The greater partitioning of dry matter to leaves, is probably the major reason why clone S15/10 gave the highest yields within this experiment.

The stems of clones S15/10 and K35 were less woody (ie, they had a higher proportion of green stem) than the stems of the other clones. The net production of green stem is determined by the rate of new stem extension and the rate of lignification. Increases in the proportion of green stem should be advantageous as it increases the photosynthetic area and could reduce the respiration load of the bush. A second advantage is that because green stem is more tender than woody stem, a higher proportion of the bush remains harvestable. This is also likely to reduce the 'creep' in the height of the plucking surface and could reduce the frequency with which the bushes need to be pruned.

Although clone S15/10 partitioned a lower proportion of dry matter to thick roots, it had a similar mass of small roots as clones 1, 6/8 and SFS150. It is these thin roots that are generally believed to be important in determining the uptake of water and nutrients from the soil. In Assam high ratios of thin to thick roots in nine month old plants of a single clone were linked to more rapid canopy growth (Chamuah, 1988). By contrast Nyirenda (1990) reported that in Malawi that high ratios of thick to thin roots were associated with vigorous clones. However this work was based on 43 month old plants grown in hessian bags (0.34 m diameter by 0.7 m depth).

Effects of drought

Drought reduced the rates of total dry matter production and the absolute rates of dry matter partitioned to leaf and green stem. Reduced partitioning of dry matter to leaves because of drought has also been reported for very young tea plants five to twelve months after propagation (Kulasegram and Kathiravetpillai, 1976) and for two to four year old clones grown in the field (Othieno, 1982b).

The xylem water potential (cf Chapter 12) and the rate of shoot extension rate (cf Chapter 9) declines when a tea plant is drought stressed. Squire and Callander (1981) proposed that in Malawi shoot extension was reduced when the xylem water potential fell below -0.8 MPa. As already discussed, during the cool season the reduced rates of partitioning to leaves and green stem were associated with decreased rates of shoot extension. Similarly the reduced partitioning of dry matter to leaves when drought stress is associated with reduced shoot extension.

Partitioning of dry matter to structural roots and woody stem was unaffected by drought. Othieno (1982b) also reported that drought had no significant effect on the dry mass of roots. This indicates that root and woody stem growth are less sensitive to low soil water potentials than that of leaves and shoots. This is at least partly due to them being nearer the water source.

The two periods of drought had no significant effect on the maximum depth of rooting. However there was an indication that drought restricted growth of thin roots in the upper 0.4 m of soil where the soil was dry.

Nyirenda (1990) and Cannell *et al.* (1990) proposed that clones with deep root systems are better able to withstand the effects of drought than those with a shallow root system. A deeper rooting depth could enable access to more water during the dry season and this could help maintain xylem water potentials. There were clonal differences in maximum rooting depth but these changed with time. Clones 1 and 207 which were initially relatively deep rooting were the most shallow rooting at the end of the 1990 dry season. More important than the maximum rooting depth may be the relative distribution of roots. Clone SFS150 partitioned a higher proportion of its thin roots at depths below 0.8 m than clones 1, 6/8 and S15/10. As reported in Chapter 5 this clone was drought resistant. However clone 1 which was also drought resistant did not show this characteristic.

CONCLUSIONS

Clone S15/10, which had the highest yield where fully irrigated, also had the highest harvest index and partitioned the highest proportion of dry matter to its leaves. The proportion of dry matter partitioned to leaves was reduced during

the cool season and by drought stress. In each case the reduction was linked to reduced shoot extension. These results could support Manivel and Hussain's (1986) proposal that the proportion of assimilates partitioned to shoot growth is determined by the 'sink capacity' of the shoots, which in turn is related to their potential growth rate.

The clones partitioned similar proportions of dry mass to stem growth, but there were clonal differences in the proportion of stem that was green. A greater proportion of green stem may provide a visible and easily determined criterion for selecting high yielding clones.

Although clone S15/10 partitioned a lower proportion of its dry matter to roots than the other clones, it maintained a similar mass of thin roots. This contrasts with the findings of Nyirenda (1990) which associated a high ratio of thick to thin roots with high vigour. The growth of thin roots was reduced in areas of dry soil and there was evidence that clone SFS150, which was relatively drought resistant, had the highest proportion of thin roots below 0.8 m. Clone 207 which had shallow roots was relatively drought susceptible. Although the drought resistance of some clones appeared to be linked with their rooting behaviour, the substantial labour required for such determinations precludes its use as a field selection technique for screening large numbers of clones.

CHAPTER 9

SHOOT EXTENSION AND DEVELOPMENT

INTRODUCTION

The dry mass of tea shoots harvested at any given time depends upon the shoot population density, the rate of shoot growth and the mean dry mass of the shoots at harvest. A systematic analysis of how these components vary between clones and how they are affected by the environment should provide guidance for future clonal selection (Tanton, 1979). A dynamic and stochastic model incorporating each of these components was reported by Fordham and Palmer-Jones (1977). This model starts with a specified population of shoots which grow at a known rate. At selected intervals shoots above a specified length are removed, the mass of these shoots are calculated from their length and a total yield is calculated. Cannell *et al.* (1990) used this type of model to describe the shoot extension of two clones and then proceeded to predict the effects of changes in harvesting interval on shoot composition. Using similar models, the effects of genotype and the environment on shoot extension rates can be quantified and used to determine yield (Figure 9.1).

In Malawi Tanton (1982a) reported that the shoot extension rate for clone SFS204 was linearly related to night temperatures between 12.5 and 20.0°C. Building on this relationship he also showed that the relative extension rates of shoots of field grown clone SFS204 were linearly related to the weekly mean air temperature over an eight month period. This relationship was described by a base temperature at which shoot extension ceased (T_{be} ; °C) and a slope (ρ_e ; mm d⁻¹ °C⁻¹ or mm mm⁻¹ d⁻¹ °C⁻¹). The value of ρ_e which defines the increment of extension per unit thermal time has been termed the thermal extension rate (Obaga and Squire, 1992). Recent work has shown that the values of T_{be} and ρ_e can vary between clones (Cannell *et al.*, 1990; Stephens and Carr, 1990).

Because the final tea quality is related to the number of expanded leaves on a harvested shoot (Owuor and Obanda, 1986), tea growers are also interested in shoot development. In systems where the tea is harvested by hand the choice of harvest interval and the principal criterion determining whether an individual shoot is harvested can also be based on the number of expanded leaves (Grice, 1982). It is therefore important to quantify clonal differences in development, and to relate these to shoot length. Recently Obaga and Squire (1992) have

proposed that the effects of clone and temperature on shoot development rate could be described in a similar way to that for shoot extension rate, by estimating a base temperature for shoot development (T_{bd}) and a thermal development rate (ρ_d).

This chapter reports the effects of season and drought on the rates of shoot extension and development for each of six clones. The measurements are also used to determine if there are differences in the lengths of the shoot internodes.

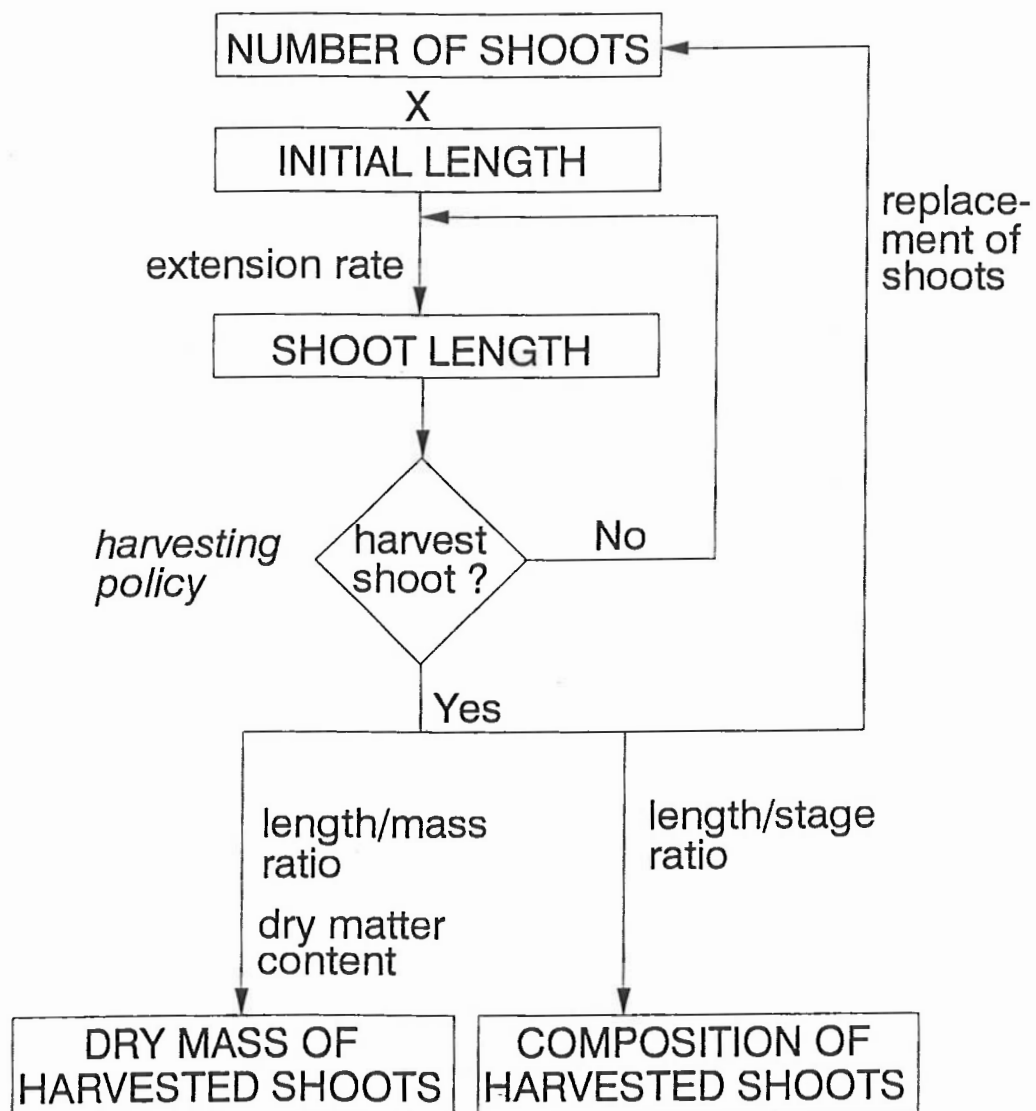


Figure 9.1. Framework for analysing the effects of shoot extension rates and number of shoots on the dry mass and composition of harvested shoots.

METHODOLOGY

Shoot extension and development were examined within the clone x drought experiment which was described in Chapter 3.

Shoot extension

Shoot extension was monitored using seventeen generations of shoots released from apical dominance at approximately monthly intervals between May 1989 and October 1990. By selecting the sample generations as buds, the possibility of choosing biased populations of fast or slow growing shoots was reduced (Stephens and Carr, 1990). For the first three generations two shoots, with at least two expanded flush leaves, were selected on three bushes within two replicates of an I_3 , I_4 or I_5 sub-plot and an I_0 , I_1 or I_2 sub-plot. For the remaining fourteen generations selected after August 1989, three shoots were identified on each of two bushes within each of the four replicates of each fully irrigated (I_5), partially irrigated (I_2) and unirrigated (I_0) sub-plots of each clone; a total of twenty four shoots per treatment combination. A shoot with two expanded flush leaves was removed, the remaining stem butt was tagged and the length of the uppermost axillary bud was measured (± 0.1 mm) with Vernier callipers. The bud length was then measured at fourteen day intervals until the shoot emerged from the bud. After emergence the length of the shoot stem from the axil to the base of the exposed bud was measured (± 1 mm) at weekly intervals until the shoot had unfurled four flush leaves.

In order to estimate shoot length from the initial bud length measurements, ten buds were selected from one fully irrigated (I_5) and unirrigated (I_0) sub-plot of each clone on two days in May and one day in September 1990. The lengths of the buds (range: 5-44 mm) and the enclosed shoots (range: 1-15 mm) were measured and the best fit linear relationship between bud and shoot length, constrained to pass through the origin, was calculated. For a given length of bud, the smaller leaved clones 1 and 207 had ($P \leq 0.05$) longer shoots than clone K35 (Table 9.1). Therefore a different conversion factor for determining shoot length from bud length was used for each of the six clones. The measurements also showed that the shoot/bud length ratio was higher ($P \leq 0.05$) at the start of the warm season in September (0.329) than at the start of the cool season in May (0.300), and was also higher ($P \leq 0.05$) for shoots within the irrigated (0.323) than the unirrigated treatments (0.304). However these changes were small in comparison to the precision of measuring bud length, which was ± 0.1 mm for

typically a length of two to four mm, and therefore no adjustment was made to the values shown in Table 9.1 for season or drought.

Table 9.1. Ratios of the enclosed shoot length to the corresponding bud length for each of six clones. Mean of data collected from irrigated and unirrigated treatments in May and September 1990 (n = 360, $r^2 = 73\%$).

Shoot/bud length ratio			
Clone	1	0.338 $\pm$ 0.016	a
	6/8	0.324 $\pm$ 0.010	az
	SFS150	0.308 $\pm$ 0.015	az
	15/10	0.303 $\pm$ 0.014	az
	207	0.335 $\pm$ 0.016	a
	K35	0.289 $\pm$ 0.014	z

Modelling shoot extension

Changes in the length of shoots (L ; mm) with time (t ; d) have been described using linear (Squire, 1979), exponential (Tanton, 1982a), logistic (Bond, 1945) and Gompertz (Smith *et al.*, 1990) models. The linear model used by Squire (1979) ignores the early part of shoot extension, whilst the other three models allow shoot extension to be modelled as a continuous process from the release of apical dominance. The exponential model (Equation 9.1) uses only two variables: an initial shoot length (L_0 ; mm) and a constant relative extension rate (RER; mm mm⁻¹ d⁻¹).

$$L = L_0 e^{\text{RER} \cdot t} \quad 9.1$$

The logistic (Equation 9.2) and Gompertz (Equation 9.3) models use three variables: a factor related to the relative extension rate (b), the time from release of apical dominance to the date of the maximum shoot extension rate (m ; d), and the final shoot length (L_f ; mm). In the logistic model the RER declines in a logistic manner from a maximum level at release of apical

dominance. In the Gompertz model the RER declines exponentially (Figure 9.2).

$$L = L_f / (1 + e^{(-b \cdot (t-m))}) \quad 9.2$$

$$L = L_f e^{-e^{-b(t-m)}} \quad 9.3$$

The RER of six shoots selected from clones 1 and S15/10 within the fully irrigated sub-plots during the wet season in January 1990 are shown in Figure 9.2. Immediately after the release of apical dominance the RERs of these shoots were low before increasing to a maximum level around the time the fish leaf began to unfurl. Eventually the RER of each shoot declined as further leaves were unfurled.

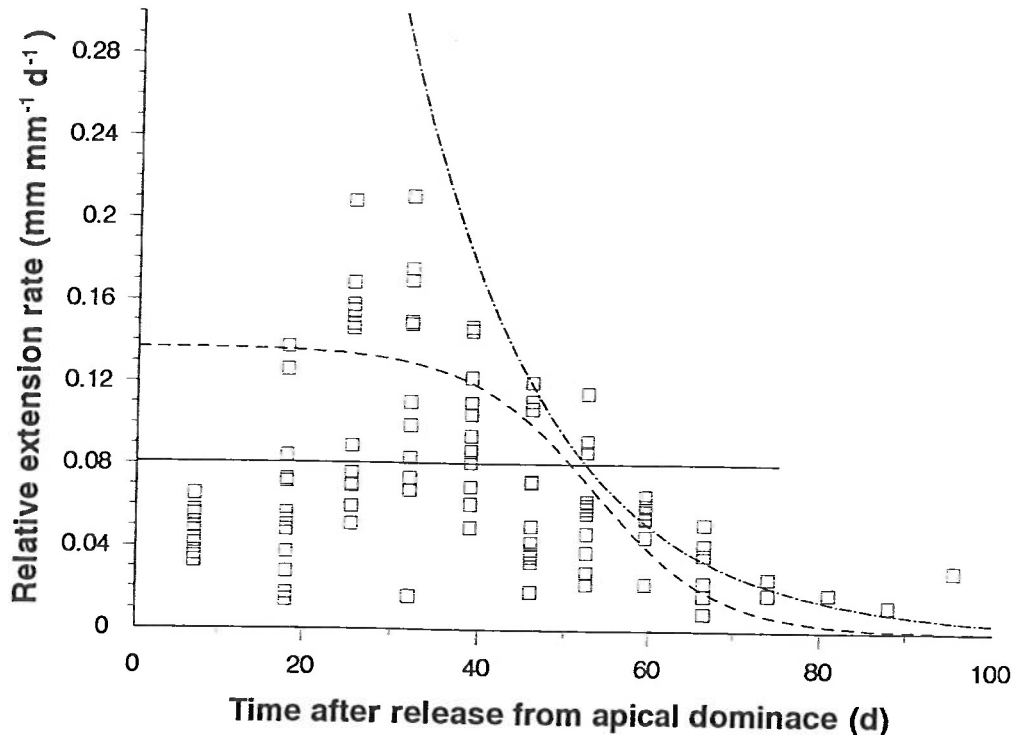


Figure 9.2. Changes in the relative extension rates of six shoots from clones 1 and S15/10 with time from release of apical dominance in January 1990. Also shown are the relative extension rates of these shoots as estimated using exponential: —, logistic: --- and Gompertz: -.-.- equations.

As shown in Figure 9.2 the Gompertz model substantially overestimated the RER of the shoots immediately after the release of apical dominance. The constant RER assumed by the exponential model provided a reasonable description of growth, but became less applicable as the shoots grew. In order to select which of the three models was most appropriate for describing clonal differences in shoot extension rate, they were used to model the extension of six shoots released from apical dominance in September 1989 (warm, dry season), January (wet season) and June 1990 (cool season) within a fully irrigated sub-plot of each clone. Shoots which died or were broken or lost before unfurling three flush leaves (4 in September, 3 in January and 10 in June) were treated as missing values.

The exponential model using only two parameters explained 94-95% of the variation in shoot length with time in each of the seasons (Table 9.2). The inclusion of a third parameter with the logistic or Gompertz model improved the fit for the warm and wet season data to over 99%. However because few data were collected after the time of maximum extension, the precision of the estimates of the final length (L_f) were poor. It was particularly difficult to estimate precise values of L_f for shoots growing at the end of the cool season when temperatures were rising. Of the twenty six shoots released from apical dominance in June 1990, which subsequently unfurled three flush leaves, the Gompertz equation could only specify values of L_f for eighteen all of which were unrealistic, being in excess of 10 m. The poor precision of these estimates of L_f in each season also skewed the estimates of the constants m and b , making it necessary to transform logarithmically all the values to obtain a normal distribution. In contrast the constants RER and L_0 calculated with the exponential model were normally distributed. Whilst the logistic model can provide a more realistic description of shoot extension, for the purpose of describing clonal, temperature and drought effects the exponential model was the most reliable. Therefore the exponential model (Equation 9.1) was used to calculate values for L_0 and the mean RER from the release of apical dominance to the unfurling of three flush leaves for each shoot. These values were then used to determine the effects of clone, season and drought on shoot extension.

Table 9.2. Best fit relationships between shoot length (L ; mm) and time (t; d) using exponential, logistic and Gompertz models for six shoots of six clones released from apical dominance during the warm dry (September 1989), wet (January 1990) and cool seasons (June 1990).

	(n)	RER (mm mm ⁻¹ d ⁻¹)		L _o (mm)	r ² (%)
Exponential $L = L_o e^{RER \cdot t}$					
warm dry	32	0.06 ± 0.014		0.64 ± 0.32	94
wet	33	0.08 ± 0.011		0.72 ± 0.26	95
cool	26	0.04 ± 0.008		0.85 ± 0.29	95
	(n)	b (mm mm ⁻¹ d ⁻¹)	m (d)	L _f (mm)	r ² (%)
Logistic $L = L_f / (1 + e^{(-b \cdot (t-m))})$					
warm dry	32	0.13 ± 0.074	72 ± 38	720 ± 2414	99
warm wet	33	0.14 ± 0.034	53 ± 7	133 ± 31	99
cool	26	0.06 ± 0.017	161 ± 66	2994 ± 5950	96
Gompertz $L = L_f e^{-e^{-b(t-m)}}$					
warm dry	28	0.08 ± 0.067	69 ± 40	204 ± 742	99
warm wet	33	0.06 ± 0.026	57 ± 15	237 ± 186	99
coo	18	0.01 ± 0.011	3307 ± 5000	- -	96

Calculation of base temperatures

The seasonal changes in the RERs of shoots from the fully irrigated plants were related to the mean air temperature (T_{mean} ; °C) during the time from selection to the mean date when shoots in that treatment had unfurled three flush leaves. The value of T_{mean} was calculated from daily maximum and minimum temperatures recorded in a Stevenson screen about 800 m from the experimental site. The best fit linear relationship between the values of RER for each clone and the corresponding values of T_{mean} were then used to establish the base temperature for shoot extension (T_{be} ; °C) and the thermal extension rate (ρ_e ; mm mm⁻¹ d⁻¹ °C⁻¹). Using mean air temperatures when the minimum air temperature is below T_{be} can cause the true value of T_{be} to be underestimated. A more accurate estimate of T_{be} can then be calculated by

modelling the diurnal variations in temperature (Allen, 1976; Stephens and Carr, 1990) and calculating the mean daily thermal time during the period of shoot extension for a range of values of T_{be} . When the correct value of T_{be} is chosen, the best fit linear relationship between RER and the mean daily thermal time will pass through the origin.

The effects of drought were expressed by relating the extension rates of the shoots in the unirrigated treatments with the corresponding rates in the fully irrigated treatments.

Shoot development

Each time that shoot lengths were measured the number of expanded leaves were also recorded. The first unfurled leaf was the 'fish' leaf and this was followed by the unfurling of successive 'flush' leaves. The length of the shoot replacement cycle (SRC; d) from the removal of apical dominance to when three flush leaves had unfurled was established for each shoot. Shoots that were broken or lost before all three flush leaves had unfurled were treated as missing values. The development rate of the shoot was then defined as the inverse of the SRC. The relationships between shoot development rates and T_{mean} for each fully irrigated clone, and the effects of drought were determined using the same procedures described for shoot extension rates.

Relationships between shoot extension and development

The best fit linear relationship between shoot length and the number of expanded leaves (inclusive of the fish leaf) was established for each shoot. The slope of this relationship corresponded to the mean internode length, and the intercept was equivalent to the mean length of a shoot without an expanded leaf. Within the fully irrigated treatments from November 1989 to October 1990 the mean value of this intercept was about 11 mm.

The mean air temperature, from the time when the mean shoot had unfurled one fish leaf to the time it had unfurled three flush leaves, was calculated for each of the six fully irrigated clones within each of the seventeen generations. The effects of clone, season and drought on internode length were then determined using the same methods described for analysing shoot extension rates.

RESULTS

Initial shoot length

There were no distinct seasonal effects on in the estimated length of shoots at release of apical dominance (range: 0.55-1.20 mm) within the fully irrigated sub-plots when released from apical dominance (Figure 9.3). However, these lengths were reduced ($P \leq 0.05$) from 1.1 to 0.9 mm in the unirrigated treatments in November and December 1989 after the imposition of drought treatments. In 1990 initial shoot lengths were lower ($P \leq 0.01$) in the fully irrigated treatments (1.0 mm) than in the unirrigated sub-plots (0.5 mm) on 25 October, thirteen weeks after the start of drought treatments. There were also differences between clones in the initial length of shoots. The initial shoot lengths for clones 1, 207 and S15/10 were longer ($P \leq 0.001$) than those for clones 6/8, SFS150 and K35 (Table 9.3).

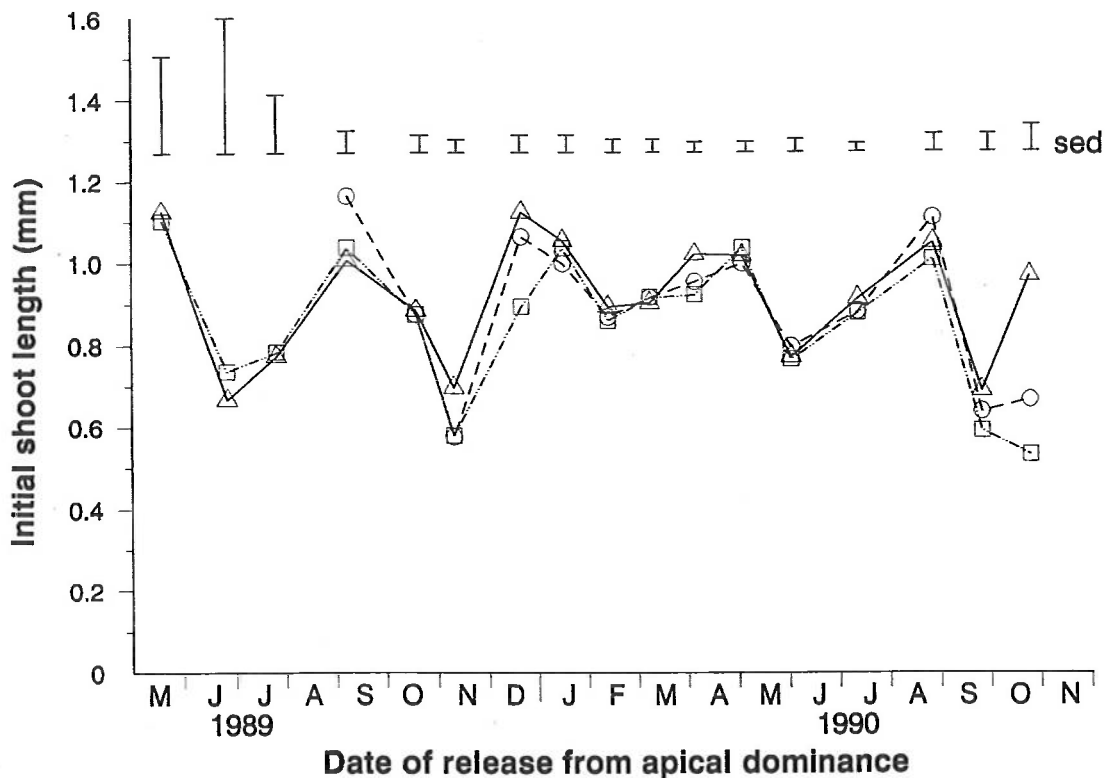


Figure 9.3. Effects of drought on the measured length of shoots at release of apical dominance for six clones. Fully irrigated (I₅): —△—, partially irrigated (I₂): --○--, and unirrigated (I₀): ---□---.

Table 9.3. Comparisons of the measured and fitted, estimated using an exponential equation, length of shoots when released from apical dominance for each of six clones between September 1989 and October 1990. The fitted values are calculated from the mean values from 14 generations and three drought treatments.

		Initial shoot length (mm)			
		Measured		Fitted	
Clone	1	1.06	a	0.99	a
	6/8	0.84		0.72	z
	SFS150	0.86		0.66	z
	S15/10	1.02	a	0.89	a
	207	1.05	a	0.83	a
	K35	0.76	z	0.60	z
sed (n)		0.03	(1008)	0.08	(14)

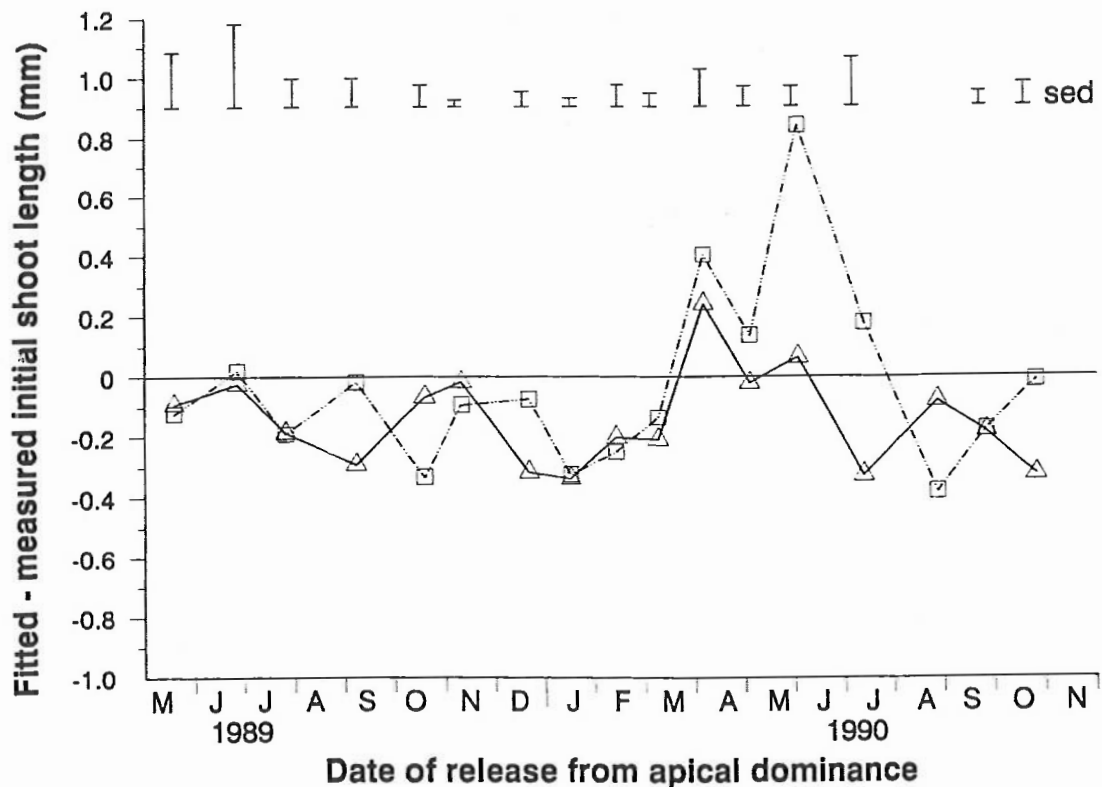


Figure 9.4. Comparisons of the seasonal differences between the measured and fitted lengths of shoots when released from apical dominance for six fully irrigated: —△— and unirrigated: —□— clones.

The fitted values of the initial shoot lengths (L_0) for the fully irrigated clones calculated with the exponential model were not significantly different from the measured values within any individual generation (Figure 9.4). The fitted values also showed similar differences between clones as the measured values (Table 9.3). The only major discrepancy between fitted and measured values occurred within the unirrigated treatments on one date during the 1990 cool season (2 June). On this date the exponential equation fitted a higher initial shoot length than was measured (Figure 9.4).

Relative extension rate

The relative extension rates of shoots within the fully irrigated treatments were highest for those released from apical dominance between October, at the end of the warm dry season, and March during the rains (0.055-0.094 mm mm⁻¹ d⁻¹) (Figure 9.5). At this time the RERs of the shoots from clones 1 and 207 (0.080-0.094 mm mm⁻¹ d⁻¹) were consistently higher ($P \leq 0.05$) than those of the slowest clones S15/10 and 6/8 (0.059-0.076 mm mm⁻¹ d⁻¹). For each of the clones the lowest RERs were for shoots released from apical dominance at the beginning of the cool season in May and June 1990 (0.029-0.049 mm mm⁻¹ d⁻¹). However in contrast to the wet season, the RERs of shoots of fully irrigated clone 1 released from apical dominance on 2 June were lower ($P \leq 0.05$) than the corresponding shoots of clones 6/8, SFS150, S15/10 and 207.

Between 85 and 92% of the seasonal variation in the RERs of shoots from each fully irrigated clone were explained by a straight line relationship with air temperature (T_{mean}) (Table 9.4). This relationship varied between clones in terms of the slope (ρ_e) and the x-axis intercept or base temperature for shoot extension (T_{be}). The values of these base temperatures were lowest for clones SFS150 and 6/8 (8.9 and 9.5°C) and highest for clones 1 and K35 (11.1 and 11.5°C), whilst the values for clones S15/10 and 207 were intermediate (10.1 and 10.3°C). Each of these base temperatures, especially those of clones 1 and K35, were above the mean minimum air temperature in June of 8.7°C. In this instance a more accurate estimate of T_{be} was derived by considering the diurnal fluctuations in temperature. This analysis, whilst estimating a similar value of T_{be} for clone SFS150 of about 9°C, estimated values for clones 1 and K35 of between 12.0 and 12.5°C which were about 1°C higher than those based on mean daily temperatures alone (Figure 9.6).

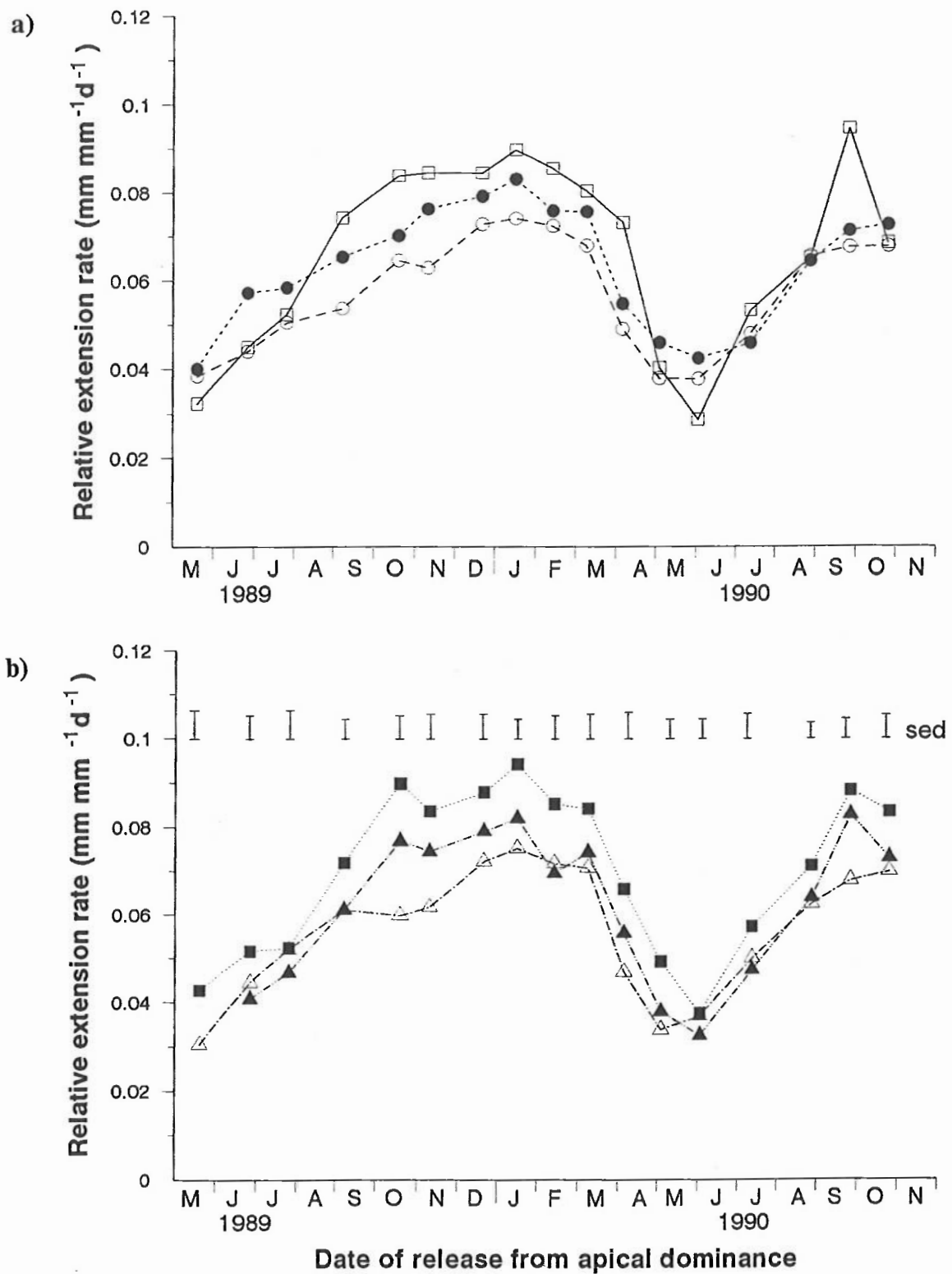


Figure 9.5. Seasonal changes in the relative extension rates of shoots from each of six fully irrigated clones, in relation to the date of removal of apical dominance. a) Clones 1: —□—, 6/8: ---○---, SFS150:●..... b) Clones S15/10: ---△---, 207: —■—, K35: ---▲---.

Table 9.4. a) Relationships between the relative shoot extension rate (RER; mm mm⁻¹ d⁻¹) and the corresponding mean air temperature (T_{mean}; °C) for each of six fully irrigated clones. The equations take the form: $RER = \rho_e \cdot T_{mean} + a$ (n=17).

		Slope, ρ_e		Y-axis intercept, a		r ²
		(mm mm ⁻¹ d ⁻¹ °C ⁻¹)		(mm mm ⁻¹ d ⁻¹)		(%)
Clone	1	0.0118	±0.0012	-0.132	±0.021	85
	6/8	0.0078	±0.0007	-0.074	±0.012	87
	SFS150	0.0080	±0.0008	-0.070	±0.014	86
	15/10	0.0086	±0.0009	-0.087	±0.015	85
	207	0.0109	±0.0008	-0.112	±0.014	92
	K35	0.0111	±0.0009	-0.126	±0.015	92

b) Estimated base temperatures for shoot extension rate for each of six fully irrigated clones, with 95% confidence intervals ^a.

		Base temperature (°C)		
		Minimum	Mean	Maximum
Clone	1	9.4	11.1	12.1
	6/8	7.5	9.5	10.7
	SFS150	6.7	8.9	10.2
	S15/10	8.2	10.1	11.3
	207	9.1	10.3	11.1
	K35	10.2	11.3	12.1

^a: The 95% confidence intervals were derived from the minimum temperature and maximum air temperatures which resulted in no extension ($P \leq 0.05$).

There seemed to be a positive correlation between the values of T_{be} and ρ_e . Clones SFS150 and 6/8 which had the lowest values of T_{be} also had the lowest values of ρ_e . Clones 1 and K35 which had the highest T_{be} also had the highest ρ_e . This correlation meant that the ranking of the fully irrigated clones in terms of their shoot extension rate varied with T_{mean}.

Effects of drought

The RERs of shoots released from apical dominance between September and October 1989 within the unirrigated treatments were reduced ($P \leq 0.05$) by the drought treatments imposed between October and November. In 1990 the first reduction ($P \leq 0.05$) in RER due to drought occurred in shoots released from apical dominance on 2 June, 55 days before the imposition of drought treatments. The severity of this reduction increased until those shoots released from apical dominance within the unirrigated treatments at the end of August, had a RER which was 40% of the corresponding value in the fully irrigated sub-plots (Figure 9.7).

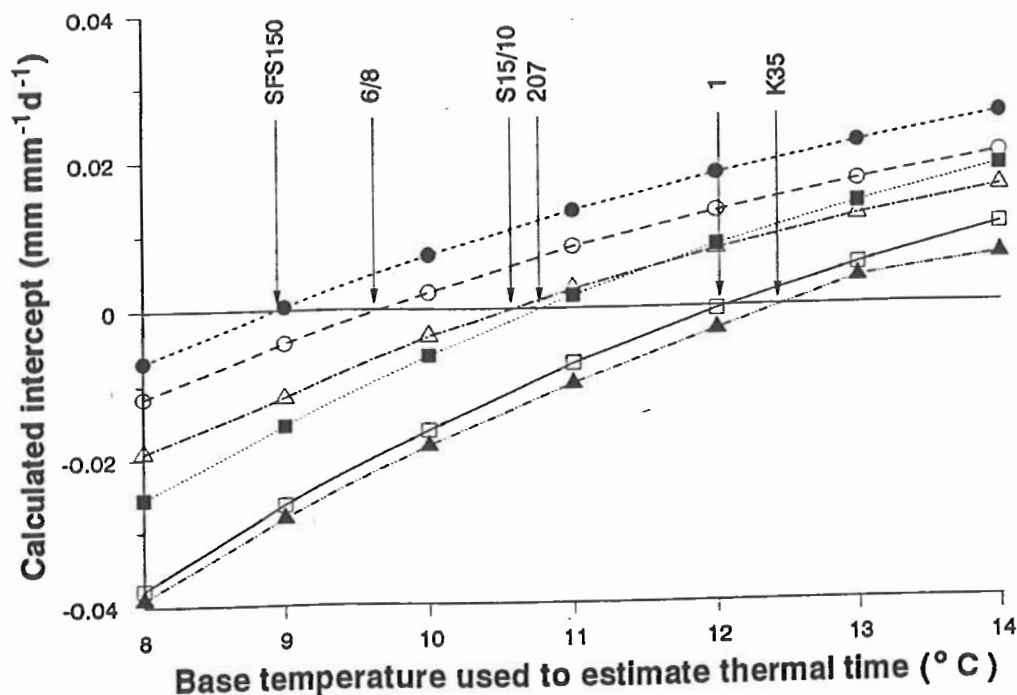


Figure 9.6. Calculated y-axis intercepts from the best fit linear relationship between relative extension rate and thermal time for each of six clones for a range of base temperatures. At the correct base temperature the y-axis intercept will equal zero.

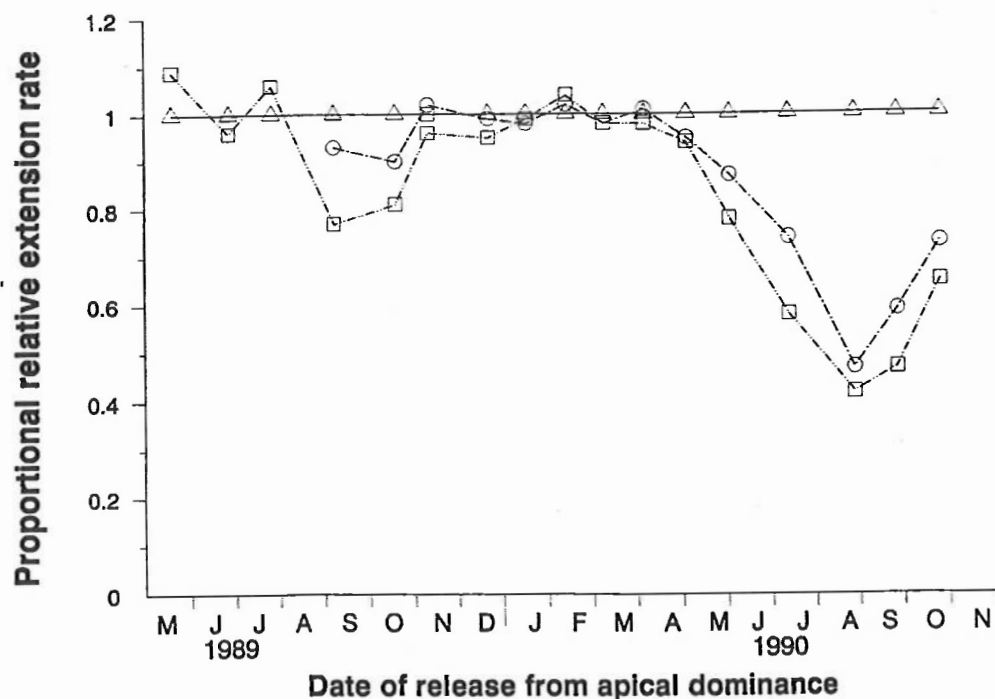


Figure 9.7. Effects of drought on the relative extension rates of shoots from six clones expressed as a proportion of the corresponding rate of shoots from fully irrigated plants, related to the month that the shoots were released from apical dominance. Fully irrigated (I_5): $\triangle$, partially irrigated (I_2): $\circ$, unirrigated (I_0): $\square$.

For those shoots released from apical dominance on 26 September 1990, there were clone x drought interactions ($P \leq 0.001$) on the values of RER (Table 9.5). In the fully irrigated treatments the RERs of shoots from clones 1, 207 and K35 were higher ($P \leq 0.05$) than those from clones SFS150, 6/8 and S15/10, but in the unirrigated sub-plots there were no significant clonal differences. Therefore at this time the shoot extension rates of clones 1, 207 and K35 were more sensitive to drought than those of the other clones.

Table 9.5. Effects of drought on the relative extension rates (RER) of shoots for each of six clones released from apical dominance on 26 September 1990.

Drought treatment		RER ($\text{mm mm}^{-1} \text{d}^{-1}$)		
		Fully irrigated I_5	Partially irrigated I_2	Unirrigated I_0
Clone	1	0.094 a	0.051 a	0.038 a
	6/8	0.068 z	0.045 az	0.034 a
	SFS150	0.071 z	0.040 z	0.035 a
	15/10	0.068 z	0.047 az	0.038 a
	207	0.088 a	0.050 az	0.036 a
	K35	0.083	0.044 az	0.039 a

sed = 0.0049, n = 24.

Shoot development

The development rates of shoots from the fully irrigated clones showed similar seasonal changes to shoot extension rates: shoots released from apical dominance in May and June at the beginning of the cool season had the slowest development rates ($0.008\text{--}0.012 \text{d}^{-1}$) (Figure 9.8). The length of the SRC of these shoots ranged from 85 days for clone 207 to 117 days for clone K35. Shoot development rates increased after the cool season and reached a plateau of $0.016\text{--}0.021 \text{d}^{-1}$ for shoots released from apical dominance at the end of the warm dry season and during the rains. The length of the SRC for shoots released from apical dominance in September 1990 ranged from 53 days for those from fully irrigated clone 1, to 75 days for those from clones 6/8 and S15/10.

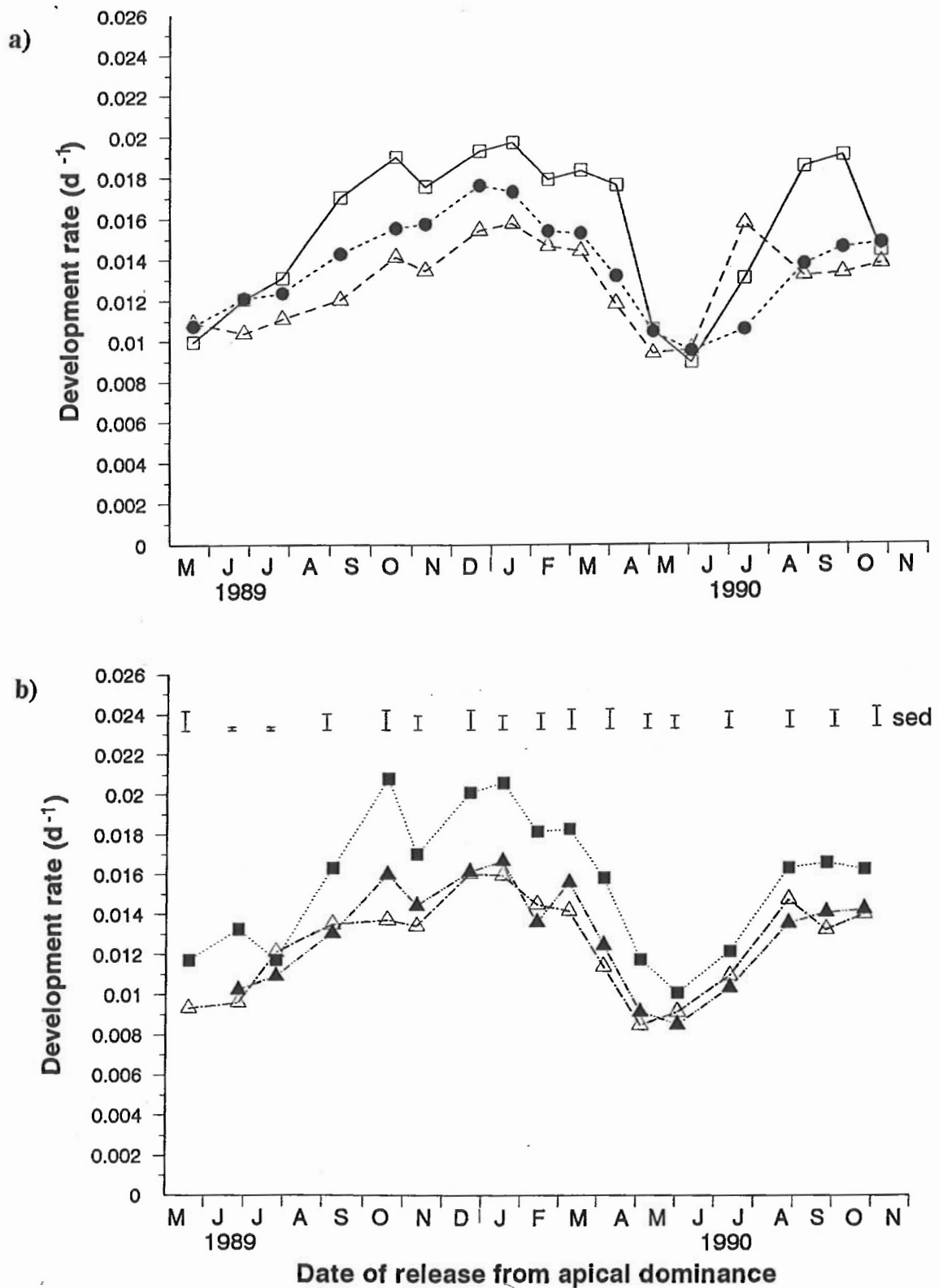


Figure 9.8. Seasonal changes in the development rates of shoots from each of six fully irrigated clones, relative to the month that they were released from apical dominance. a) Clones 1: —□—, 6/8: —○—, SFS150: —●—. b) Clones S15/10: —△—, 207: —■—, K35: —▲—.

The shoot development rates for fully irrigated clones 1 and 207 were consistently higher ($P \leq 0.05$) than for the slowest fully irrigated clone, except for clone 1 in June 1990. At this time the shoot development rate for clone 1 was similar to that for the slowest clone. This low development rate for clone 1 during the cool season was offset by high development rates for shoots released from apical dominance in August and September 1990 (Figure 9.8). The shoot development rates for clones S15/10 and K35 were similar to those for clone 6/8 which were usually the slowest.

Table 9.6 a). Relationships between the shoot development rate ($1/\text{SRC}$; d^{-1}) and the corresponding mean air temperature (T_{mean} ; $^{\circ}\text{C}$) for each of six fully irrigated clones. The relationship takes the form : $1/\text{SRC} = \rho_d \cdot T_{\text{mean}} + a$ ($n=17$)

		Slope ρ_d ($\text{d}^{-1} \text{ } ^{\circ}\text{C}^{-1}$)		Y-axis intercept a (d^{-1})		r^2 (%)
Clone	1	0.0019	± 0.0003	-0.017	± 0.005	75
	6/8	0.0012	± 0.0001	-0.007	± 0.002	84
	SFS150	0.0014	± 0.0001	-0.010	± 0.002	86
	15/10	0.0014	± 0.0002	-0.011	± 0.003	81
	207	0.0019	± 0.0002	-0.017	± 0.004	81
	K35	0.0017	± 0.0001	-0.015	± 0.002	89

b) Estimated base temperatures for shoot development rate for each of six fully irrigated clones, with 95% confidence intervals^a.

		Base temperature ($^{\circ}\text{C}$)		
		Minimum	Mean	Maximum
Clone	1	5.1	8.7	10.6
	6/8	2.9	6.1	8.2
	SFS150	4.4	7.0	8.7
	S15/10	4.7	7.8	9.7
	207	5.7	8.6	10.4
	K35	7.4	9.2	10.5

^a: The 95% confidence interval was derived from the minimum and maximum air temperatures which resulted in no development ($P \leq 0.05$).

Between 75 and 89% of the seasonal variation in the shoot development rates of each fully irrigated clone was explained by a straight line relationship with the mean air temperature (Table 9.6). Like the clonal ranking of T_{be} , the values of T_{bd} were lowest for clones 6/8 and SFS150 (6.1 and 7.0°C) and highest for clones 1 and K35 (8.7 and 9.2°C). However for all of the clones the base temperature for shoot development (range: 7.0-9.2°C) was lower than that for extension (range: 8.9-11.3°C). Because each of the values of T_{bd} were below or very close to the minimum monthly air temperature, the estimates of T_{bd} calculated using daily mean temperatures were similar to those calculated with an allowance for the diurnal changes in temperature. As with shoot extension, clones with low base temperatures for development also tended to have a low thermal development rates (ρ_d).

Effects of drought

The drought treatments imposed between October and November 1989, reduced ($P \leq 0.05$) the development rates of shoots released from apical dominance within the unirrigated sub-plots between September and December 1989 (Figure 9.10). In 1990 drought reduced ($P \leq 0.05$) the development rates of shoots released from apical dominance between 2 June and 26 October. The effects of drought were greatest on those shoots which were released from apical dominance within the unirrigated treatments on 27 August. The development rates of these shoots were about 50% of the corresponding values within the fully irrigated treatment.

There were clone x drought interactions ($P \leq 0.05$) on the development rates of shoots released from apical dominance between July and October 1990. Shoots from clones 1 and 207 which had the highest shoot development rates when fully irrigated, were similar to those of most other clones when drought stressed (Table 9.7).

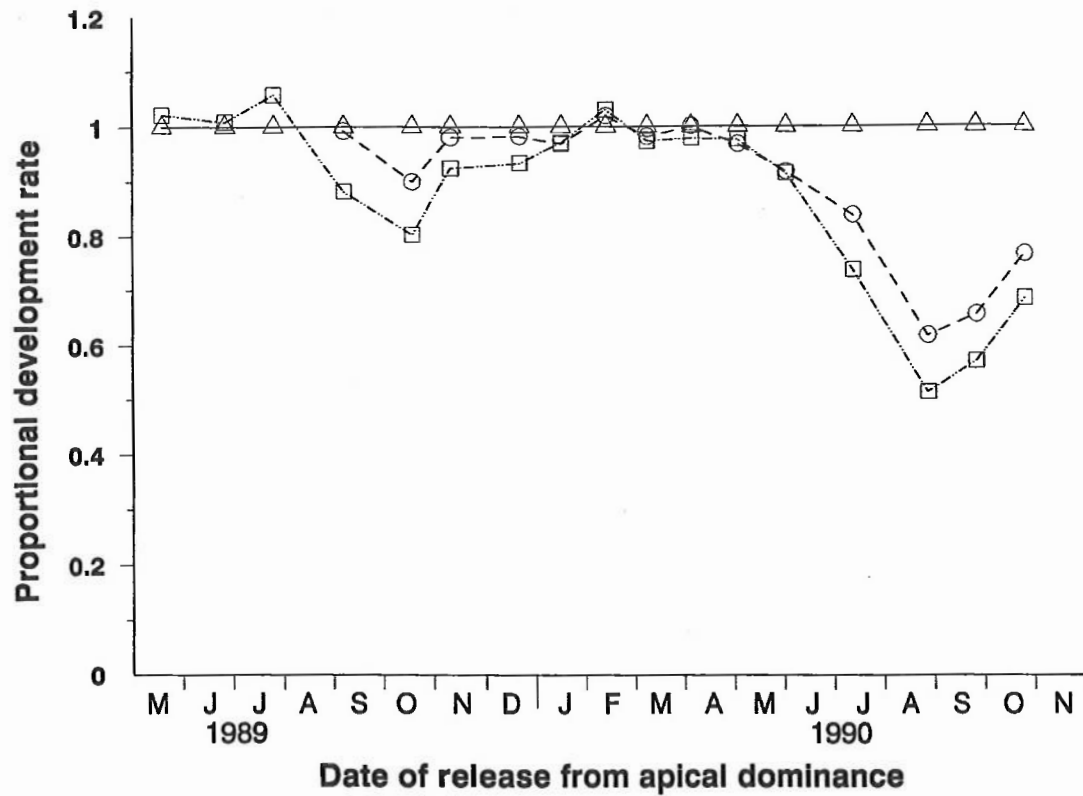


Figure 9.9. Effects of drought on the mean development rates of shoots from six clones, as a proportion of the corresponding rate for shoots from fully irrigated plants, related to the month that the shoots were released from apical dominance. Fully irrigated (I_5): $\triangle$, partially irrigated (I_2): $\circ$, unirrigated (I_0): $\square$.

Table 9.7. Effects of drought on the development rates of shoots released from apical dominance on 26 September 1990 for each of six clones.

Drought treatment		Development rate (d^{-1})					
		Fully irrigated I_5		Partially irrigated I_2		Unirrigated I_0	
Clone	1	0.0190	a	0.0116	a	0.0096	a
	6/8	0.0135	z	0.0096	z	0.0077	z
	SFS150	0.0148	z	0.0096	z	0.0087	az
	15/10	0.0136	z	0.0101	az	0.0091	az
	207	0.0169		0.0104	az	0.0086	az
	K35	0.0147	z	0.0095	z	0.0090	az
sed = 0.0008, n = 24							

Relationships between shoot length and stage

The mean internode length, between the fish leaf and the third flush leaf, of shoots from fully irrigated clones showed a similar seasonal changes as the relative extension rates (Figure 9.10). Internode lengths were longest for shoots released from apical dominance at the end of the warm dry season and the early part of the wet season, when air temperatures were highest, and were shortest for shoots released from apical dominance in June at the beginning of the cool season.

The internode lengths of shoots released from apical dominance within the fully irrigated treatments from December 1989 to March 1990, or from September to the last measurements in October 1990 were similar for all the clones. However, shoots of fully irrigated clone 1 released from apical dominance during the cool season (June to August 1990) had shorter ($P \leq 0.05$) internodes (range: 7.5-14.0 mm) than those of the other clones (range: 11.0-26.0 mm).

Between 59 and 72% of the seasonal change in the internode lengths of the shoots from each fully irrigated clone was explained by a straight line relationship with mean air temperature (Table 9.8). Clone SFS150 which had the lowest base temperature for shoot extension, also had the lowest base temperature for internode length. Similarly clones 1 and K35 which had the highest values of T_{be} , also had the highest base temperatures for internode length. For each clone the internode length increased by between two and four mm per °C rise in T_{mean} above the corresponding base temperature. This temperature response was least for clone SFS150 and greatest for clone 1.

Effects of drought

Drought imposed in October and November 1989 reduced ($P \leq 0.05$) the mean internode length of shoots which were released from apical dominance in September and October. In 1990 drought reduced ($P \leq 0.05$) the internode lengths of those shoots released from apical dominance between early June and October.

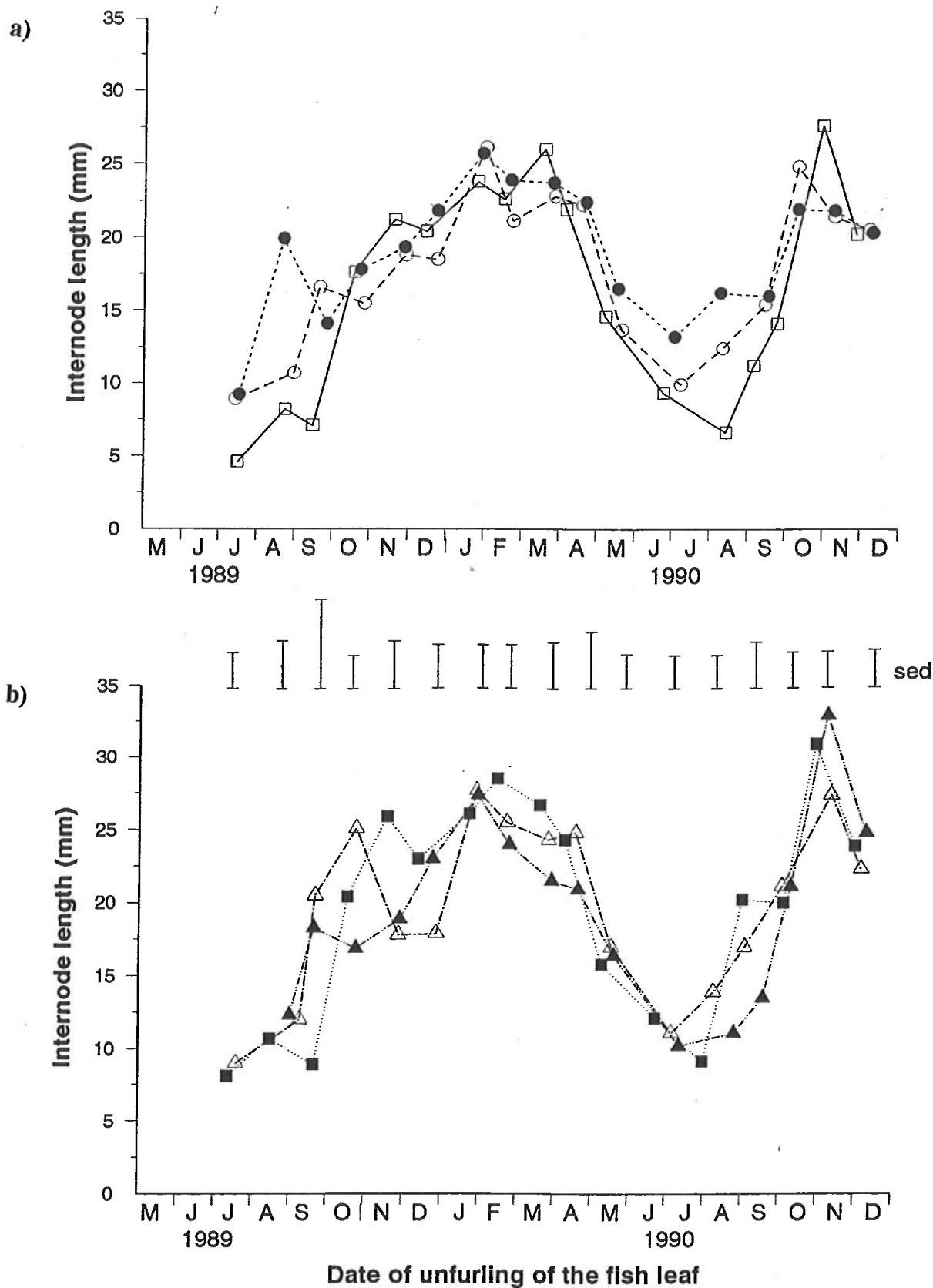


Figure 9.10. Seasonal changes in the mean internode lengths of shoots from each of six fully irrigated clones, relative to the date that they unfurled the fish leaf. a) Clones 1: —□—, 6/8: ---○---, SFS150:●..... . b) Clones S15/10: —△—, 207: —■—, K35: —▲— .

Table 9.8 a). Relationships between the mean length of shoot internodes (between the fish leaf and third flush leaf)(i ; mm) and the mean air temperature (T_{mean} ; °C) for each of six fully irrigated clones. The relationship takes the form : $i = \rho_i \cdot T_{\text{mean}} + a$ ($n=17$).

		slope ρ_i (mm)		y-axis intercept a (mm °C ⁻¹)		r^2 (%)
Clone	1	3.81	±0.64	-48.5	±10.9	68
	6/8	2.71	±0.46	-28.6	±7.9	68
	SFS150	2.05	±0.38	-15.8	±6.6	64
	15/10	3.19	±0.49	-34.8	±8.5	72
	207	3.67	±0.61	-42.7	±10.4	69
	K35	3.62	±0.77	-43.2	±13.3	59

b) Estimated base temperatures for internode length for each of six fully irrigated clones, with 95% confidence intervals ^a.

		Base temperature (°C)		
		Minimum	Mean	Maximum
Clone	1	10.2	12.7	13.9
	6/8	6.7	10.5	12.3
	SFS150	1.5	7.7	10.4
	S15/10	7.8	10.9	12.5
	207	8.6	11.6	13.1
	K35	7.4	12.7	13.7

^a: The 95% confidence intervals were derived from the minimum and maximum temperatures which resulted in no extension per additional unfurled leaf ($P \leq 0.05$).

DISCUSSION

Shoot extension

The rates of shoot extension for each of six clones under varying drought regimes were modelled using an exponential equation. The fitted values of initial shoot length closely corresponded to the actual measured values. The RERs of the shoots from the fully irrigated clones ranged from 0.030 to 0.095 mm mm⁻¹ d⁻¹ and were normally distributed. These values are similar to those (0.025-0.080 mm mm⁻¹ d⁻¹) established for well-fertilized mature clone 6/8 at Ngwazi (Stephens and Carr, 1992a).

The relative extension rates of shoots from fully irrigated clones were lowest during the cool season, and highest during the warm dry season and at the

beginning of the wet season. Most of this seasonal variation was explained by a straight line relationship between RER and the mean air temperature, described by an x-axis intercept (T_{be}) and a slope (ρ_e). The values of T_{be} and ρ_e varied between clones.

The lowest T_{be} was 8.9°C for clone SFS150, which is similar to the value (10.4°C) reported for the same clone in Malawi (Cannell *et al.*, 1990). However the values of T_{be} for clones 6/8 (9.5°C) and K35 (11.3-12.4°C) were substantially lower than those (14.8-14.9°C) reported for the same clones by Cannell *et al.* (1990). The values reported by Cannell *et al.* were derived from measurements taken during the ten months from November, when mean air temperatures are 24°C, to the end of the subsequent cool season when the corresponding temperatures are 17-19°C. The early measurements were therefore taken at higher temperatures than the later measurements. Confounded with this trend in temperatures, the bushes were pruned four months before the first measurements in November. It is generally known that shoot extension rates are greater in recently pruned bushes, and it is therefore probable that the measurements of Cannell *et al.* (1990) confounded the effects of temperature on shoot extension with those of time from pruning. This may explain why they estimated higher base temperatures than those reported here.

Apart from the above measurements, the estimation of T_{be} and the ranking of clones by base temperature were generally similar to those reported elsewhere. The value for clone 6/8 (9.5°C) is close to the value of 10°C suggested for the shoots of a mature stand of clone 6/8 also at Ngwazi (Stephens and Carr, 1992a). The value of 10.1°C for clone S15/10 is within the wide range of 7.3-11.6°C reported for the same clone by Obaga and Squire (1992) in Kenya. The high ranking of the value for clone 1 (11.1-12.0°C) in comparison to most of the other clones, was also reported in a comparison of three clones by Stephens and Carr (1990).

There was a positive correlation between the values of T_{be} and ρ_e . The data presented by Cannell *et al.* (1990) from Malawi also showed that the clones with the highest values of T_{be} had the highest values of ρ_e . One explanation for this in regions where there are seasonal changes in temperature, such as Southern Tanzania and Malawi, is that higher shoot extension rates during the warm season are not only a direct result of high temperatures, but they can also be increased by the relocation of the starch built up in the stem and structural roots during the cool season (Stephens and Carr, 1992a). This effect could also

explain why the RERs of shoots of fully irrigated clone 1 released from apical dominance in September 1990, at the end of the cool season, were greater than those released from apical dominance at the end of October (Figure 9.5). This change in the allocation of reserves tends to emphasise the clonal differences in temperature response. This may explain why, so far, it has been easier to determine clonal differences in temperature response in regions like Malawi and Southern Tanzania where there is a seasonal climate, than by comparing extension rates over a range of altitudes in Kenya, where the seasonal changes in temperature are minimal. If this is so, then selection programmes for clones with a low base temperature will be more effective if carried out in regions at high latitudes.

The step changes in T_{be} reported by Stephens and Carr (1990; 1992a) for mature stands of clones 1 and 6/8 were not readily apparent in these younger plants. This could be a result of younger bushes having smaller starch reserves or since there was incomplete ground cover, shoot and soil temperature could be more closely coupled with air temperature. The values of T_{be} presented here are also based on measurements of relative extension rates calculated over a longer period of time than the linear extension rates reported by Stephens and Carr (1990, 1992a).

The correlation between T_{be} and ρ_e meant that the shoots of those clones with a low base temperature did not necessarily have the highest extension rates at high temperatures (Figure 9.11). For example the mean RERs of shoots from clone 1 were below those of clone SFS150 during the cool season, but were higher during the warm season. This change in ranking corresponds to the differences between these clones in the seasonal distribution of yield (cf Chapter 5). Clone SFS150 yielded more during the cool season than clone 1, but produced less than clone 1 once temperatures had increased. These clonal differences in T_{be} and ρ_e therefore have important implications for yield distribution in areas where the T_{mean} is close to the base temperatures (8-12°C) during part of the year. By selecting clones with a low T_{be} the peaks and troughs in yield associated with synchronisation of growth can be smoothed. This could allow easier scheduling of labour for harvesting leaf, and easier planning of transport and factory requirements.

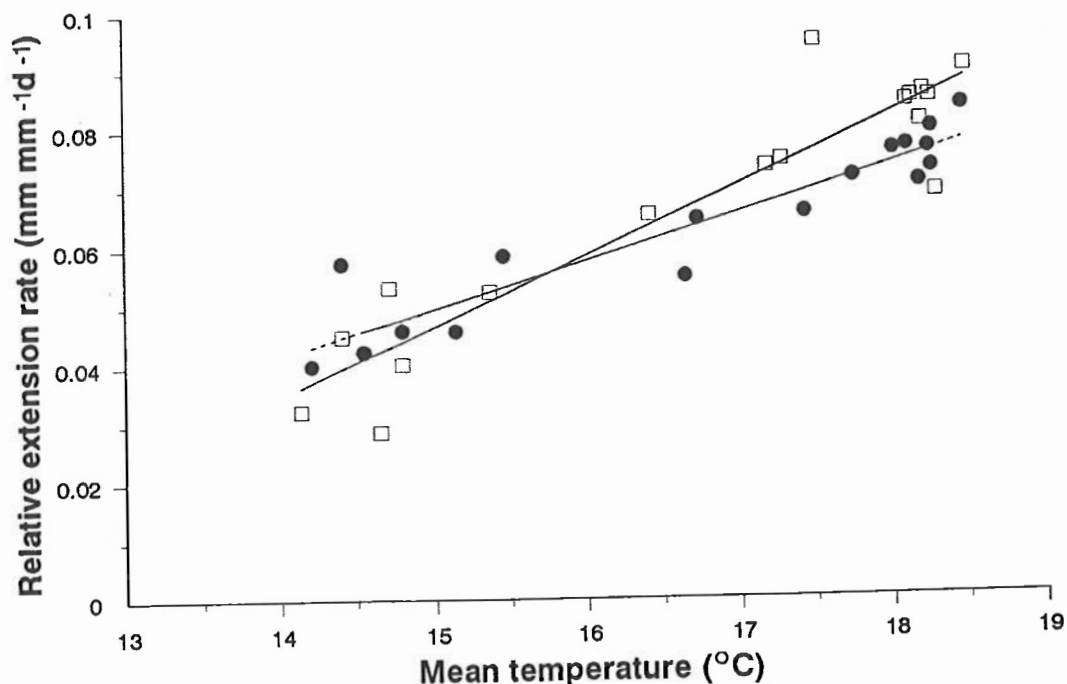


Figure 9.11. Relationships between the relative extension rates and mean air temperature for shoots of irrigated clones 1: □ and SFS150: ●.

Shoot development

The two small leaved 'China' type clones (207 and 1) unfurled leaves faster than the larger leaved clones during the main growing season. This is in contrast to work at UPASI in India which showed that the rates of leaf unfurling by seven clones were similar (Murty and Sharma, 1989). The lack of clonal differences in India may be a result of measurements being taken at higher mean air temperatures (range: 20-26°C) than at Ngwazi (range: 14-18.5°C). Further work on clonal differences in the rate of leaf unfurling have been initiated at Ngwazi so that these apparent differences can be studied in finer detail.

Rates of shoots development varied with mean air temperature and were described by values for T_{bd} and ρ_d for each fully irrigated clone. The base temperatures for development were 1.7 to 3.5°C lower than those for extension. Since shoot extension was estimated to cease at a higher temperature than development, the mean internode length (which is linked to the ratio of

extension rate to development rate) will tend to zero at the base temperature for extension. Therefore the temperatures responses of the mean internode length were similar to those of shoot extension rates with the shortest internodes occurring during the cool season.

Effects of drought

Drought reduced shoot extension and development rates in both 1989 and 1990. Because the exponential model was used to calculate the rates of extension and development over quite long periods of time (48 to 143 days) it is not possible to define with this technique the SWD at which shoot development or extension was first reduced. However the results do show that the effects of drought were greater on shoot extension than shoot development (Figures 9.8 and 9.10). This is also substantiated by the observation that drought reduced the mean internode length of shoots. The reduction by drought of the length of shoots with a specified number of expanded leaves has also been reported for a mature stand of clone 6/8 by Stephens and Carr (1992a). Therefore in terms of temperature and drought responses shoot extension was more sensitive to the environment than development. A practical implication of this is that a harvest interval based on shoot development is likely to be more stable than one based on shoot extension.

There were also clonal differences in the responses to drought of shoots released from apical dominance in September 1990 during the middle of the dry period. In the unirrigated treatments the relative rates of shoot extension were similar for all clones, but in the fully irrigated plots the RERs were greatest for clones 1, 207 and K35. At this time, those shoots which were extending fastest were therefore the most sensitive to drought. Stephens and Carr (1989) also reported that the effects of drought on shoot growth were related to the proportion of fast growing shoots.

CONCLUSIONS

Shoot extension was successfully modelled using an exponential function which estimated only two constants: an initial shoot length and a relative extension rate, which was normally distributed. This model provided a reliable description

of shoot length from the release of apical dominance to the time the shoot had unfurled three flush leaves.

Between 82 and 92% of the seasonal variation in the RERs of the shoots from each fully irrigated clone was explained by a linear relationship with mean air temperature. There were differences between clones in the slope (ρ_e) and the x-axis intercept (T_{be}) of this relationship. High values of T_{be} tended to be associated with high values of ρ_e . The shoots of clone SFS150, which had low values for both these constants, showed a more stable extension rate than those of clone 1 and this corresponded to differences in the seasonal distribution of yield. In regions where the mean air temperature is close to the values of T_{be} reported here (range: 8-12°C), a more even seasonal yield distribution is obtained from clones with a low T_{be} .

The base temperatures for shoot development were 1.7 to 3.5°C lower than those for extension in all clones. This meant that the mean internode length of shoots was reduced at low temperatures and showed seasonal changes similar to shoot extension rates. Shoot extension rates were also more sensitive than shoot development to drought. Therefore in regions where there are seasonal changes in air temperature or drought stress a harvest interval based on shoot development is likely to be more stable than one based on shoot extension.

The modelling of shoot development and shoot extension provides the first stage in understanding clonal differences in seasonal yield distribution and also in the composition of harvested shoots. These are discussed further in Chapter 10.

CHAPTER 10

SHOOT MASS AND POPULATION DENSITY

INTRODUCTION

In Chapter 9 the responses of the shoot extension and development rates of six clones to temperature and drought were described. The total dry mass of harvested shoots also depends upon the fresh mass and dry matter content of each individual shoot, and the total number of shoots (Figure 9.1).

The fresh mass of a harvested shoot can be determined from the length of the shoot at harvest and the relationship between fresh mass and length (Fordham and Palmer-Jones, 1977). This has been described both as a linear (Palmer-Jones, 1974) and as an exponential relationship (Smith *et al.*, 1990). Alternatively the fresh mass of the harvested shoot can be determined from the number of expanded leaves on the harvested shoot and the relationship between this and fresh shoot mass. Stephens and Carr (1992b) reported that this relationship was linear ($0.16\text{--}0.35 \text{ g leaf}^{-1}$) for a mature stand of clone 6/8.

The dry matter content of harvested shoots is often assumed for convenience to be a constant 22.5% (TRFK, 1990) or 22.0% (Cloughley, 1981). However Cloughley (1981) reported that the mean dry matter content of shoots harvested during the main growing season in Malawi ranged from 19.8% for one clone to 22.9% for another. He related this to clonal differences in the ratio of leaf to stem. The dry matter content of a tea shoot can also be increased by low temperatures (Cloughley *et al.*, 1983) drought and poor nutrition (Stephens and Carr, 1992b).

The total number of harvested shoots depends upon the shoot population density (Tanton, 1979). Clonal differences in the shoot population density for three clones were reported by Stephens and Carr (1990) from counts of the number of shoots with an unfolded fish leaf per unit area. Values ranged from 50-400 shoots m^{-2} for two broad leaved 'Assam' type clones to 350-1200 shoots m^{-2} for the small leaved clone 1. They also reported clonal differences in the proportion of shoots that were actively growing. Whilst this technique does not include all the shoots growing on the bush, many of which are in the form of buds, it does allow comparisons to be made between clones.

In this chapter the composition, fresh mass and dry matter content of harvested shoots and the shoot population density of six clones under different drought regimes are analysed and discussed.

METHODOLOGY

Measurements were taken within the clone x drought experiment which was fully described in Chapter 3.

Composition and mass of harvested shoots

Shoot composition was determined from samples (range: 195-205 g) taken at random from the shoots harvested from two replicates of the fully irrigated (I_5) and unirrigated (I_0) sub-plots of each clone from February 1990 to May 1991. From July 1990 to May 1991 the number of replicates was increased to three. The shoots within each sample were sorted into those which were actively growing, dormant and broken. The active shoots were then further sub-divided into shoots with one, two, three, four or five expanded leaves. The number of shoots within each class was counted and expressed as a proportion of the total number of unbroken shoots, or active shoots. The proportion of broken shoots on a mass basis was typically 20-35%.

The fresh mass of shoots in each class was also weighed (± 0.1 g) and divided by the number of shoots to determine the mean fresh mass of each type. The mean fresh shoot mass for the whole sample was calculated by dividing the total fresh mass of unbroken shoots by the corresponding number. These data were grouped into four periods corresponding to the wet (February to May 1990, and December 1990 to May 1991), cool (June to August 1990) and warm dry seasons (September to November 1990). Within each of these seasons the relationships between fresh shoot mass and the number of expanded leaves were determined for the actively growing shoots of each fully irrigated clone.

Dry matter content

The dry matter contents of the harvested shoots were determined from 25-80 g samples collected on seven harvest dates between March and November 1990. These samples were taken from two (from March to July 1990) and later three replicates (from August to November 1990) of the fully irrigated (I_5) and

unirrigated (I_0) sub-plots of each clone. The samples were oven dried at 80-90°C for 24 hours, re-weighed and used to determine the dry matter content at harvest.

An analysis of comparable dry matter content data collected over one complete year from an adjacent nitrogen x irrigation experiment was used to identify the important variables determining the dry matter content. The variables considered were potential soil water deficit (SWD), mean air temperature (over the preceding day, 10 days, 1, 2 and 3 months), rainfall (over the preceding day and 2 days), vapour pressure deficit, and fertilizer application. A step-wise regression showed that three factors: the potential SWD, the mean air temperature during the preceding two months and the fertilizer application accounted for 65% of the annual variation in dry matter content. Using the same two environmental factors, but substituting clone for fertilizer application, an identical step-wise regression was used to analyse the data collected from the clone x drought experiment.

Shoot population density

Two measures of shoot population density were taken. From May 1989, nine months after planting in the field, until July 1990 when the fully irrigated bushes had achieved 35-65% ground cover the total number of shoots per bush were counted. The bushes were planted at a spacing of 1.2 x 0.8 m. From February 1990 to May 1991 shoot density was counted within the area of a 0.1 m² quadrat placed in the centre of selected bushes. Shoots were identified once the terminal bud had visibly begun to expand, in the same way as described by Stephens and Carr (1992b).

The total number of active and dormant shoots per bush were counted at two to four week intervals from May until August 1989 on three selected bushes within two replicates of an I_5 , I_4 or I_3 and an I_2 , I_1 or I_0 sub-plot of each clone. From September 1989 the numbers were recorded at two week intervals on three (September 1989 to March 1990) and later two (April 1990 to July 1990) bushes within each of the four replicates of the fully irrigated (I_5), partially irrigated (I_2) and unirrigated (I_0) sub-plots of each clone. After the first harvest of shoots on 4 December 1989 shoot numbers were always counted between one and six days after a harvest.

From February 1990 until May 1991 the numbers of active and dormant shoots were counted within a 0.1 m² quadrat placed in the centre of selected tea bushes, two to three days after each harvest. Two bushes were sampled in each of the four replicates of the fully irrigated (I₅), partially irrigated (I₂) and unirrigated (I₀) sub-plots of each clone. Both the whole bush and the quadrat measurements were used to determine the clonal, seasonal and drought effects on the total population density of shoots and the proportion of shoots that were actively growing.

RESULTS

Composition of harvested shoots

The relative composition of shoots harvested between February 1990 and May 1991 from the irrigated treatments of each clone are shown in Figure 10.1. The mean proportion of harvested shoots with an active terminal bud gradually decreased from 78-92% between February and May 1990, to 49-73% between December 1990 and May 1991.

There were also significant clonal differences in the relative composition of harvested shoots, as illustrated by the results from the fully irrigated treatments during the wet season from December 1990 to May 1991 (Table 10.1). The proportion of shoots harvested with an active terminal bud from clones S15/10, 6/8 and 207 (76-77%) were higher ($P \leq 0.05$) than those from clones 1 and K35 (58-66%). The harvested samples with the lowest ($P \leq 0.05$) proportion of active shoots came from clone SFS150 (49%).

There were also differences ($P \leq 0.05$) between clones in the composition of the harvested active shoots. The proportion of shoots with one or two leaves was highest in clone 6/8 and lowest in clone 1. Clone 1 had the highest proportion of active shoots with three or four leaves. The proportion of active shoots harvested with five leaves, which was highest for clone 1 (0.2%), comprised such a small proportion of the total they were grouped with the shoots with four expanded leaves.

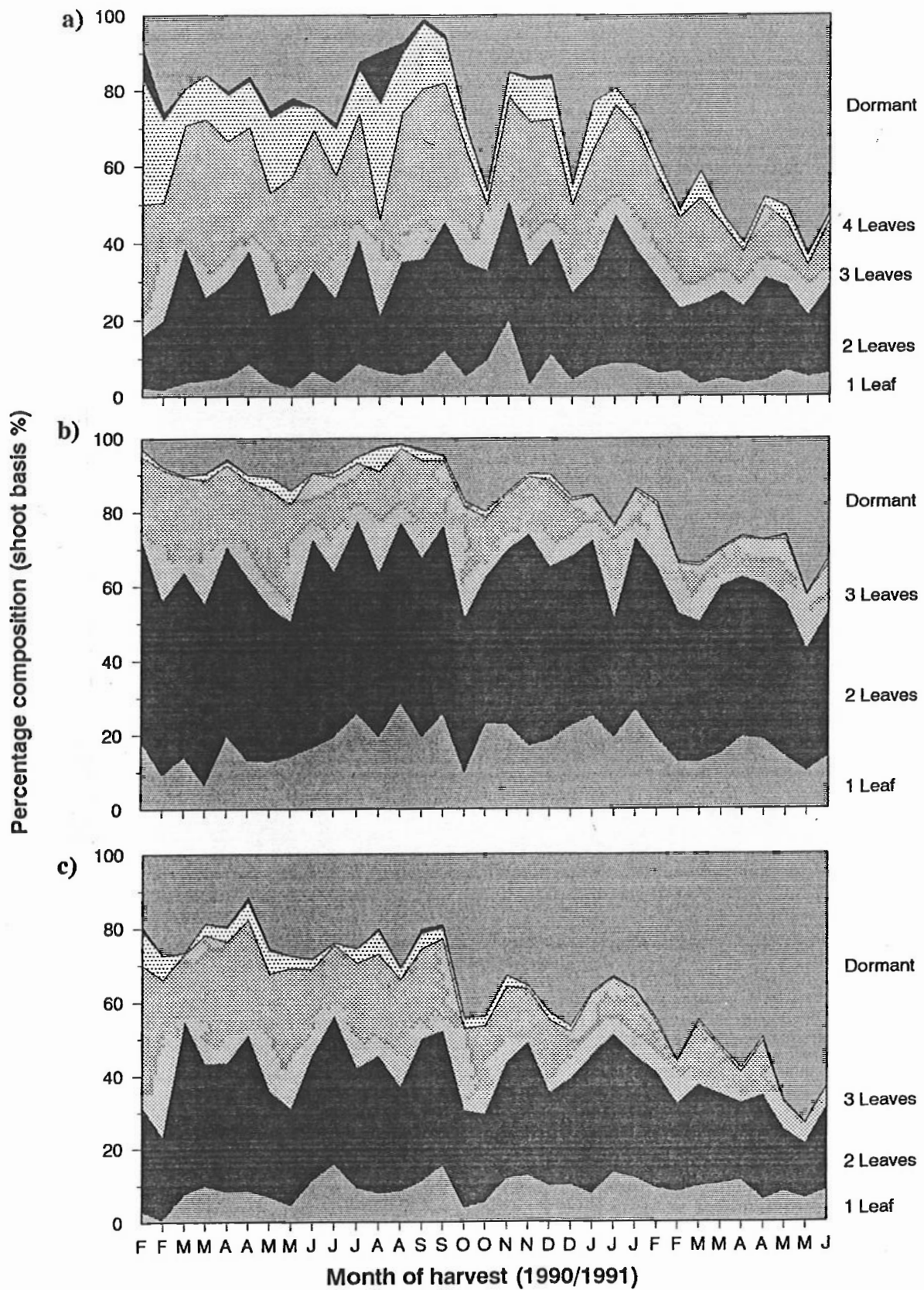


Figure 10.1.a-c. Seasonal changes in the composition of unbroken shoots harvested from each of six fully irrigated clones: a) clone 1, b) clone 6/8, c) clone SFS150

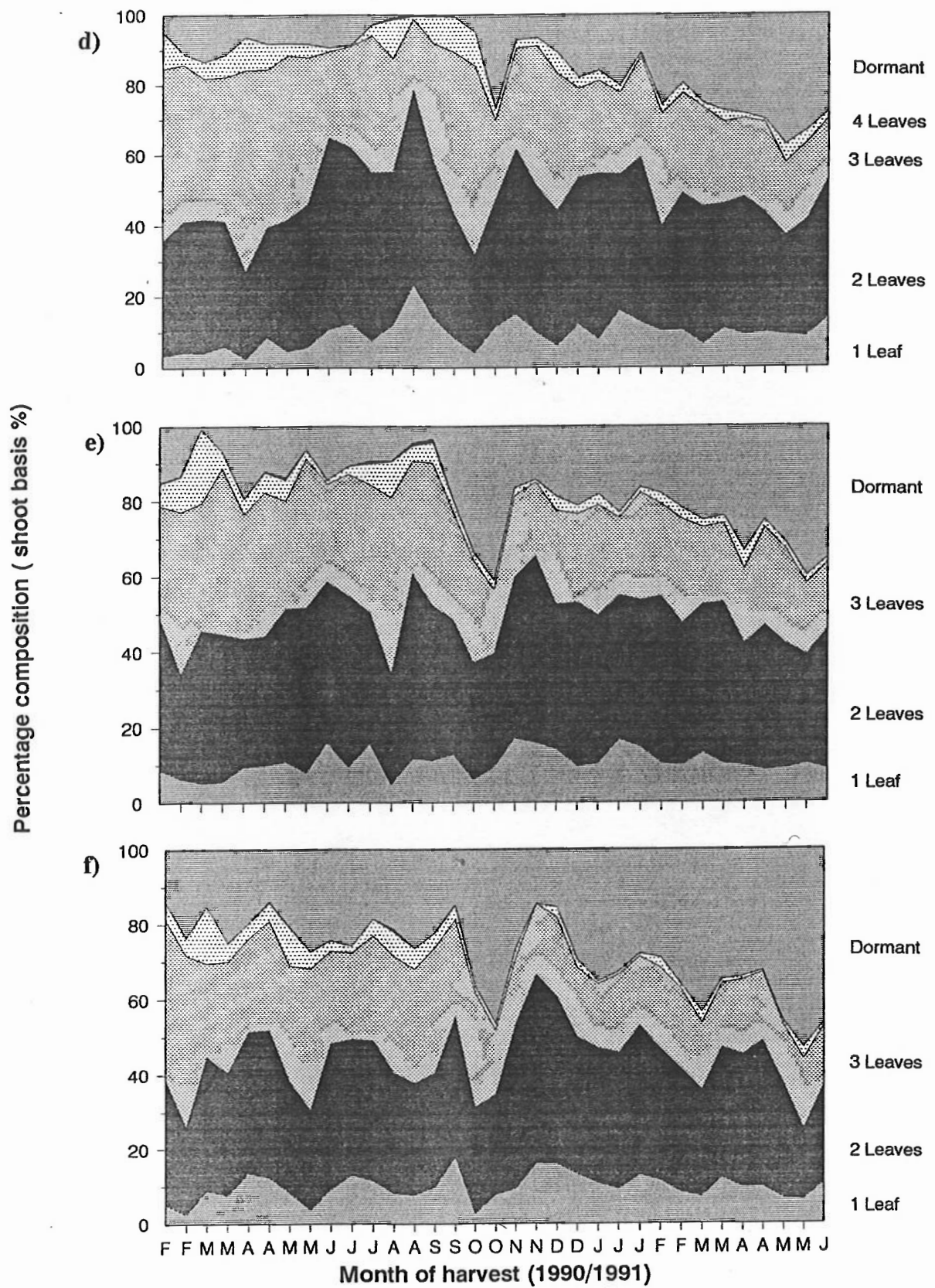


Figure 10.1.d-f. Seasonal changes in the composition of shoots harvested from six fully irrigated clones: d) clone S15/10, e) clone 207 and f) clone K35.

Table 10.1. Proportion of harvested shoots (on a numbers basis) with an active terminal bud and the proportions of these shoots with one, two, three and four expanded leaves from each of six fully irrigated clones during the wet season from December 1990 to May 1991.

		Proportion of unbroken shoots that were active (%)	Composition of active shoots (%)			
			One leaf + bud	Two leaves + bud	Three leaves + bud	Four leaves + bud
Clone	1	58	11 z	42 z	39 a	8 a
	6/8	76 a	24 a	55 a	20 z	1 z
	SFS150	49 z	19	53 a	26	2 z
	S15/10	77 a	13 z	49	34	4
	207	76 a	15	50	32	3
	K35	66	16	53	29	2
sed (n=39)		2.0	2.0	1.0	2.4	-a

a: Significant differences for the four leaves + bud data were calculated using an angular transformation.

The first significant ($P \leq 0.05$) effect of drought on shoot composition occurred following the imposition of drought treatments from the end of July 1990. Although very few shoots were harvested from the unirrigated treatments between mid-October and mid-December, over the complete warm dry season (September to November 1990) the mean proportion of active shoots was lower ($P \leq 0.05$) from the unirrigated sub-plots (73%) than where fully irrigated (80%).

Relationships between fresh shoot mass and development

The mean fresh mass of individual harvested shoots with three expanded leaves from the fully irrigated treatments declined from 1.26 g between February and May 1990 to 0.92 g during the following cool season (June to August). The mean fresh mass of this type of shoot then remained relatively constant averaging 1.07 g in the warm dry season (September to November 1990) and 1.02 g during the subsequent wet season (December 1990 to May 1991).

Throughout the year there were consistent clonal differences ($P \leq 0.05$) in the fresh mass of shoots with three expanded leaves harvested from the fully irrigated treatments (Table 10.2). The fresh mass of these shoots was almost twice as high from clones S15/10 and K35 (1.1-1.7 g) as from clones 1 and 207 (0.5-0.9 g). The corresponding shoots from clones 6/8 and SFS150 were of intermediate mass (0.8-1.4 g).

Table 10.2. Mean fresh mass of a harvested shoot with three expanded leaves for each of six fully irrigated clones during four seasons from February 1990 to May 1991.

Fresh mass of shoot with three expanded leaves (g)									
Season		Wet Feb. - May 90		Cool June - Aug. 90		Warm dry Sept. - Nov. 90		Wet Dec. 90 - May 91	
Clone	1	0.75	z	0.63	z	0.66	z	0.60	z
	6/8	1.37		0.82		1.05		1.02	
	SFS150	1.26		1.02		1.15		1.06	
	S15/10	1.70	a	1.38	a	1.36	a	1.36	a
	207	0.88	z	0.59	z	0.74	z	0.74	
	K35	1.60	a	1.11		1.47	a	1.31	a
sed		0.097		0.039		0.088		0.038	
n		16		12		18		39	

The mean fresh mass of harvested shoots with three expanded leaves (Figure 10.2) from some of the fully irrigated clones, most notably clones K35 and S15/10, fluctuated in a series of peaks and troughs which started at the beginning of the warm dry season in 1990 and continued into the wet season. Over this period the harvest interval was relatively constant (range: 12-16 days). Shoot mass appeared to peak approximately every eight weeks or at every fourth harvest. These peaks in shoot mass coincided with troughs in the yield of harvested shoots and shoot population density (cf Figure 10.5).

The relationships between the fresh mass (M ; g) and the number of expanded leaves on a harvested shoot (n_L) for each season were best described by exponential rather than linear relationships. This relationship (Equation 10.1) included two constants: the mass of the shoot with no expanded leaves (M_0 ; g) and the relative increase in mass per unfurled leaf (b_M):

$$M = M_0 e^{b_M \cdot n_L} \quad 10.1$$

There were clonal differences ($P \leq 0.001$) in the value of M_0 (Table 10.3; Figure 10.3), but the model was not improved ($P \leq 0.05$) by including different values of b_M . The mean fresh mass of a shoot with a specified number of expanded leaves harvested from fully irrigated clones K35 and S15/10 was about twice that from clones 1 and 207.

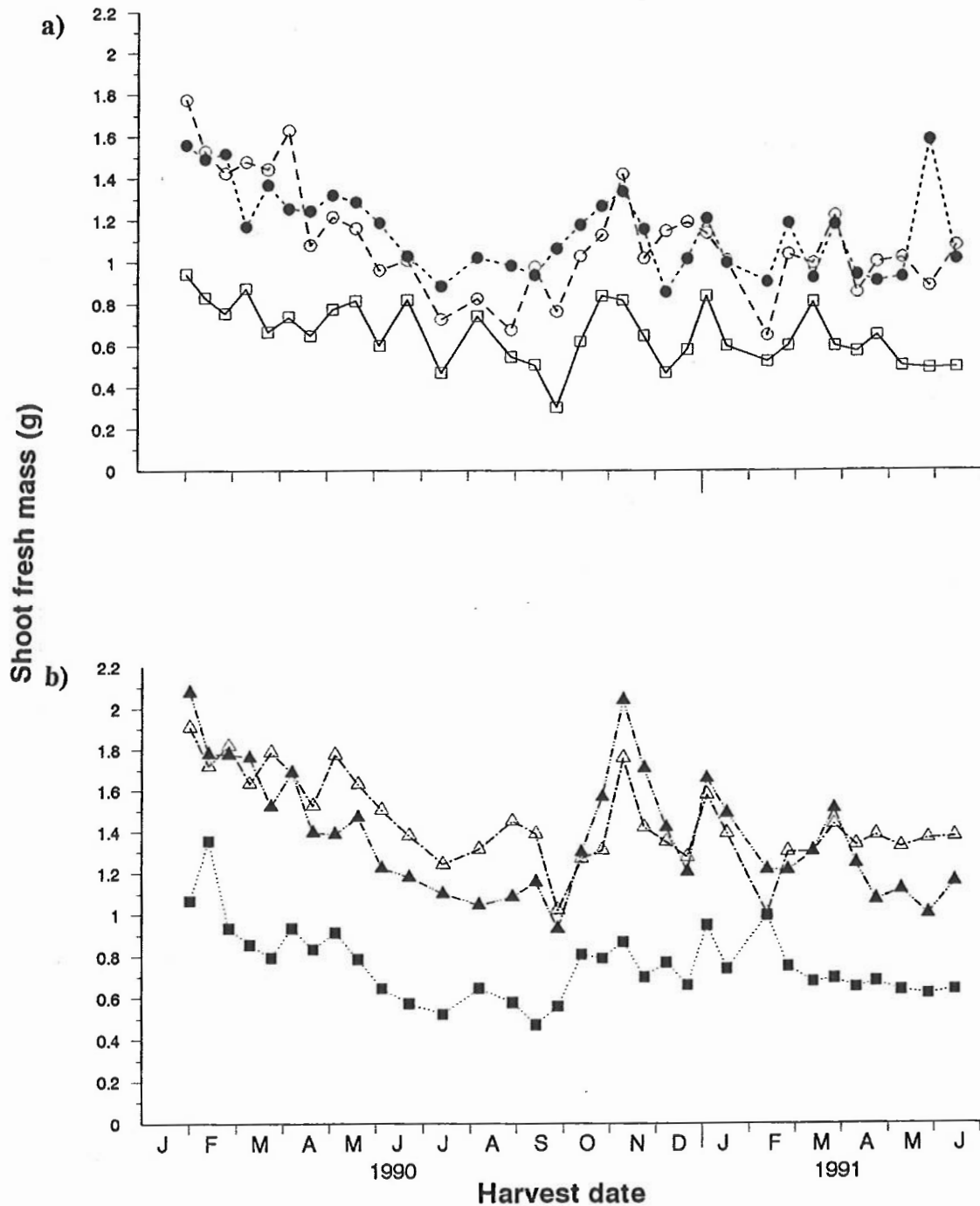


Figure 10.2.

Seasonal changes in the mean fresh mass of harvested shoots with an active terminal bud and three expanded leaves from each of six fully irrigated clones. a) Clones 1: —□—, 6/8: ---○---, SFS150:●...... b) Clones S15/10: ---△---, 207: —■—, K35:▲......

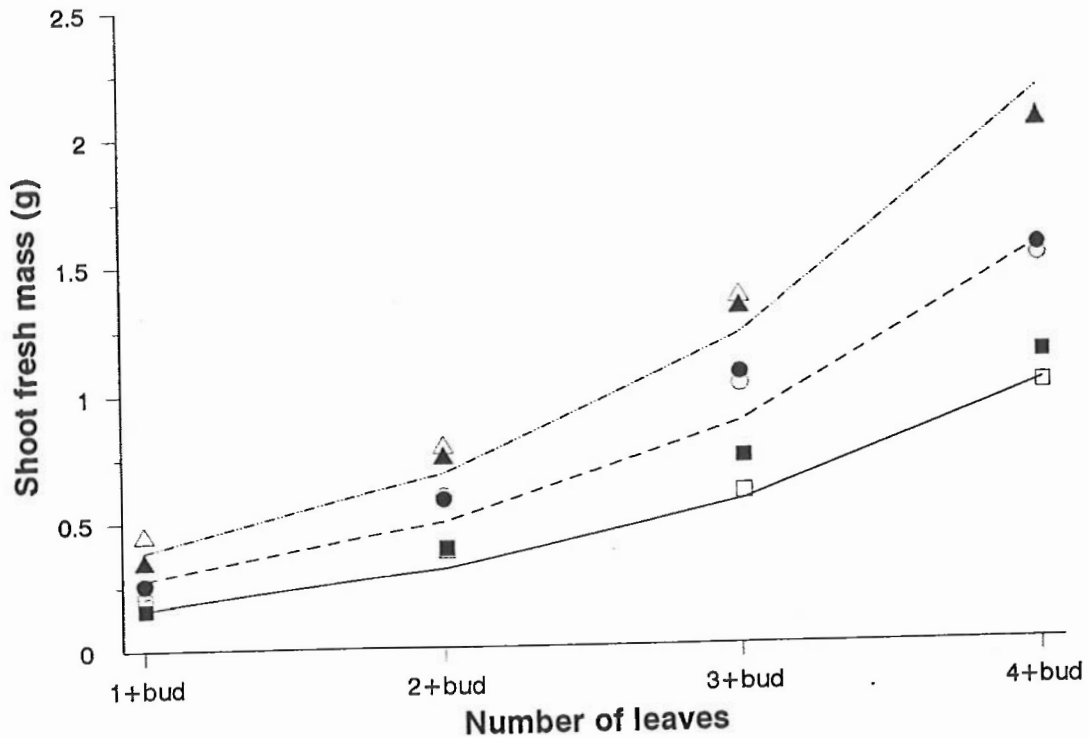


Figure 10.3. Relationships between the fresh mass and the number of expanded leaves for shoots harvested from each of six clones during the wet season from December 1990 to May 1991. Clones 1: □, 6/8: ○, SFS150: ●, S15/10: △, 207: ■ and K35: ▲.

Table 10.3. Mass of a harvested shoot with no expanded leaf (M_0) and the relative increase in mass per expanded leaf (b_M) for each of six clones for each of four seasons from February 1989 to May 1991.

Season	Wet Feb.- May 90	Cool June- Aug. 90	Warm dry Sept.- Nov. 90	Wet Dec. 90- May 91
b_M (g g ⁻¹)				
	0.57 ±0.010	0.57 ±0.011	0.54 ±0.015	0.57 ±0.009
M_0 (g)				
1	0.13 ±0.005	0.10 ±0.004	0.11 ±0.006	0.10 ±0.004
6/8	0.22 ±0.009	0.14 ±0.006	0.17 ±0.010	0.16 ±0.005
SFS150	0.22 ±0.008	0.17 ±0.008	0.18 ±0.011	0.16 ±0.006
S15/10	0.29 ±0.012	0.22 ±0.009	0.23 ±0.013	0.21 ±0.007
207	0.16 ±0.007	0.11 ±0.005	0.11 ±0.014	0.11 ±0.004
K35	0.25 ±0.010	0.17 ±0.007	0.24 ±0.015	0.22 ±0.007
n	739	561	516	1641
r ² (%)	83	86	75	76

Mean fresh shoot mass

The mean fresh mass of an individual harvested shoot was calculated by dividing the total mass of unbroken shoots by their number. The mean fresh mass of shoots harvested from the fully irrigated treatments declined from a mean of 1.00 g between February and May 1990 to 0.69 g during the 1990 cool season (June to August). It then remained relatively constant averaging 0.73 g during the warm dry season and 0.65 g during the wet season from December 1990 to May 1991. There were clonal differences ($P \leq 0.001$) in the mean fresh mass of a harvested shoot in each of the seasons as shown in Table 10.4. The mean fresh mass of the harvested shoots from fully irrigated clones S15/10 and K35 (range: 0.83-1.41 g) was always higher ($P \leq 0.05$) than that from the other clones (range: 0.46-1.01 g). The mean shoot mass was always lowest for clone 1 or clone 207 (range: 0.46-0.76 g).

Table 10.4. The mean fresh mass of a shoot harvested from each of six fully irrigated clones for each of four seasons from February 1990 to May 1991.

		Mean fresh mass of a harvested shoot(g)							
Season		Wet		Cool	Warm dry		Wet		
		Feb. - May 90		June - Aug. 90	Sept. - Nov. 90		Dec. 90 - May 91		
Clone	1	0.76	z	0.62	0.51	z	0.46	z	
	6/8	0.93		0.56	0.65		0.58		
	SFS150	1.01		0.70	0.77		0.61		
	S15/10	1.41	a	0.97	1.03	a	0.92	a	
	207	0.69	z	0.46	0.46	z	0.48	z	
	K35	1.19		0.83	0.96	a	0.83		
sed		0.08		0.04	0.08		0.03		
n		16		12	18		39		

Dry matter content

Regression analysis showed that the potential SWD, the choice of clone and the mean air temperature over the previous two months explained 69% of the variation in dry matter content of the harvested shoots (Table 10.5). In this table the dry matter content of each clone is standardised to an air temperature of 17°C, which is close to the mean air temperature at Ngwazi, and for a SWD of

zero. The mean dry matter content of shoots harvested from clone 1 was 2.0 to 3.6% points higher than those from for the other clones. The dry matter content was increased by higher potential SWDs ($0.034\% \text{ mm}^{-1}$) and was reduced by higher air temperatures ($-0.36\% \text{ }^{\circ}\text{C}^{-1}$) within the range of 13 to 19°C .

Table 10.5. The best fit linear regression between the dry matter content of harvested shoots from each of six clones, potential soil water deficit (SWD) and air temperature over the preceding two months. $n = 163$, $r^2 = 69\%$.

		Dry matter content of harvested shoots ^a (%)	Effect of potential SWD (% mm^{-1})	Effect of air temperature during preceding two months (% $^{\circ}\text{C}^{-1}$)
Clone	1	24.2	0.0335	-0.362
	6/8	20.9		
	SFS150	20.7		
	S15/10	22.3		
	207	22.3		
	K35	22.3		

^a: The dry matter contents are standardised for an air temperature of 17°C during the preceding two months and for a potential SWD of zero.

Total shoot population density

The total number of shoots per bush in the fully irrigated sub-plots increased from between 15 and 35 in May 1989, nine months after planting, to between 62 and 148 in February and 114 to 226 in June 1990. The mean daily increase in shoot number from May 1989 to June 1990 ranged from about 0.25 shoots d^{-1} for clones S15/10 and K35 to 0.4-0.5 shoots d^{-1} for clones 1 and 207 (Figure 10.4).

The first measurements within the central part of the bush were taken in February 1990. On this date the population densities in the centre of the fully irrigated bushes ($170\text{-}360 \text{ shoots m}^{-2}$) were higher than that for the complete bush (about $64\text{-}154 \text{ shoots m}^{-2}$), as would be expected for bushes with incomplete ground cover. The shoot population density in the centre of the bush also gradually increased with time reaching $570\text{-}850 \text{ shoots m}^{-2}$ in February 1991 (Figures 10.5a and c).

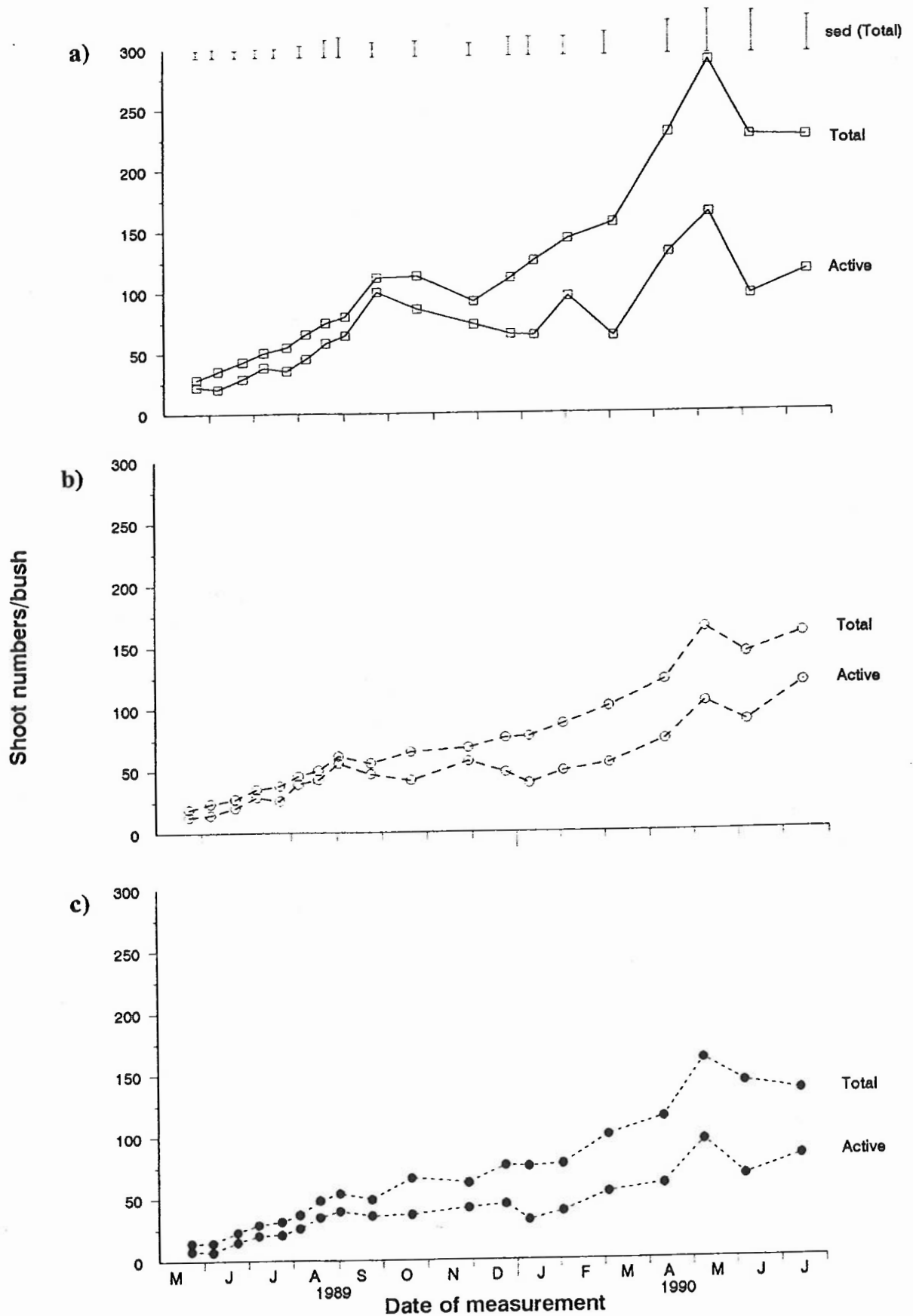


Figure 10.4.a-c. Changes in the total number of active and dormant shoots per bush for each of three clones from May 1989 to June 1990. Clones a) 1, b) 6/8 and c) SFS150.

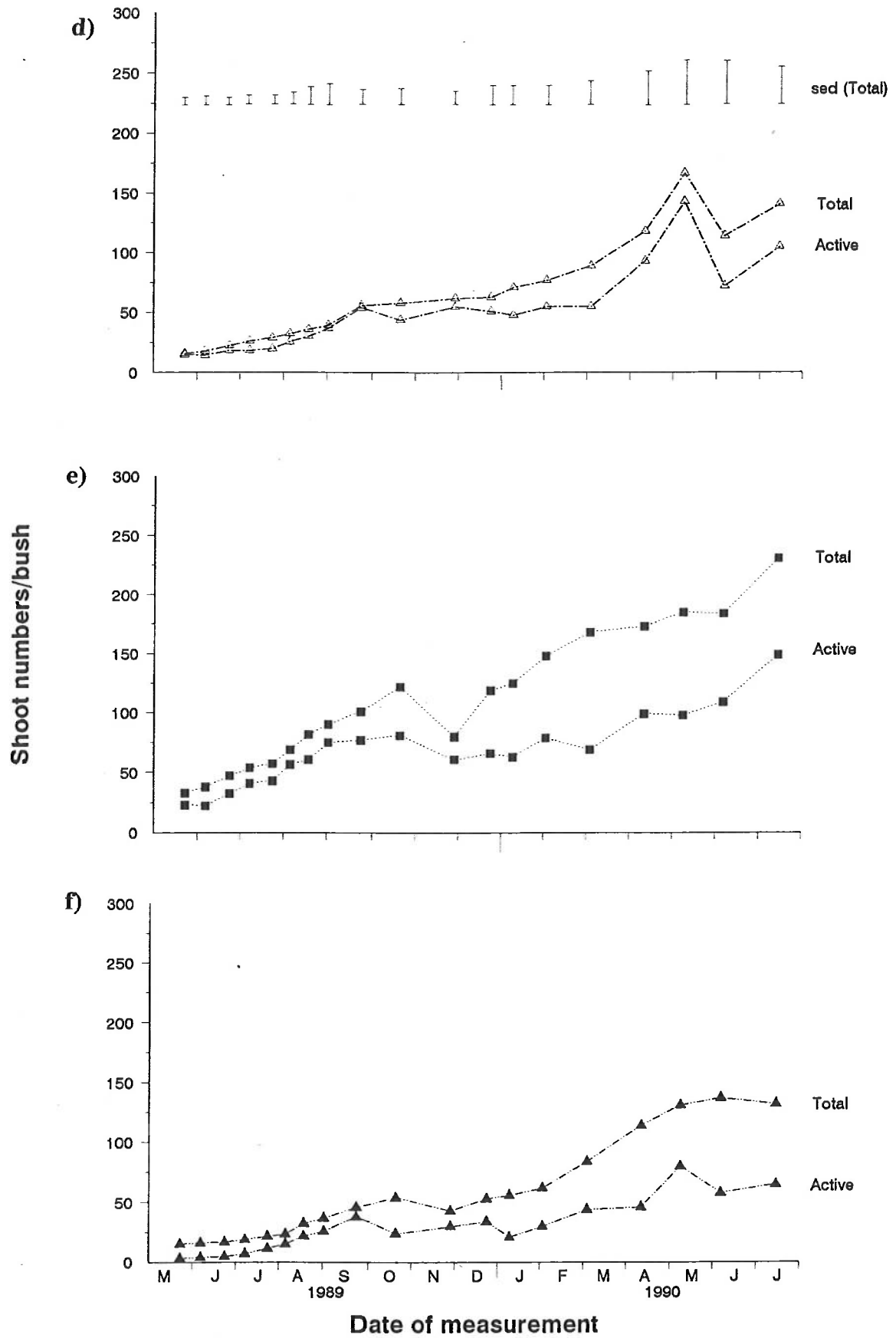


Figure 10.4.d-f. Changes in the total number of active and dormant shoots per bush for each of three clones from May 1989 to June 1990. Clones d) S15/10, e) 207 and f) K35.

The clonal differences ($P \leq 0.001$) shown in total shoot population density in both the whole bush and quadrat measurements of fully irrigated clones at the beginning of February 1990 were typical of measurements obtained during the year. On this date the number of shoots per bush for clones 1 and 207 (144-148) were higher ($P \leq 0.01$) than the other clones (62-89). The quadrat measurements also showed that the shoot population densities of clones 1 and 207 (280-360 shoots m^{-2}) were higher ($P \leq 0.05$) than clones K35, SFS150 and S15/10 (170-185 shoots m^{-2}).

Despite the steady increase in the shoot population density of the fully irrigated clones on an annual basis, during the cool season in 1990 the shoot population density remained relatively constant or declined (Figure 10.5). Shoot numbers only began to rise again in August reaching a peak at the end of September prior to the first peak in yield from the fully irrigated clones in October. This peak was most pronounced in clone 1 (Figure 10.5a). Clones 207 and K35 which also have high base temperatures for shoot extension rate also showed distinct peaks in shoot population density at this time. In the three clones with lower base temperatures (clones SFS150, 6/8 and S15/10) the fluctuations were less prominent as illustrated by clone SFS150 (Figure 10.5). There were also peaks in shoot population density (of varying intensity) in the fully irrigated treatments at the end of November, the end of January and the end of March. Each of these occurred prior to peaks in the yield of harvested shoots.

Effects of drought

There were no significant effects of the drought treatments imposed in October and November 1989 on the total number of shoots. However drought imposed from the end of July in 1990 reduced ($P \leq 0.05$) shoot density in the centre of the bush from 300-480 shoots m^{-2} in the fully irrigated treatments to 185-420 shoots m^{-2} where unirrigated in mid-September (Figure 10.5). This difference was only sustained until early December as the shoot populations in the unirrigated treatments (450-800 shoots m^{-2}) temporarily exceeded ($P \leq 0.01$) those in the fully irrigated sub-plots (370-590 shoots m^{-2}) after the start of rains in mid-November. This was the only time when clone $\times$ drought interactions ($P \leq 0.05$) on total shoot population were found. The total shoot populations of clones 1 and 207 were higher ($P \leq 0.05$) than those of the other clones in the unirrigated sub-plots, but they were not significantly different from clones 6/8, SFS150 and S15/10 where fully irrigated.

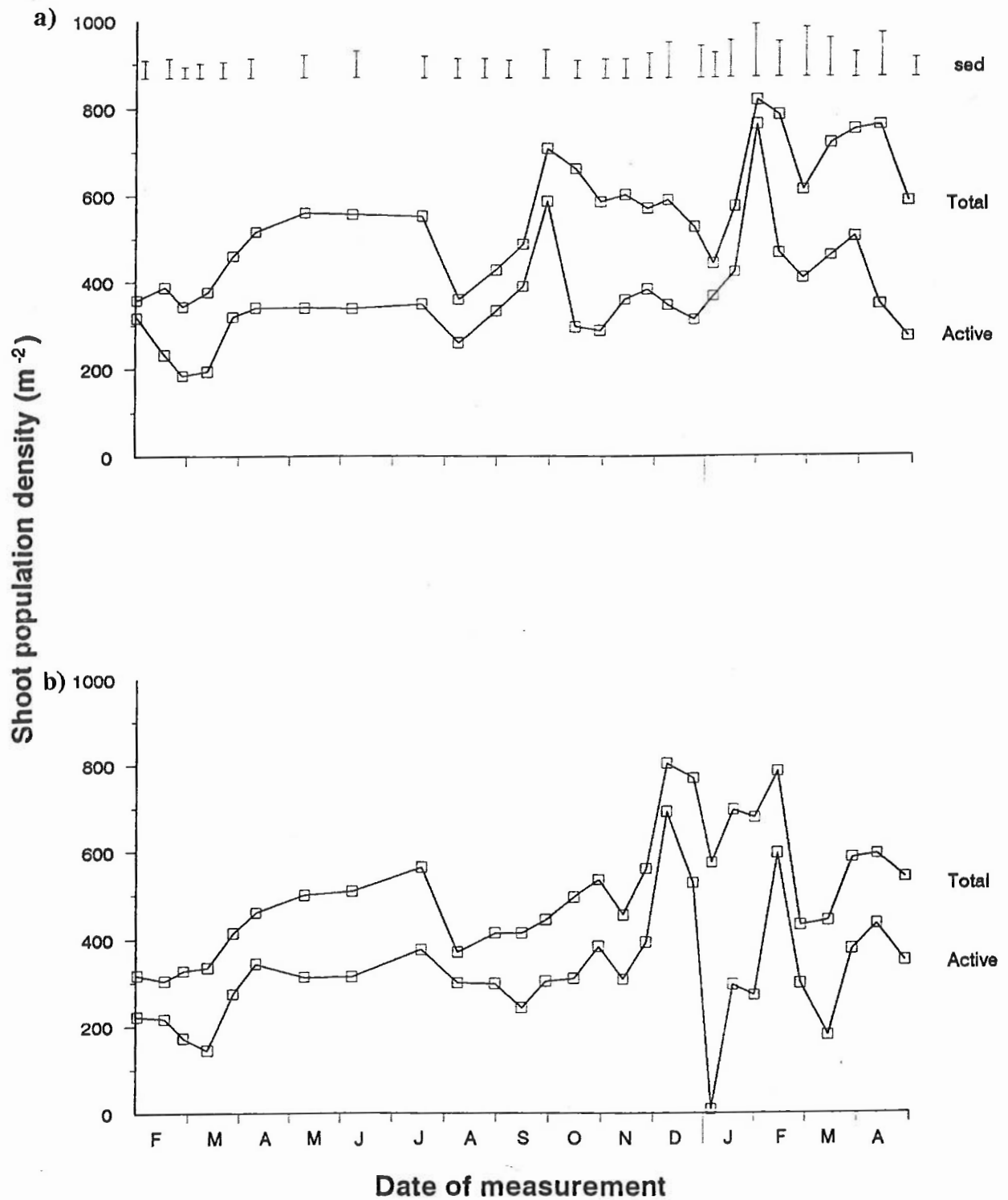


Figure 10.5.a-b. Seasonal changes in the population density of active and dormant shoots with the centre of the bushes of a) fully irrigated and b) unirrigated clone 1.

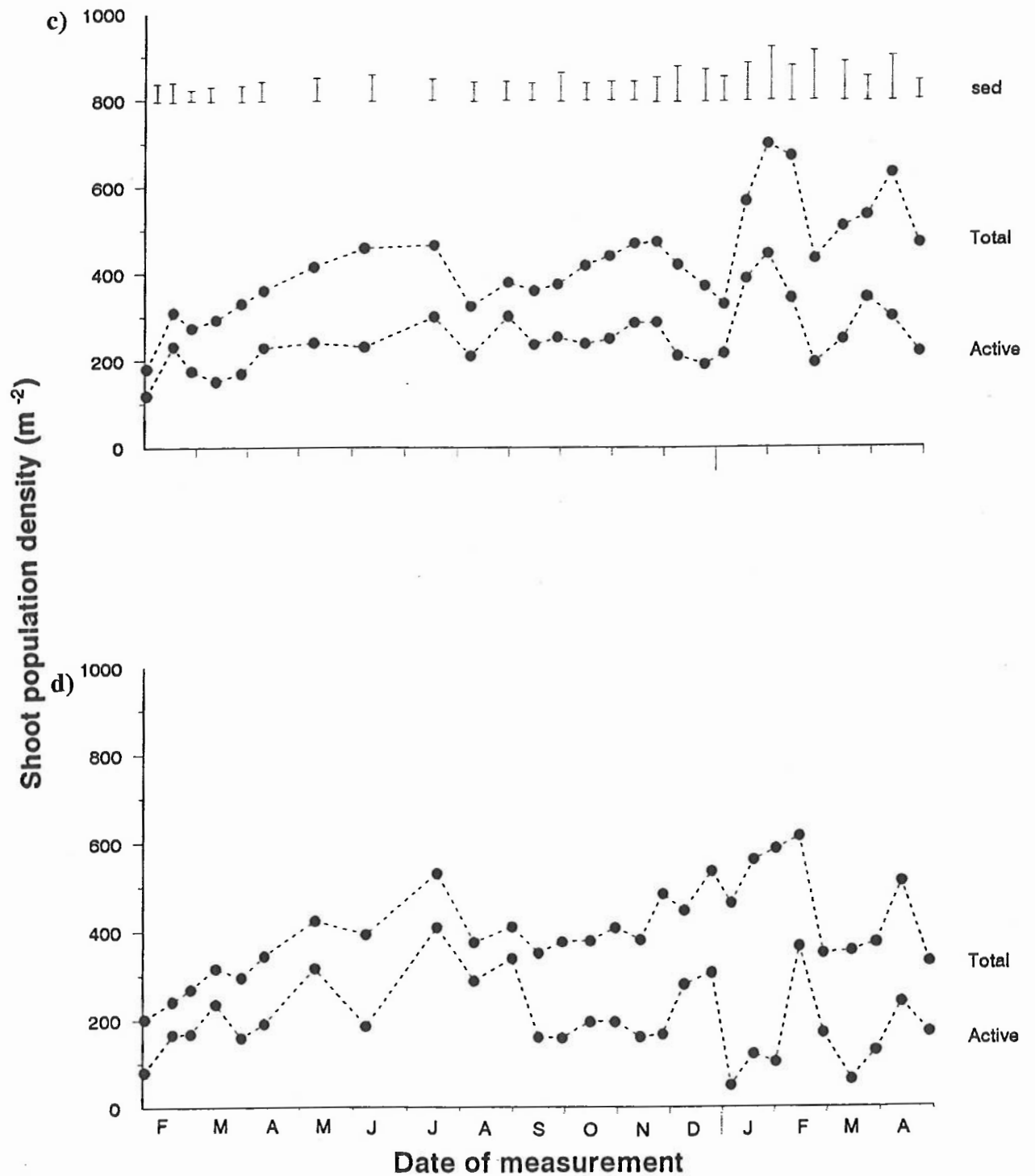


Figure 10.5.c-d. Seasonal changes in the population density of active and dormant shoots with the centre of the bushes of c) fully irrigated and d) unirrigated clone SFS150.

Proportion of actively growing shoots

There were consistent clonal differences ($P \leq 0.05$) in the proportion of active shoots on each date the whole bush was examined. On the first date of measurement in May 1989 the proportion of active shoots was greatest ($P \leq 0.05$) for clone S15/10 (92%) and lowest ($P \leq 0.05$) for clone K35 (22%). The effects of time and clone on the proportion of active shoots in the centre of the fully irrigated bushes were determined from a linear regression of the percentage active shoots against days after 1 February 1990. The proportion of variation explained by these variables was low ($r^2 = 20\%$) because of seasonal fluctuations, but there was a tendency for the proportion of active shoots to decrease with time ($-0.014\% \text{ d}^{-1}$) (Table 10.6). As with the whole bush measurements the initial proportion of active shoots was highest for clone S15/10 (82%); the proportions were lowest for clones SFS150 and K35 (60-63%).

The proportion of active shoots within the fully irrigated treatments varied during the season reaching peaks at the end of September, the end of November and mid January. These were more accentuated for clone 1 than clone SFS150 and occurred before peaks in yields.

Table 10.6. Y-axis intercepts for the linear relationships between the proportion of shoots that were active, within the central 0.1 m^2 of a bush, and time (t; d) for each of six fully irrigated clones ($n = 1415$, $r^2 = 20\%$). The equation took the form: $y (\%) = -0.0138(\% \text{ d}^{-1}) \cdot t + a$

		Y-axis intercept 'a' (%)	
Clone	1	67.4	± 1.22
	6/8	73.7	± 1.45
	SFS150	62.8	± 1.45
	S15/10	82.4	± 1.45
	207	74.2	± 1.45
	K35	60.2	± 1.45

Effects of drought

The synchronisation of shoot extension in the unirrigated plots at the end of the dry season resulted in more extreme fluctuations in density of active shoots, than in the fully irrigated sub-plots (Figure 10.5). Prior to the first peak in yield, the proportion of active shoots within the unirrigated plots was between 63 and 97%. Immediately after these shoots were harvested the proportion of active shoots on the bush declined to between 1 and 13% before rising again in mid-February and mid-April. There were frequent clone x drought interactions ($P \leq 0.05$) on the proportion of active shoots during this period, primarily as a result of the more stable behaviour of clone SFS150 in comparison to the other clones (Figure 10.5).

DISCUSSION

Shoot composition and mass

The active shoots harvested from clone 1 comprised a higher proportion of shoots with three expanded leaves than those from clone 6/8 between December 1990 and May 1991. During this period shoots of clone 1 were extending faster than those of clone 6/8, but there were no significant clonal differences in internode length (cf Chapter 9). Since the clones were harvested at the same time, the shoots harvested from the faster extending clone 1 would be expected to have more leaves. Whilst this explains why the composition of shoots from clone 1 differed from clone 6/8, it does not explain the high proportion of active shoots with three expanded leaves harvested from clone S15/10. Clone S15/10 had a shoot extension rate similar to clone 6/8. Further research is required to determine the reason for the high proportion of shoots with three leaves harvested from clone S15/10. One reason could be possible clonal differences in the number of expanded leaves left on the bush after harvest.

An empirical exponential relationship between shoot mass and the number of expanded leaves was described for each clone. This is similar to the exponential relationship between shoot mass and length recognised by Tanton (1979) and described by Smith *et al.* (1990). The additional increase in shoot mass for each extra leaf is probably due to continued expansion of the lower leaves and also the secondary thickening of the stem. Stephens and Carr (1992a) reported that the relationship between the mass and the number of leaves of shoots harvested

from clone 6/8 was approximately linear. Of the six clones studied, the relationship between mass and number of leaves was most linear for clone 6/8.

Clones 1 and 207, which had the highest shoot extension and development rates during the warm dry and wet seasons, did not produce the heaviest shoots. The mean fresh mass of a harvested shoot was more affected by clonal differences in the mass to stage (or length) relationship than the differences in shoot extension or development. It was clones with a high mass/leaf ratio, such as clones S15/10 and K35, rather than those with a high extension rate which produced the heaviest shoots. Because harvested tea shoots are sold on the basis of mass rather than length, these clonal differences in shoot mass per stage or per length are of direct commercial importance.

There were also important clonal differences in dry matter content. For a given fresh mass of harvested shoots, the dry mass of shoots of clone 1 were typically 2.0-3.6% points higher than the other clones. This higher dry matter content of clone 1 offers potential savings to the tea producer in transport requirements and also storage capacity for withering at the factory. The clonal variations in dry matter content also indicate that in a clonal field trial where a constant dry matter content is assumed, real yield differences of up to 16% can go unnoticed. If greater precision than this is required in evaluating clones then it is important that clonal differences in dry matter content are determined.

Shoot dormancy

During 1990 up to 45% of the harvested shoots were dormant. This was substantially higher than the proportion of uppermost axillary buds measured for shoot extension which became dormant. The majority of the harvested dormant shoots must therefore have originated from other sources such as secondary axillary buds, or they were shoots developing from a lower level in the canopy. The selection of the uppermost axillary buds therefore only represents a proportion of the total shoot population. The full effects of this bias in sampling needs to be considered if the shoot extension rates reported in Chapter 9 are used to model yield.

Bond (1945) related the initiation of dormancy to the reduction in the vascular supply of nutrients to the bud during extension. This link between dormancy and nutrition has also been shown by Stephens and Carr (1992a) who reported that nitrogen deficiency led to a greater proportion of dormant shoots. The results

presented here also show that there are significant clonal differences in the proportion of the harvested shoots that are dormant. This proportion was lowest for clone S15/10, which also gave the highest yield (cf Chapter 5), and showed the greatest partitioning to leaves and shoots (cf Chapter 8). This apparent link between dormancy and yield and partitioning is worthy of further study, and may be a potential selection criterion for high yield.

Shoot population density

The two 'China' type clones had shoot population densities almost twice those of the other clones. Obaga and Squire (1992) proposed that clones with high shoot extension and development rates will also tend to have high shoot population densities. This is because their shoots reach a harvestable size earlier and therefore if more than one shoot replaces each harvested shoot, the increase in shoot population density per unit time will be greater. A second possible explanation is that the shoots of the smaller leaved clones are not so apically dominant over neighbouring buds as the heavier shoots of the 'Assam' type clones. This too would allow a higher proportion of axillary buds to grow in the smaller leaved clones and would lead to higher shoot population densities.

The high shoot population densities of the 'China' type clones were in direct contrast to their lower shoot mass. This antagonistic relationship between shoot mass and density has been reported before by Cannell *et al.* (1988). In this experiment although there were clonal differences both in shoot mass and shoot population density of fully irrigated clones 1, 207, SFS150, 6/8 and K35, their annual yields were similar. Therefore there appears to be no advantage in increasing shoot population density without considering shoot mass, or vice versa. Results from an adjacent irrigation x fertilizer experiment showed that the population density of shoots increased and the mean mass of shoots decreased during the pruning cycle of a closely managed stand of clone 6/8 (Burgess, 1990). Under commercial conditions where the tea is harvested by hand, the greater number of actions required to harvest a given mass of tea means that people are reluctant to work in fields with small shoots. Therefore it is advantageous in terms of labour productivity to select those clones which produce the heaviest shoots of acceptable quality. Shoot population density can then be increased through improved nutrition and field management.

CONCLUSIONS

The proportions of active shoots with more than two expanded leaves were generally highest in those clones which had the highest extension and development rates. However the clonal differences in the mean mass of harvested shoots were primarily caused by differences in the relationship between mass and stage, rather than by differences in composition.

There were significant clonal differences in the dry matter content of harvested shoots, which should be taken into account in clonal field trials. Selection for a high dry matter content would also offer potential savings in transport and withering costs.

Although up to 45% of the shoots harvested in 1990 were dormant, few of the uppermost axillary buds selected in the shoot extension measurements ever became dormant. This suggests that these extension measurements relate to a biased sample of the total shoot population and this needs to be considered in any future modelling of tea yield.

There were clonal differences in the proportion of harvested shoots, and the proportion of the total shoot population density which are active. Clone S15/10 which had the highest proportion of active shoots also gave the highest annual yield of tea where fully irrigated and showed the greatest partitioning to leaves and shoots. Further work is required to determine the links between these variables. A high proportion of active shoots may potentially be used as a selection criterion for high yield.

Since there was an antagonistic relationship between the shoot population density and the dry mass of harvested shoots, shoot population density and shoot dry mass must be considered together when used as selection criteria.

CHAPTER 11

COMPARISONS OF THREE TECHNIQUES FOR MEASURING STOMATAL CONDUCTANCE

INTRODUCTION

To grow, the tea canopy must maintain the turgidity of its leaves and stems by balancing transpiration losses with the water supply from the roots. The rate of water loss per unit area of leaf (E_L ; $\text{mmol m}^{-2} \text{s}^{-1}$) is determined by the difference between the partial pressure of water vapour in the leaf and the atmosphere (dw ; kPa kPa^{-1}), and the leaf conductance (g_L ; $\text{mmol m}^{-2} \text{s}^{-1}$) (Equation 11.1).

$$E_L = dw \cdot g_L \quad 11.1$$

The value of dw , assuming constant atmospheric pressure, is more normally expressed as the vapour pressure deficit (VPD; kPa). The VPD is primarily determined by the humidity and temperature of the atmosphere, because the air within the leaf is kept close to saturation. The main plant factors controlling water loss are therefore the total leaf area (cf Chapter 6) and the leaf conductance. Leaf conductance comprises the cuticular and stomatal conductance which act in parallel. The capacity of the cuticle of a tea leaf to conduct water vapour is very low ($0.2\text{-}0.4 \text{ mm s}^{-1}$ or about $8\text{-}16 \text{ mmol m}^{-2} \text{s}^{-1}$, Nagarajah, 1979) and therefore, as in most crops, the diffusion of water vapour out of the leaf is primarily determined by the stomatal conductance. Once the water vapour has left the leaf it continues to move by diffusion until it reaches an area of turbulence. The conductance over this boundary layer is usually large (greater than 65 mm s^{-1} or about $3000 \text{ mmol m}^{-2} \text{s}^{-1}$) for individual leaves exposed to direct sunlight (Idso, 1990). It therefore follows that the water loss at a given VPD from an area of well exposed leaf at the surface of a tea canopy is primarily determined by the stomatal conductance.

Transient and steady state porometry

A wide range of techniques have been used to monitor the behaviour of tea stomata, of which one of the most common has been the transient porometer.

The principle of this porometer is described by Monteith and Bull (1970). A small chamber containing a humidity sensor is clamped onto a leaf and the transit time required for an increase in humidity to reach a preselected level is measured. Whilst the theoretical relationship between the transit time and the stomatal conductance has been described (Monteith *et al.*, 1988), in practice it is difficult to quantify the effects of water absorption by the chamber and the response lag of the humidity sensor. The measured transit times are therefore calibrated using transit times recorded at the same humidity and temperature from a calibration plate with holes of known conductance.

Using a transient porometer on clone SFS204 in Malawi, Squire (1978) found that stomatal conductances closely followed solar radiation levels during the wet season. They rose from 1-2 mm s⁻¹ (40-80 mmol m⁻² s⁻¹) at dawn to approximately 6 mm s⁻¹ (230 mmol m⁻² s⁻¹) at midday, before declining in the afternoon. In the dry season the relationship between conductance and radiation became curvilinear, and conductance appeared to be light saturated at 300-400 W m⁻². By contrast Callander and Woodhead (1981) using a transient porometer on mature clonal Assam-type tea in Kenya, found that stomatal conductances were highest in the early morning and then declined during the day. This corresponded to simultaneous micro-meteorological measurements of canopy conductance which were related to both radiation and VPD. Similar morning peaks followed by a steady decline during the day have also been found on potted tea plants grown in greenhouses in Sri Lanka (Sandanam *et al.*, 1981; Nagarajah, 1981).

Stomatal conductance can also be measured with a steady state constant flow porometer (Parkinson and Legg, 1972; Day, 1977). The leaf to be measured is clamped within a chamber and is then exposed on both sides to a turbulent flow of air at a known flow rate and humidity. Stomatal conductance is then calculated from the change in the humidity of the air passing through the chamber. This type of porometer has not been used extensively on tea, but has been used on other tropical crops such as oil palm (Smith, 1989) and cassava (El-Sharkawy and Cock, 1990).

Infiltration score

A third method which has been used to determine the behaviour of tea stomata is the infiltration score technique as modified by Wormer (1965). Wormer used a series of iso-propanol/water mixtures (Table 11.1), which varied in surface

tension and viscosity, to determine the behaviour of coffee stomata. The procedure for tea is described by Carr (1969) who related stomatal opening to the score of the liquid mixture with the highest proportion of distilled water which entered the leaf within ten seconds. The entry of the liquid mixture is shown by the appearance of small dark spots.

Table 11.1. Concentrations on a volume basis of iso-propanol and distilled water in a series of infiltration score mixtures.

Score	1	2	3	4	5	6	7	8	9	10	11	12	13
iso-propanol (%)	100	95	90	85	80	75	70	65	60	55	50	45	40
water (%)	0	5	10	15	20	25	30	35	40	45	50	55	60

Although there is no definite understanding of the exact nature of the infiltration process for tea, it seems that the darkened spots are created by the infiltration of the liquid mixtures through the stomata into the mesophyll layer of the leaf. Hack (1974) reviewed the evidence that the water potential of the mesophyll could limit infiltration and concluded that at all times the water potential of the mesophyll of field grown cotton was sufficiently low to draw the liquids into the leaf. He therefore concluded that the limiting step determining infiltration was the geometry of the stomata and in particular the angle of the cell wall past the smallest constriction (Figure 11.1).

Using the infiltration score technique on fully irrigated clone 1 in Tanzania Carr (1969) found that stomatal opening was greatest in the morning at about 08.00 h. The stomata then closed partially during the middle of the day and on most days re-opened in the late afternoon. A similar diurnal saddle shape response was found on different clones during dry weather conditions in Kenya (Carr, 1977a; Othieno, 1978b). However during the wet season infiltration scores remained constant after midday (Othieno, 1978b).

There is therefore no consistent description of stomatal behaviour for tea bushes (Squire and Callander, 1981). The porometry work suggests that under some conditions it is closely related with solar radiation (Squire, 1978), and elsewhere with both solar radiation and VPD (Callander and Woodhead, 1981). Much of the infiltration score work has shown a midday decline in stomatal opening associated with high VPDs with little apparent response to incident solar radiation (Carr, 1977a; Othieno, 1978b).

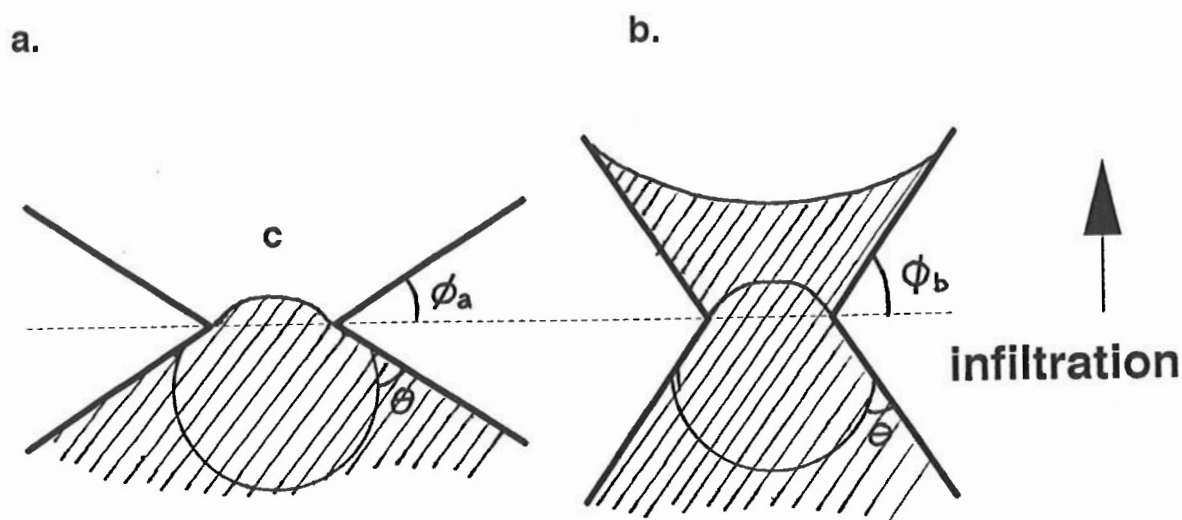


Figure 11.1.

Schematic diagrams showing the capacity of a liquid with a contact angle θ to rise in a conical capillary. Situation a represents a partially closed stoma with a diverging wall angle of $\phi_a = 30^\circ$ and situation b represents an open stoma with a diverging wall angle of $\phi_b = 60^\circ$. The meniscus of an approaching liquid with a contact angle $\theta = 45^\circ$ is shown. In the converging position the penetrating pressure is always positive and the liquid rises to position c in each case. At the constriction the liquid only continues to infiltrate if ϕ is greater than θ , as in case b. (Adapted from Weyers and Meidner, 1990).

In addition to analysing diurnal changes transient porometers have also been used to determine clonal differences in stomatal conductance (Squire, 1976; Sandanam *et al.*, 1981). Differences in stomatal opening have also been identified between clones (Carr, 1977b; Othieno, 1978b).

In this chapter the diurnal stomatal behaviour measured using a transient and a steady state porometer are compared and related to infiltration score readings taken at the same time. The absolute and relative measures of stomatal conductance of six fully irrigated clones are also compared with infiltration score values.

METHODOLOGY

Comparisons of a transient and a steady state porometer

The two porometers examined were the AP3 transient porometer (hereafter called the AP3) produced by Delta-T Devices Ltd, Cambridge and the steady state porometer (hereafter called the LCA-2) which forms part of the LCA-2 photosynthesis system produced by ADC Ltd, Hertfordshire. The leaf chamber for this system is manufactured by PP Systems, Hitchin, Hertfordshire.

The procedures for calculating stomatal conductance with the AP3 are described in Appendix C. The values of the resistances of the calibration plate were based on the most recent recommendation of the manufacturer (Chris Nichol, personal communication, 1991) (Table 11.2). These values, based on finite element analysis, are higher than those originally supplied with the equipment and therefore for a given transit time they lead to a higher estimate of conductance.

Table 11.2. Comparison of the original and currently recommended resistance values for each of the positions on the calibration plate for an AP3 porometer.

Plate position	Resistance (s mm^{-1} at 20°C & 100 kPa)	
	Original	Recommended
1	2.25	2.27
2	1.09	1.07
3	0.65	0.61
4	0.29	0.25
5	0.13	0.085
6	0.04	0.034

To allow comparison with the LCA-2 results, the calculated stomatal resistances from the AP3 were converted to the inverse: a stomatal conductance. These were then expressed in the units of $\text{mol m}^{-2} \text{s}^{-1}$ using Equation 11.2, where T ($^{\circ}\text{C}$) is the temperature of the conductance reading and P (kPa) is the atmospheric pressure (Parkinson, 1985). The atmospheric pressure (P) at the experimental site (altitude = 1800 m) was assumed to be 81.6 kPa (Doorenbos, 1976):

$$g(\text{mol m}^{-2} \text{s}^{-1}) = g(\text{mm s}^{-1}) 4.66 [273/(273 + T)][P/101.3] \quad 11.2$$

The porometers were compared using measurements taken on leaves within the fully irrigated (I_s) and unirrigated (I_0) treatments for each of the six clones within

the clone x drought experiment fully described in chapter 3. Stomatal conductances were only measured over an area of 56 mm² on the abaxial side of the leaf with the AP3. In contrast the LCA-2 measured the combined conductance of both sides of a larger leaf area (625 mm²). Because stomata only occur on the abaxial surface of tea leaves it was assumed that there was only significant transpiration from the lower surface. If there was water loss from the upper surface, the LCA-2 would have estimated higher conductances than the AP3.

To account for the variability of stomatal conductance between leaves, five leaves each on a different bush were examined to provide a mean value for each clone x drought treatment at any one time. All the selected leaves were healthy mature leaves fully exposed to the incident sunlight. On mornings when there was dew the leaves were dried on both sides with tissue paper before measurement.

All measurements taken with the AP3 between 09.00 and 17.00 h were usually completed within 20-40 s of the chamber being placed on the leaf. As shown in Figure 11.2a, the stomatal conductance gradually declined the longer the sensor head remained on the leaf. This decline has been reported before (Bell and Squire, 1981) and can be attributed to a stomatal reaction to the lack of light within the chamber.

There has recently been considerable concern about high VPDs within porometer chambers causing stomatal closure (Idso *et al.*, 1988; Idso, 1990). It is now agreed that the 'deficit within the porometer should be kept as close as possible to the external air' (Monteith, 1990). With the AP3 this was achieved by altering the humidity within the chamber so that it followed that of the ambient air. However in the LCA-2 for all measurements dry air (<10% RH) was pumped into the chamber. When the stomatal conductances of leaves placed within the LCA-2 chamber were examined over a prolonged period of time, there was only limited stomatal closure over the first two minutes (Figure 11.2b). Assuming that the stomata did not respond within the first fifteen seconds, tea stomata were not immediately sensitive to dry air and the LCA-2 should have produced valid stomatal conductance readings. Measurements on potato, field bean, wheat and barley with a similar steady state system have also shown that conductance did not decline significantly until two minutes after the porometer was attached (Day, 1977).

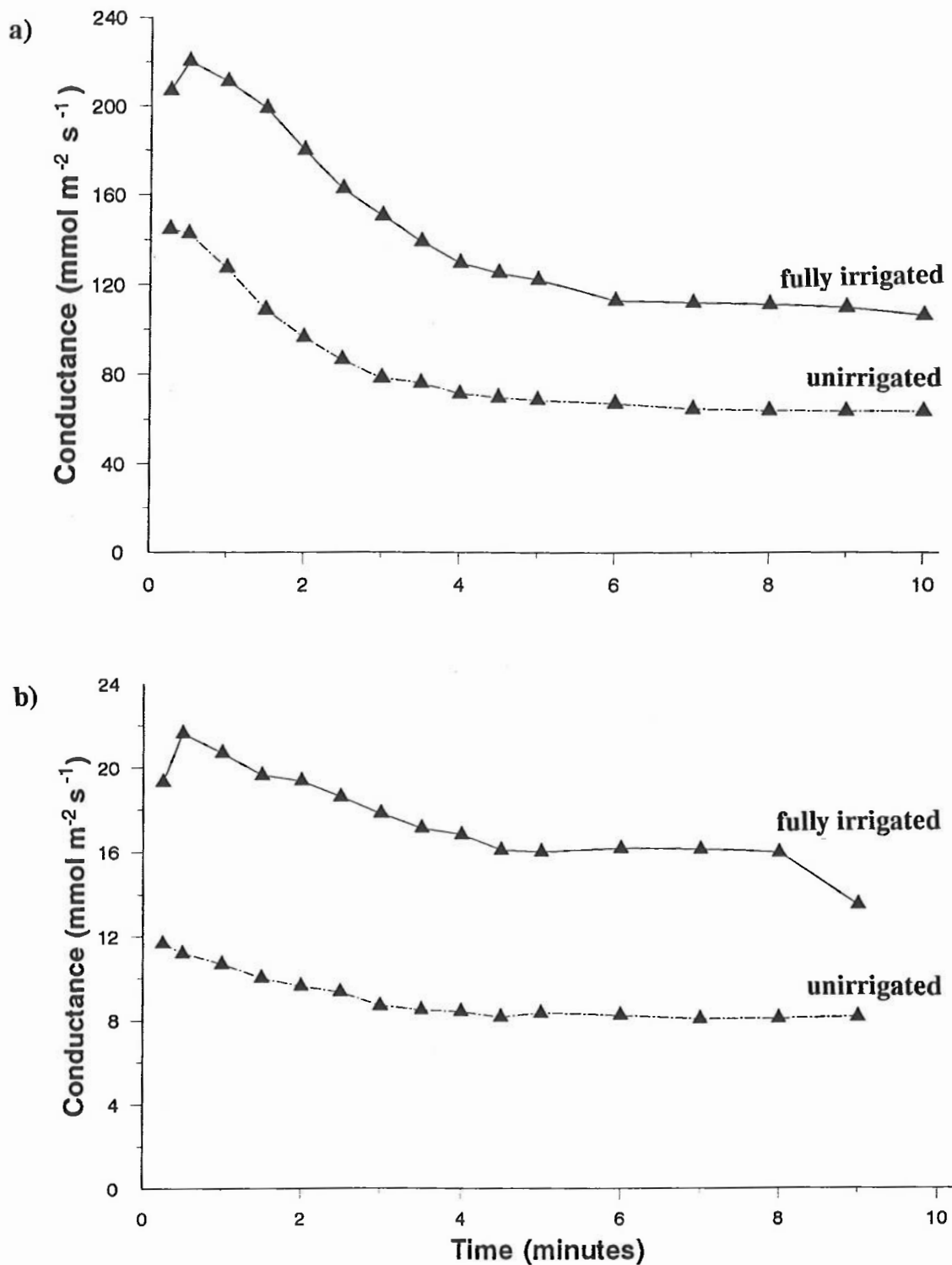


Figure 11.2. Effects of the time that the porometer was attached to the leaves of fully irrigated (I_5) and unirrigated (I_0) clone K35, on the measured stomatal conductance using a) an AP3 and b) an LCA-2 porometer.

Diurnal behaviour of stomata

The diurnal changes in the stomatal conductance of tea within experiment N10 were measured with the AP3 on seven days between September and mid-November in 1989, and on ten days between June and November in 1990. There were no consistent patterns in diurnal behaviour in 1989. This was attributed to problems with calibration at the beginning and the end of the day when temperatures were below 20°C and the relative humidity was greater than 60% (cf Appendix C). In 1990, especially between September and November, a more consistent pattern emerged. The data for 3 October 1990 were typical for this period and they are presented in the results with simultaneous measurements of conductance taken with the LCA-2.

Values of stomatal conductance

The mean conductances from 10.00 to 16.00 h for each of the six clones within fully irrigated (I_5) and unirrigated (I_0) treatments were measured using the AP3 porometer on five days during the warm dry season in 1989, between 29 September and 25 October. In 1990 corresponding measurements were taken on four days between 19 September and 1 November. Over similar periods the stomatal conductances of the same treatments were also measured with the LCA-2 (Smith, personal communication; Smith, 1991a). The values obtained using each system within the fully irrigated treatments were compared to determine the capacity of each porometer to measure stomatal conductance in absolute terms.

Both porometers were sent for recalibration in 1991 to their respective manufacturers in the U.K., who reported no 'significant' faults. They were then compared under controlled conditions by measuring the conductance of prepared samples consisting of Celgard 2400 (Hoechst Celanese, Charlotte, North Carolina), which is an inert porous hydrophobic polypropylene sheet. These trials were carried out with the help and supervision of representatives from both manufacturers (Delta-T Ltd and PP Systems Ltd). Three replicate samples to cover a range of conductances were prepared by placing together 1, 2, 4, 8, 16 or 32 (50 mm x 50 mm) sheets of Celgard. These samples were then backed by blotting paper and held together around the edges and the back with sealing tape. On the front side the Celgard remained exposed (30 x 30 mm) and at the back a removable tape was placed to allow rewetting of the blotting paper (Figure 11.3). The conductances of the Celgard samples within each replicate set were measured with the AP3 and LCA-2. Because there was some water loss

from the back of the samples, the conductance measurements with the LCA-2 were repeated using an aluminium waterproof backing.

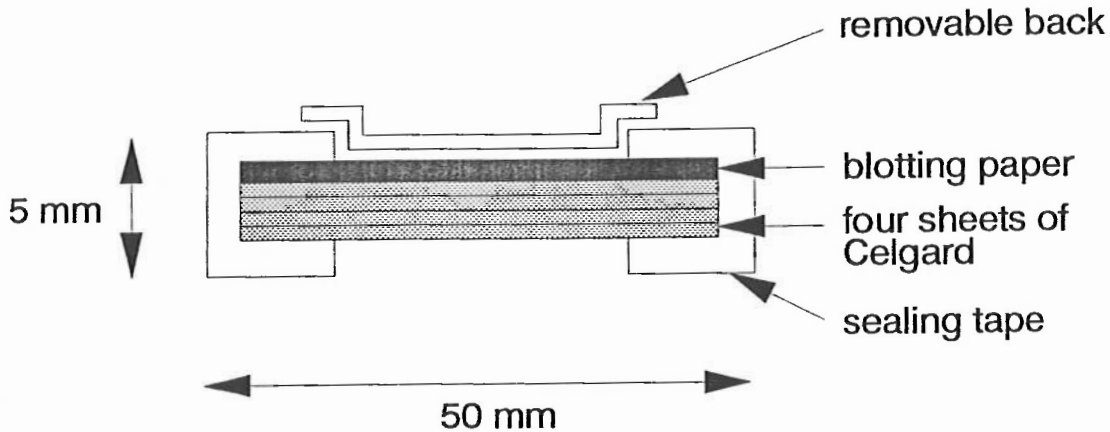


Figure 11.3. Schematic diagram showing the construction of a Celgard sample with four Celgard sheets.

Comparisons of clones

The mean values used to compare absolute stomatal conductances in 1989 and 1990 were also used to determine the ranking of the six irrigated clones by the two porometers.

Infiltration score

Thirteen small vials were numbered and filled with iso-propanol containing increasing proportions of distilled water according to the series established by Wormer (1965) (Table 11.1). These liquid mixtures were used to determine the infiltration score of the leaves of plants within the same clone and drought treatments studied with the porometers. As with the porometry measurements five healthy mature leaves fully exposed to sunlight were examined to obtain a mean value for each treatment. The range of scores obtained within a particular treatment at a given time was generally narrow (± 2) implying that there was little bias in using a mean infiltration score. The diurnal change in infiltration score was measured for the fully irrigated and unirrigated treatments of each clone on two days in 1989 and on nine days between July and late-November in 1990. The results for one day (3 October 1990) were compared with the

porometer results. The ranking of the mean 10.00 to 16.00 h infiltration scores for each fully irrigated clone measured between September and November in 1989 and 1990 were also compared with the porometry measurements.

RESULTS

Comparison of the porometers

Diurnal changes in stomatal behaviour

The diurnal changes in stomatal conductance were measured using the two porometers on 3 October 1990. During this day solar radiation followed a regular pattern (Figure 11.4) rising from zero at 07.00 h to a plateau of about $1700 \mu\text{mol PPFD m}^{-2} \text{ s}^{-1}$ (730 W m^{-2}) from 11.00 to 16.00 h before declining to zero by 18.30 h. The air temperature, measured using an Assmann psychrometer at the surface of the canopy, rose from 12.5°C at 07.00 h to 26°C at midday. The VPD increased from 0.2 kPa at dawn to a mean of 2.0 kPa during the afternoon, before declining to 0.6 kPa at sunset. The mean day-time (09.00 to 15.00 h) windspeed measured at a height of 2 m above short grass at a meteorological station 800 m from the experimental site was 2.9 m s^{-1} . The measured SWD within the unirrigated treatments was about 110 mm.

The AP3 transient porometer estimated high stomatal conductances before 08.30 h, when the leaves within the fully irrigated sub-plots were still covered with dew. (Figure 11.5a). High conductances in the early morning were also apparent on other days when there was dew, but on 11 October 1990 when there was little dew and the porometer was allowed to dry between individual leaves conductances were lower. After the dew had evaporated and the leaf surfaces were dry, the stomatal conductances (most notably those of clones 1, SFS150 and 6/8) continued to decline steadily towards midday. For five of the six clones there was a slight increase in conductance from 13.00 to 15.00 h, but the overriding pattern was a steady decline to minimum values at sunset. The conductances in the unirrigated clones were lower and remained relatively constant throughout the day (Figure 11.5b).

High conductances before 8.30 h, associated with dew, were also measured using the steady state LCA-2 porometer (Figure 11.6). Conductances declined for most clones, even after the dew had evaporated, to reach minimum values at 11.00 h and then remained relatively constant until dusk.

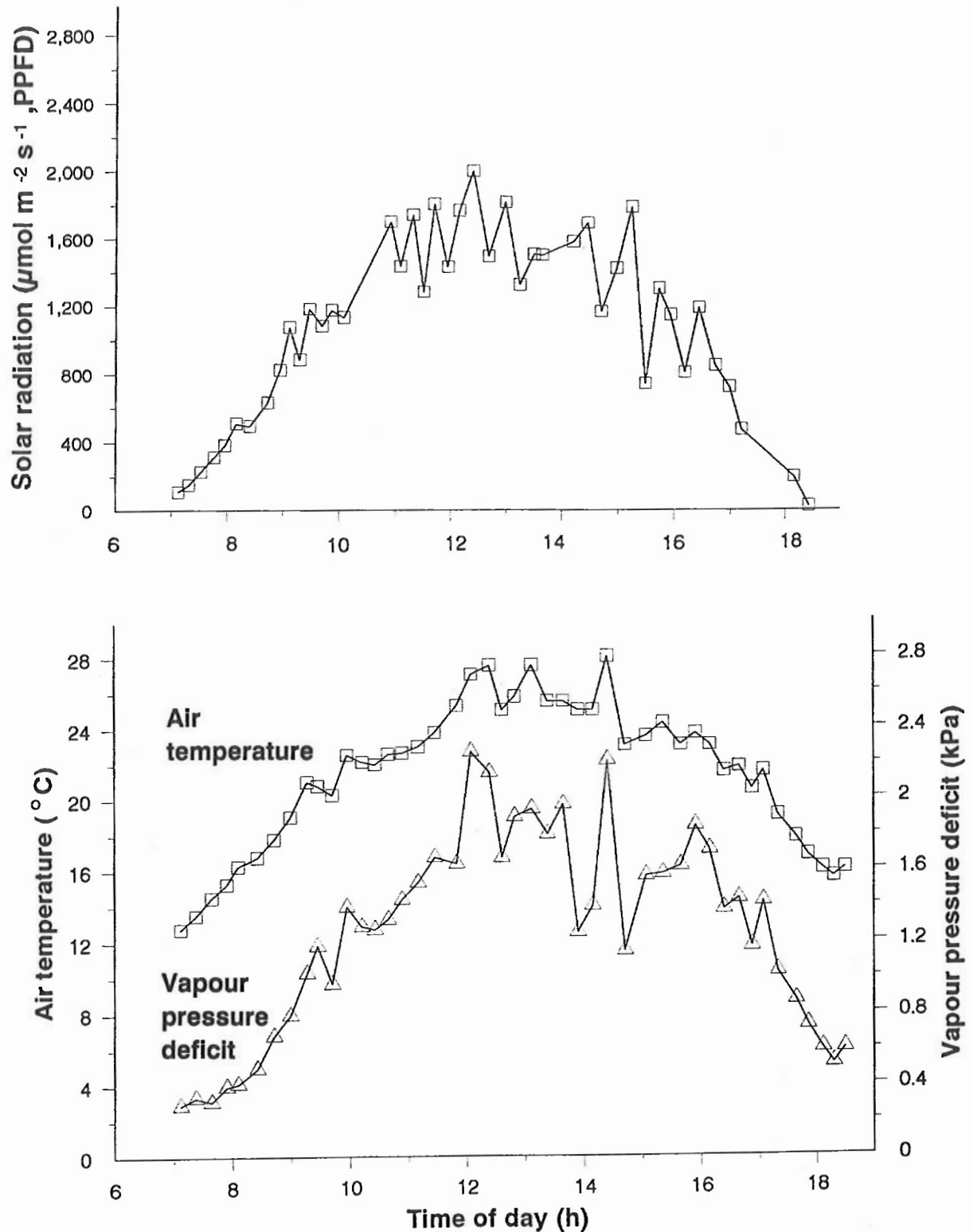


Figure 11.4. Diurnal changes in incident solar radiation (photosynthetically active photon flux density), air temperature and vapour pressure deficit measured at the canopy surface on 3 October 1990.

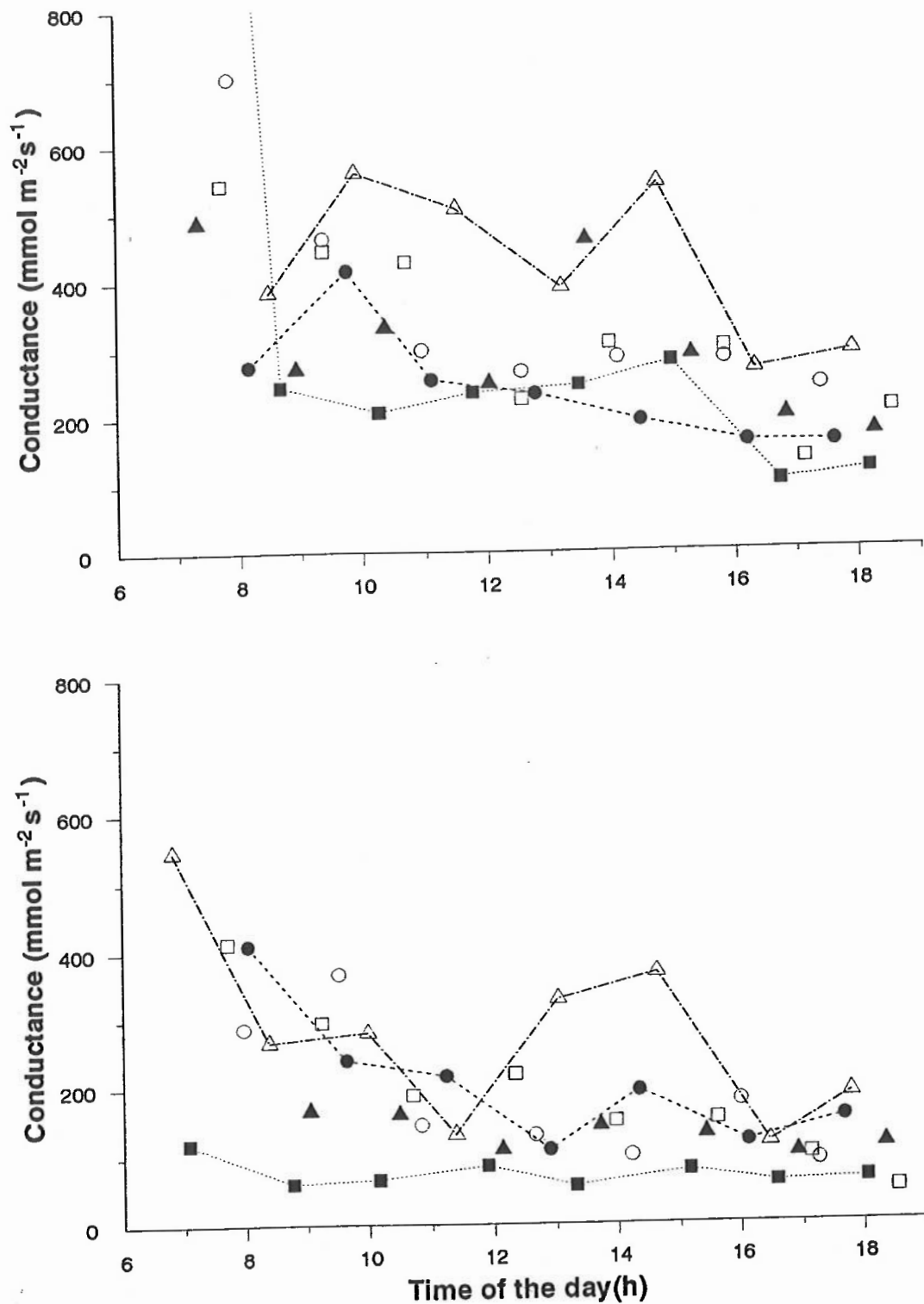


Figure 11.5.

Diurnal changes in stomatal conductances for each of six clones which were a) fully irrigated and b) unirrigated, measured using an AP3 porometer on 3 October 1990. Clones 1: □, 6/8: ○, SFS150: ●, S15/10: △, 207: ■ and K35: ▲.

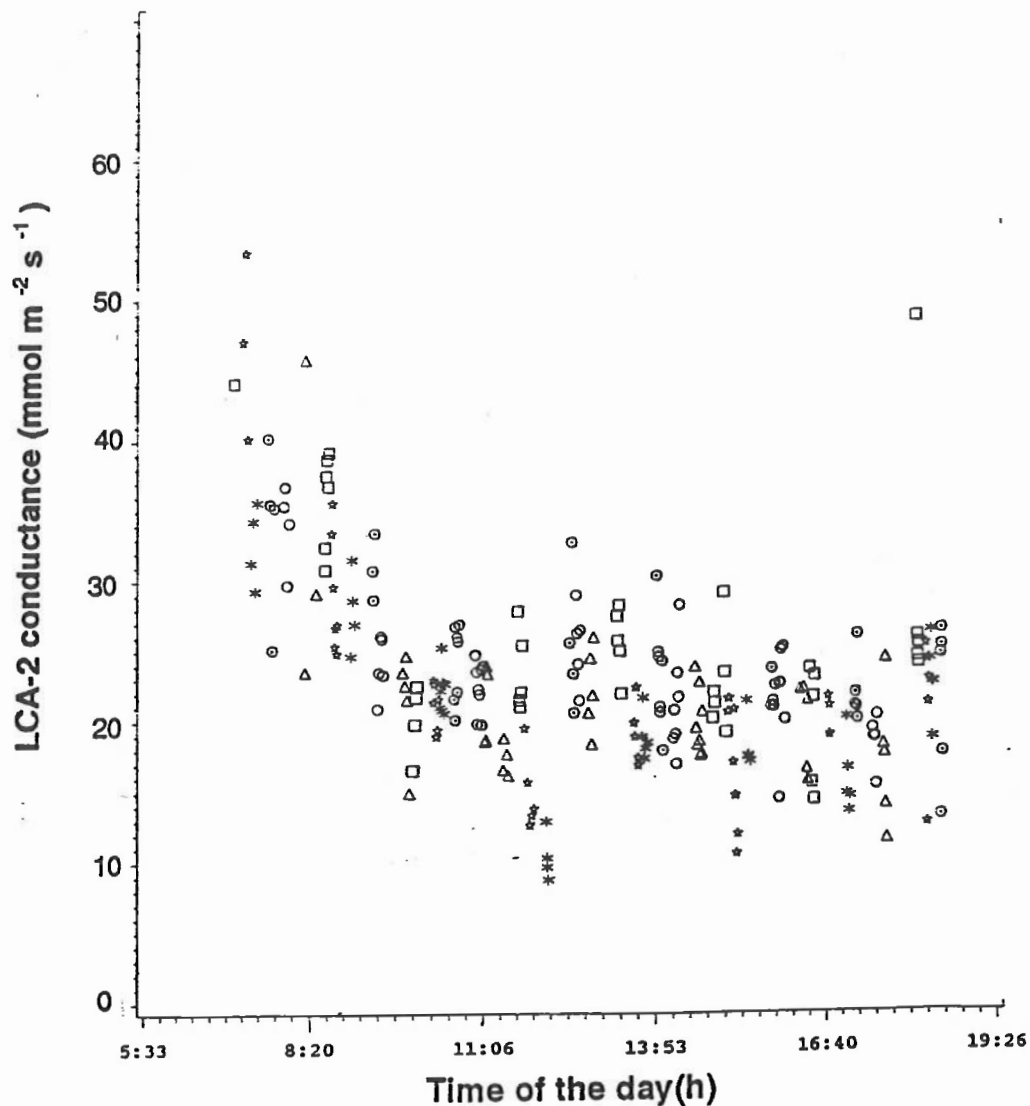


Figure 11.6. Diurnal changes in the stomatal conductances measured for each of six fully irrigated clones measured using a LCA-2 on 3 October 1990 (Smith, personal communication). Clones 1: $\circ$, 6/8: $\circ$, SFS150: Δ , S15/10: $\square$, 207: $*$ and K35: $*$.

Comparison of mean day-time stomatal conductances

The stomatal conductances shown in Figures 11.5 and 11.6 were both measured on the same day within identical treatments. However the mean values measured between 10.00 and 16.00 h in the fully irrigated treatments with the AP3 ($200\text{--}500 \text{ mmol m}^{-2} \text{ s}^{-1}$) were about ten times higher than those measured with the LCA-2 ($20\text{--}30 \text{ mmol m}^{-2} \text{ s}^{-1}$).

Differences between the two techniques were also apparent during the warm dry season in 1989, when the mean 10.00 to 16.00 h conductances for each of the six

fully irrigated clones measured with the AP3 ($250\text{--}350 \text{ mmol m}^{-2} \text{ s}^{-1}$) were about five times higher than the equivalent conductances ($55\text{--}70 \text{ mmol m}^{-2} \text{ s}^{-1}$) measured with the LCA-2 (Figure 11.7). In 1990 over a similar time period the differences were more stark. Whilst the mean conductances estimated with the AP3 ($220\text{--}410 \text{ mmol m}^{-2} \text{ s}^{-1}$) were similar to those in 1989, the conductances estimated with the LCA-2 had fallen to less than 10% of the AP3 values ($23\text{--}28 \text{ mmol m}^{-2} \text{ s}^{-1}$).

The reasons for these differences in absolute measurement of stomatal conductance were examined by first sending the porometers to the manufacturers for calibration. The manufacturers reported no significant faults. The porometers were then compared in 1991 using Celgard samples. These measurements showed that for the same samples, the conductances estimated using the AP3 were 2 to 2.5 times higher than those using the LCA-2 (Figure 11.8).

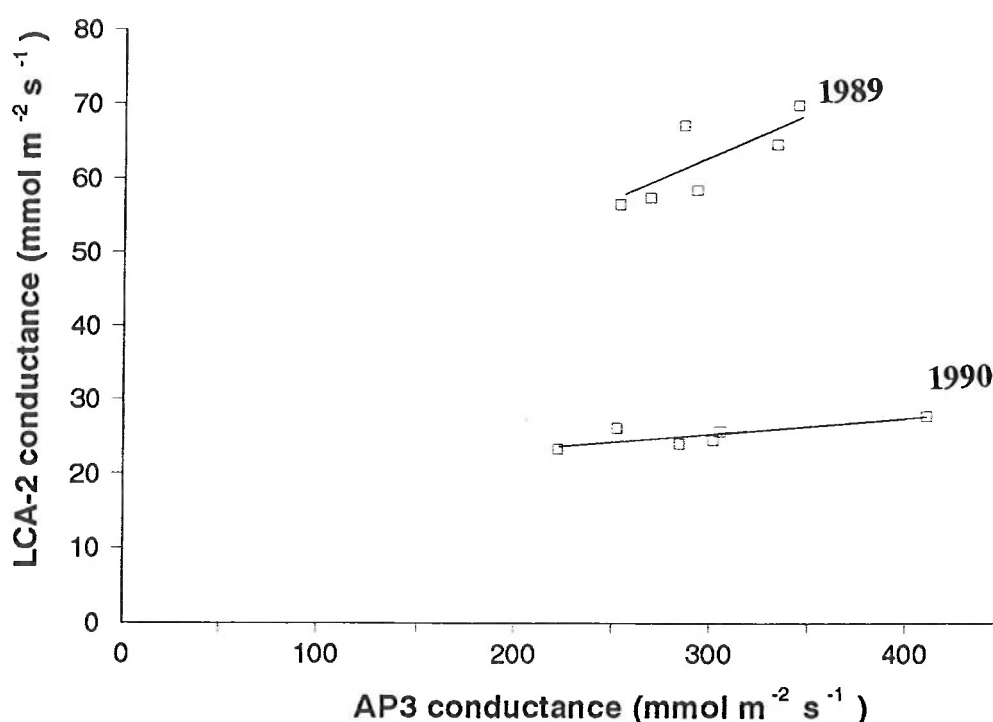


Figure 11.7. Comparisons of the AP3 and LCA-2 porometers in their measurements of the mean 10.00 to 16.00 h stomatal conductances for each of six fully irrigated clones in 1989 and 1990.

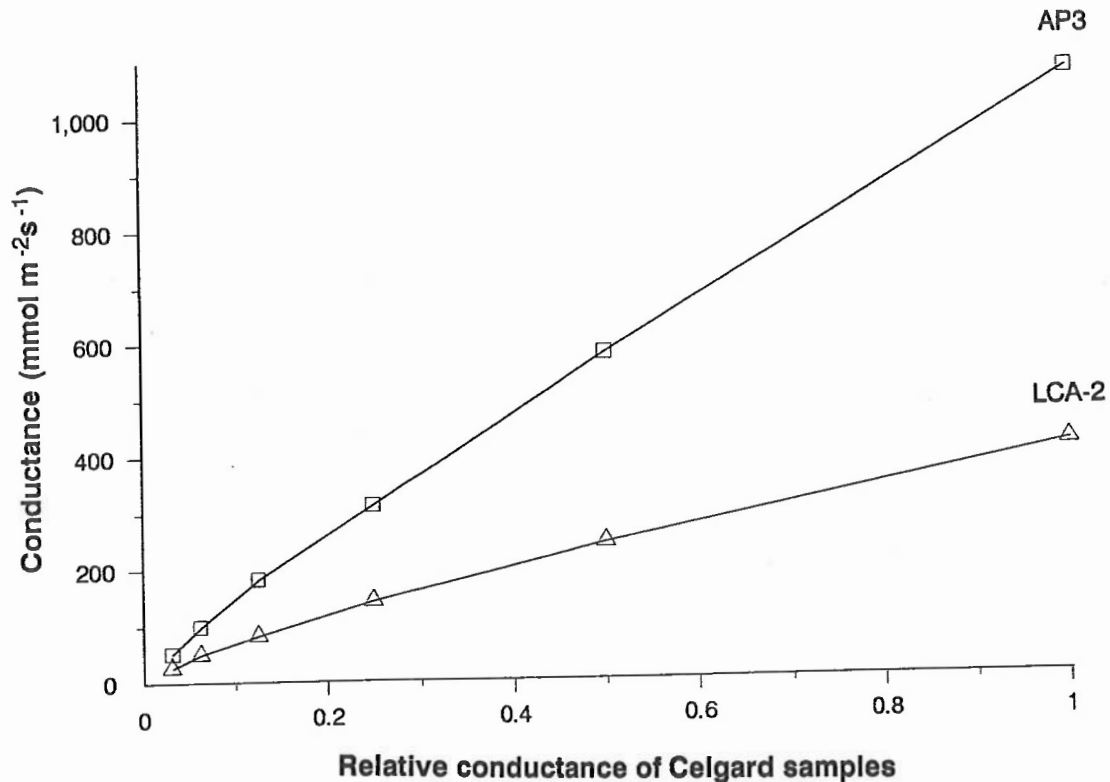


Figure 11.8. Comparison of the measured conductances for each of six Celgard samples using an AP3 and an LCA-2 porometer.

Comparison of clones

The mean stomatal conductance of each of the six fully irrigated clones in 1989 and 1990, estimated using each of the porometer, was expressed as a proportion of the mean conductance for the six clones measured by the corresponding porometer. This was to highlight the capacity of the porometers to rank the stomatal conductances of the clones (Table 11.3). Both of the porometers ranked clones S15/10 and 6/8 as having high conductances and ranked clones K35, 207 and 1 as having low conductances. The values of clone SFS150 were intermediate. Of the two techniques, the conductances estimated using the AP3 showed the greatest relative difference between the clones. For example: clone S15/10 was estimated with the AP3 to have a conductance 63% higher than clone 207 in 1990, compared to only a 14% difference estimated with the LCA-2.

Table 11.3. Mean Stomatal conductances (10.00 to 16.00 h) measured with AP3 and LCA-2 porometers during the warm dry season in 1989 and 1990 for each of six fully irrigated clones ^a. To highlight the ranking of clones the conductances are expressed as proportion of the corresponding mean conductance.

Porometer type		Relative stomatal conductance					
		AP3		LCA-2			
		1989	1990	1989	1990		
Clone	1	0.86 z	0.96	0.92 z	0.96 z		
	6/8	1.16 a	1.03	1.11 a	1.04 a		
	SFS150	0.96 z	0.85	1.09 a	1.00		
	S15/10	1.12 a	1.38 a	1.03	1.09 a		
	207	0.91 z	0.75 z	0.91 z	0.95 z		
	K35	0.99 z	1.02	0.94 z	0.97 z		
mean (mmol m ⁻² s ⁻¹)		298	296	62.8	25.0		
sed (n)		21 (95)	19 (75)				

^a: The AP3 measurements were taken from 29 September to 25 October in 1989 and from 19 September to 1 November in 1990. The mean LCA-2 results for similar time periods were adapted from Smith (unpublished; 1991a).

Infiltration score

Diurnal behaviour of stomata

The infiltration score measurements on 3 October 1990 showed that stomatal opening increased from 07.00 to 09.00 h in the fully irrigated treatments (Figure 11.9), a trend which was also apparent on other days. Stomatal opening then declined for most clones, whilst it stayed high for clone K35. There was no evidence of stomatal closure or opening at the end of the day. In the unirrigated treatments stomatal opening was reduced from the irrigated levels after 8.00 h and continued to remain low and relatively constant throughout the day.

Clonal differences

There were clonal differences ($P \leq 0.01$) in mean infiltration score (10.00 to 16.00 h) in both 1989 and 1990 (Table 11.4). In both years fully irrigated clones K35 and 6/8 had high infiltration scores, whilst those of fully irrigated clones 1 and 207 were low.

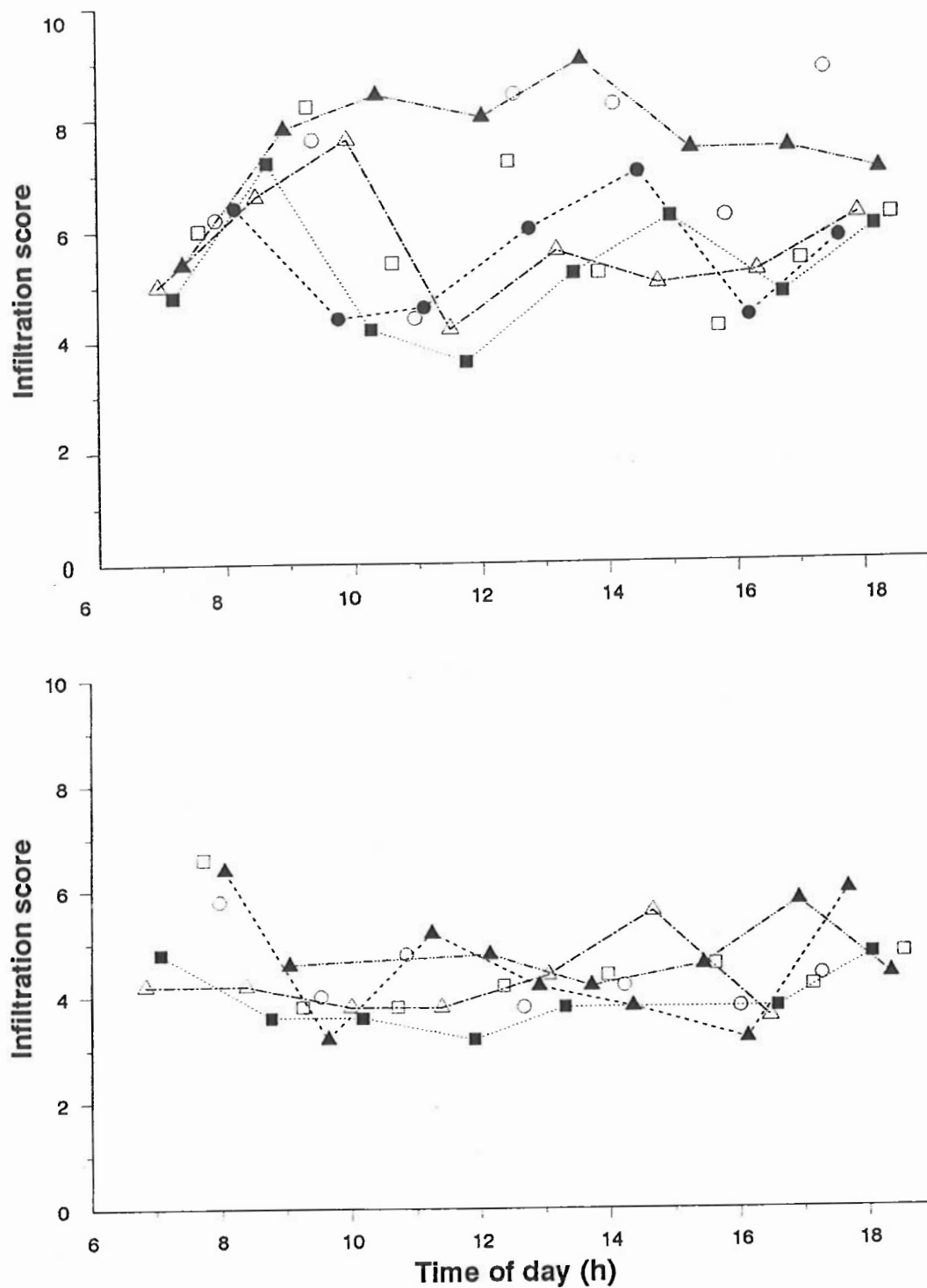


Figure 11.9.

Diurnal changes in the infiltration score for each of six a) fully irrigated and b) unirrigated clones measured on 3 October 1990. Clones 1: $\square$, 6/8: $\circ$, SFS150: $\bullet$, S15/10: $\triangle$, 207: $\blacksquare$, K35: $\blacktriangle$.

Table 11.4. Mean infiltration scores (10.00 to 16.00 h) for each of six fully irrigated clones during the warm dry seasons in 1989 and 1990.

Year		Infiltration score			
		1989		1990	
Clone	1	5.4	z	5.7	
	6/8	6.3	az	6.5	
	SFS150	6.6	a	6.0	
	S15/10	6.0	az	5.5	z
	207	5.8	az	5.2	z
	K35	6.6	a	7.2	a
sed		0.5		0.22	
n		30		75	

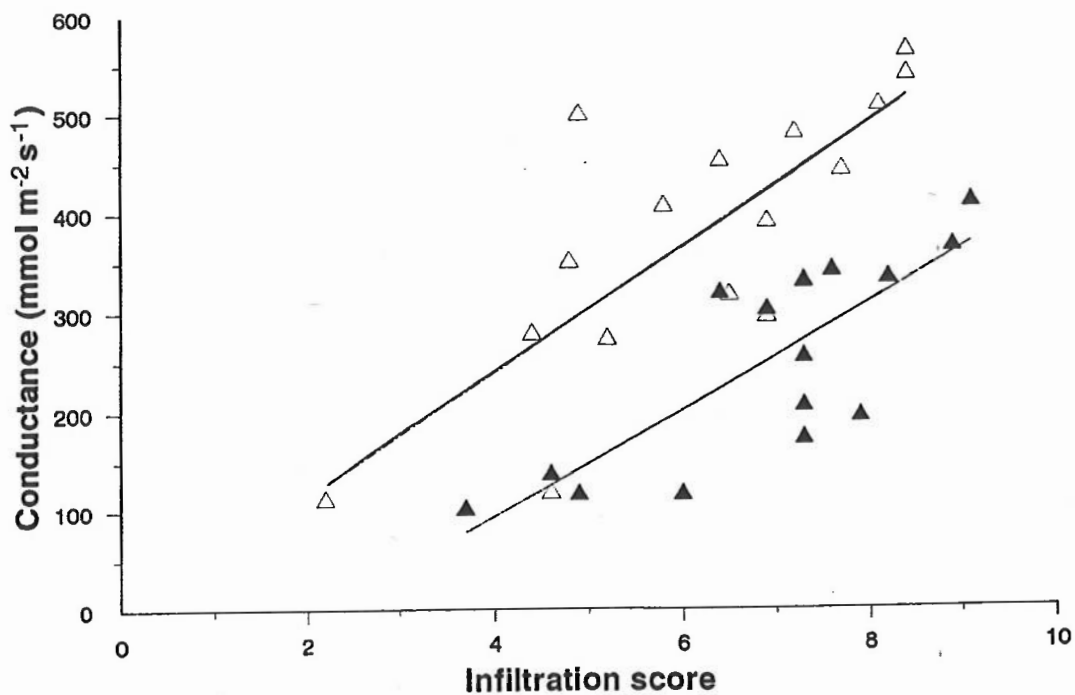


Figure 11.10. Relationships between mean stomatal conductances (10.00 to 16.00 h), measured with an AP3 porometer, and the corresponding infiltration scores for fully irrigated and unirrigated clones S15/10: △ and K35: ▲ during the 1990 dry season.

The relative rankings of the infiltration scores for clones 6/8, SFS150, 1 and 207 were similar to those obtained with the porometers. However they did not indicate the high stomatal conductance of clone S15/10 and low conductance of clone K35 which were apparent with the porometry measurements. These two clones show that the relationship between the daily mean conductance (10.00 to 16.00 h) and corresponding infiltration score can vary with clones (Figure 11.10).

DISCUSSION

Diurnal stomatal behaviour

Both porometers estimated very high early morning stomatal conductances, which were associated with morning dew. These high values could have been caused by the leaves being wet, or alternatively because the leaves were wet (and the associated VPD was minimal) stomatal conductances could actually have been high. The sensitivity of stomata to VPD has been reported in tea (Callander and Woodhead, 1981) and in a range of other crops including sunflower, cotton and tree species (Turner, 1991), vegetables (Bakker, 1991) and cassava (El-Sharkawy and Cock, 1990). Because of the presence of dew the effect of stomatal conductance on transpiration at this time of the day is unlikely to be important.

None of the techniques showed strong positive relationships with incident solar radiation. Although infiltration scores increased between 07.00 and 09.00 h, they did not decline in the evening. Although the measurements taken with the AP3 suggested that conductances declined in the late afternoon, this was not substantiated by the LCA-2. This lack of response may be a result of the very low levels of radiation needed for full stomatal opening. Hsiao (1973) considered that most crops showed full or nearly complete stomatal opening at light intensities corresponding to 10% of full sunlight. At Ngwazi this would be equivalent to about $200 \mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD, or about 100 W m^{-2} total solar radiation, levels which were achieved by 08.00 h and maintained until 17.30 h when there was no cloud. These values are lower than the $300\text{--}400 \text{ W m}^{-2}$ light saturation point for stomatal conductance tea reported by Squire (1978). Further work, preferably within an environment where the VPD can be controlled, is required to determine the response of stomatal conductance to solar radiation.

None of the techniques showed a distinctive diurnal change in stomatal conductance when solar radiation levels were high and there was no dew. This may have been due to the relatively constant VPDs and air temperatures between 10.00 and 16.00 h. However measurements made with the AP3 porometer, particularly for some clones, showed that gradual stomatal closure occurred during the day. This pattern of a high morning conductance followed a steady decline throughout the rest of the day is similar to the wet season infiltration score measurements of Othieno (1978b) in Kenya. It also corresponds with the porometry measurements of Callander and Woodhead in Kenya (1981), and Nagarajah (1981) and Sandanam *et al.* (1981) in Sri Lanka. The infiltration score technique provided no evidence for the re-opening of the stomata in the late afternoon reported by Carr (1977a) and Othieno (1978b) in Kenya.

Each of the techniques showed that there was greater stomatal closure (lower stomatal conductances) in the unirrigated treatments. For all methods this tended to be a consistent decrease throughout the day.

Calibration of the transient porometer

Although the conductances estimated with the AP3 porometer at low temperatures and at high humidities were sensitive to the calibration procedure (cf Appendix C), the values estimated during the middle part of the day (10.00 to 16.00 h) were consistent between the two years (220-410 mmol m⁻² s⁻¹). These values are higher than previously reported maximum stomatal conductances for tea of 48 to 77 mmol m⁻² s⁻¹ (Nagarajah, 1981; Sandanam *et al.* 1981; Callander and Woodhead, 1981). The highest reported value is about 230 mmol m⁻² s⁻¹ for tea in Malawi (Squire, 1978). The conductances measured with the AP3 were also higher than the typical maximum conductances of approximately 200 mmol m⁻² s⁻¹ (5 mm s⁻¹) for woody plants cited by Jones (1983). It is therefore probable that the AP3 was consistently overestimating the conductance. This could have been caused by the choice of the resistance values for the calibration plate and/or by the width of the chamber at the leaf-chamber interface.

Decreasing the resistance value of calibration plate position 5 from 0.13 to the recommended value of 0.085 s mm⁻¹ (Table 11.2) increased the calculated conductances within that range (400-600 mmol m⁻² s⁻¹) by about 50%. Whilst it is currently believed that the new value is the 'actual' value, the fact that such a change in recommendation is possible means that the absolute measurements

obtained with the AP3 are questionable. Over-estimates of conductance could also have been caused by the poor definition of the end of the chamber (Figure 11.11). Because the foam pad rose above the level of the leaf chamber, the area of exposed leaf was larger than the area of the porometer chamber. This may have resulted in a greater quantity of water vapour entering the chamber and therefore a higher estimated conductance (John Wood, personal communication). In the new Delta-T AP4 porometer this potential problem has been avoided by extending the sides of the polypropylene chamber so that they touch the leaf.

These differences may explain why the AP3 porometer estimated conductances for the Celgard samples up to two and half times higher than those measured by the LCA-2 porometer. The possibility of inherent differences in calibration between 'correctly calibrated' porometers has also been raised following field measurements taken at a recent international workshop on field instrumentation in Italy (Dugas, 1991).

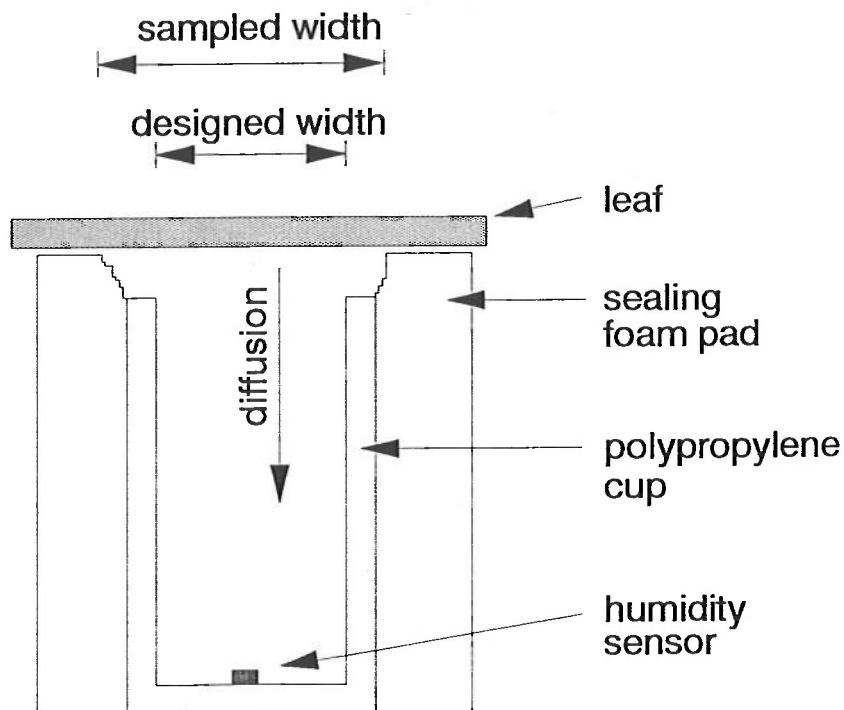


Figure 11.11. Vertical section across the narrow width of the cup of an AP3 porometer showing the effect of a raised foam pad on the area of leaf sampled.

Calibration of the steady state porometer

Although up to a two and a half fold difference was explained by the Celgard measurements, this was still smaller than the differences found in the field in Tanzania. The probable reasons for the outstanding disagreement are associated with field calibration. Although the measurements taken with the AP3 porometer were consistent between the years, the values obtained within the fully irrigated treatments with the LCA-2 declined from 55-70 mmol m⁻² s⁻¹ in 1989 to 24-28 mmol m⁻² s⁻¹ in 1990. The most likely source of error is therefore the field calibration of the LCA-2. A sensitivity analysis of the LCA-2 conductance calculations shows that such major changes in conductance could only be caused by incorrectly measuring the flow rate or the humidity. The flow rates were correct on return to the U.K., and therefore the most likely source of error was the humidity measurement. Even though the values recorded by the humidity sensor were reported to be 'within 5% of its true value' by the manufacturers, even such 'small' offsets can cause large changes in the calculated stomatal conductance if the humidity of the air leaving the porometer is low (McDermitt, 1990).

These problems with calibration highlight the need for some simple and quick method of checking the calibration of steady state porometers in the field. The need for a technique of standardising porometer calibrations has been raised before (Landsberg *et al.*, 1975), but still no commonly accepted method has been found. The use of Celgard samples offers a potentially simple and relatively quick way to check the calibration of porometers.

Ranking of clones by porometry

Despite the large differences in absolute conductance both porometers ranked the stomatal conductances of the fully irrigated clones in a similar order. This therefore gives the operator some confidence in the use of porometers for ranking the stomatal conductances of different clones. Greater relative differences in clonal conductances were found with the AP3 porometer than with the LCA-2.

Use of infiltration score

The disagreements between the porometers in the absolute levels of conductance made it futile to estimate the relationships between values of

infiltration scores and values of stomatal conductance. Although the infiltration score technique ranked the stomatal opening of most of the clones in a similar order to the stomatal conductance measured with the porometers, the rankings for clones S15/10 and K35 were different. This indicates that the relationships between infiltration score and conductance varies with clone. This may be caused by clonal differences in stomatal density (Sandanam *et al.*, 1981) or geometry. Because infiltration depends primarily upon the geometry of the 'widest' stomata, infiltration scores will not necessarily increase at higher stomatal densities, even though this will tend to increase the stomatal conductance. Therefore porometry is the preferable technique for determining clonal differences in stomatal conductance.

CONCLUSIONS

The two porometers ranked the stomatal conductances of six irrigated clones in a similar and consistent order. Porometry therefore provides a reliable technique for determining relative differences in stomatal conductance. A greater relative spread of conductances was obtained using the AP3 porometer than the LCA-2, and therefore the AP3 may more readily identify clonal differences.

The mean day-time conductances measured using the LCA-2 porometer were only 20% of the corresponding values estimated using the AP3 porometer in 1989, and less than 10% in 1990. The major reason for the change over the two years was probably incorrect calibration of the LCA-2 humidity sensor. It is also possible that the AP3 porometer consistently overestimated conductances by up to 2.5 fold in both years. These problems with calibration mean that the absolute measurements of stomatal conductance must be treated with caution. For example the calculation of transpiration rates from these measurements of stomatal conductance is not recommended. The use of Celgard samples provides a potential means of standardising porometer calibration.

There were positive linear relationships between the daily mean infiltration scores and the corresponding stomatal conductances measured using an AP3 porometer. However the ranking of clones in terms of infiltration score was different to that for stomatal conductance for two clones (K35 and S15/10) within a group of six.

Both porometers estimated high early morning conductances, which were associated with morning dew. After the dew had evaporated the conductances of

most clones tended to decline steadily throughout the rest of the day. The infiltration score measurements on irrigated plants also showed maximum stomatal opening in the morning.

CHAPTER 12

STOMATAL CONDUCTANCE AND XYLEM WATER POTENTIAL

INTRODUCTION

Cell expansion is reduced when the water potential within the xylem (ψ_x ; MPa) of any crop falls below a critical value. The critical value of ψ_x for shoot extension of tea in Malawi is considered to be about -0.8 MPa (Squire and Callander, 1981). Individual cells, shoots and even whole plants may die at even lower levels of ψ_x (Ludlow and Muchow, 1990).

The value of ψ_x depends upon the difference between the water potential of the soil (ψ_s ; MPa) and the atmosphere (ψ_a ; MPa) and how efficiently the roots and stomata conduct water. Typical values for ψ_s range from zero at saturation to -1.5 MPa at permanent wilting point. Although the capacity of the atmosphere to draw water is usually described in terms of a vapour pressure, it can also be expressed as an equivalent atmospheric water potential (Koide *et al.*, 1989). A VPD of 1.5 kPa at 23°C, which is close to the mean afternoon value in October at Ngwazi, is equivalent to a value of ψ_a of about -104 MPa. Values of ψ_x for tea can vary from -0.1 to -2.1 MPa (Othieno, 1978b), indicating that the greatest potential difference occurs between the xylem and the atmosphere. The conductance of water vapour at this stage is primarily determined by the stomata. Both stomatal conductance (g_s ; mmol m⁻² s⁻¹) and xylem water potential have therefore been suggested as useful parameters for identifying high yielding and/or drought resistant clones.

In conditions where the soil was wet, Squire (1976) in Malawi reported that for a range of clones low values of ψ_x were positively correlated with high yield. He suggested that this was because high yielding clones were photosynthetically more active and produced a higher concentration of osmotica in the leaf cells than low yielding clones. The higher concentration of osmotica resulted in lower day-time values of ψ_x .

By contrast the capacity of some clones to maintain high values of ψ_x under dry soil conditions, has been related with visual observations of drought resistance (Carr, 1977b; Othieno, 1978b). Carr (1977b) also examined the slope of the best fit linear relationship relating values of ψ_x of an individual clone to corresponding values for a group of clones, representing an environmental

mean, over a range of drought stresses. Those clones which had shallow slopes were generally drought resistant. Using the same technique in Burundi Renard *et al.* (1979) were able to determine successfully the relative drought resistance of twenty out of twenty four clones.

Othieno (1978b) in Kenya related the lower values of ψ_x of the 'drought susceptible' clones to their 'greater demand for water' which he associated with wide open stomata. In a comparison of three clones in Sri Lanka, Sandanam *et al.* (1981) also reported that the most drought susceptible clones had the highest stomatal conductance, especially in the dry treatments. By contrast Carr (1971a) in Southern Tanzania reported that under dry soil conditions clone 1, which is drought resistant (cf Chapter 5), had wider open stomata than seedling tea of a similar age which was drought susceptible. In later experiments in Kenya, Carr (1977a; 1977b) also reported that the stomata of 'drought resistant' clones tended to be wider than those of 'drought susceptible' clones in dry soil. Rather than focussing on these absolute differences Carr (1977b) suggested that the slope of the best fit linear relationship between the infiltration scores of a individual clone to the corresponding mean infiltration scores of the group of clones under study could perhaps be used to determine drought resistance.

In this chapter the stomatal conductances, xylem water potentials and their interaction are examined for each of six clones under differing drought regimes in Southern Tanzania.

METHODOLOGY

Stomatal conductance

Stomatal conductances were measured with a Delta-T AP3 porometer using the procedures described in Appendix C and Chapter 11. The stomatal conductances within each fully irrigated (I_5) and unirrigated (I_0) treatment of each clone were measured at approximately one and a half hour intervals between 10.00 and 16.00 h on seven days between 29 September and 17 November in 1989 and on ten days between 1 June and 1 November in 1990. Within each treatment at each visit the stomatal conductance was measured for five healthy mature leaves fully exposed to the incident sunlight.

Xylem water potential

The xylem water potentials of healthy 90-120 mm long tea shoots were measured using an Arimad-2 pressure chamber marketed by ELE International Ltd, Hertfordshire. Three shoots were taken at approximately one and a half hour intervals between 10.00 and 16.00 h from each fully irrigated and unirrigated treatment of each clone on the same dates as the porometry measurements. Each clone x drought treatment was usually visited seven to eight times on each day. In 1990 the shoots were obtained from the guard rows of each treatment, but in 1989 a proportion of the shoots were also harvested from within the experimental sub-plots.

The selected shoots were cut and carried to a central point, where the lower 10 mm of the shoot was cut again. The shoot was then placed in the chamber within 60 s of being removed from the bush. Although the second cut may have caused errors in the absolute value of ψ_x (Squire *et al.*, 1981), this would be systematic in all treatments. The length of shoot protruding out of the chamber, which was typically 40 mm, was the minimum that enabled easy observation of the cut stem. Using compressed CO₂ the pressure chamber was pressurised at a rate of 1.2 MPa min⁻¹ until the pressure was estimated to be within 0.4 MPa of an equilibrium value of ψ_x . The rate of increase in pressure was then reduced to 0.3 MPa min⁻¹. If the chamber was pressurised quicker than this there was a tendency to underestimate the value of ψ_x (Table 12.1). The value of ψ_x was assumed to be equal to the negative of the pressure within the chamber when air bubbles first appeared at the cut surface of the stem.

Table 12.1. Effects of different rates of increasing the pressure within the chamber on the measured value of xylem water potential (n=8).

Rate of increasing the pressure (MPa min ⁻¹)	Xylem water potential (MPa)	
0.1	-0.46	±0.065
0.3	-0.45	±0.038
1.2 then 0.3	-0.45	±0.054
1.2	-0.57	±0.078
2.5	-0.60	±0.046

A preliminary experiment showed that in contrast to the work of Baughn and Tanner (1976) and Leach *et al.* (1982) it was not necessary to cover the shoot with clingfilm prior to excision to prevent transpiration losses affecting the value of ψ_x .

RESULTS

Stomatal conductance

During the warm dry season in 1989 the stomatal conductances of fully irrigated clones S15/10 and 6/8 were higher ($P \leq 0.05$) than those of clones 1 and 207 (Table 12.2). In 1990 the mean stomatal conductances of the fully irrigated clones ($330 \text{ mmol m}^{-2} \text{ s}^{-1}$) were close to those estimated in the previous year ($284 \text{ mmol m}^{-2} \text{ s}^{-1}$). The ranking of these clones was also similar with clone S15/10 having the highest ($P \leq 0.05$) values followed by clone 6/8. The mean conductance of fully irrigated clone 6/8 was not significantly greater than that of clone 1, but was higher ($P \leq 0.05$) than those of clones SFS150 and K35. Clone 207 had the lowest ($P \leq 0.05$) stomatal conductance.

Table 12.2. Mean stomatal conductances (10.00 to 16.00 h) for each of six fully irrigated clones measured with an AP3 porometer during the warm dry season in 1989 (9 September to 17 October) and the dry season in 1990 (1 June to 1 November).

		Stomatal conductance ($\text{mmol m}^{-2} \text{ s}^{-1}$)	
		1989	1990
Clone	1	232 z	337
	6/8	327 a	361
	SFS150	279	296
	S15/10	312 a	429 a
	207	271	233 z
	K35	284	305
Mean		284	330
sed (n)		18 (120)	18 (185)

Effects of drought

Stomatal conductances were reduced ($P \leq 0.001$) by drought on 6 November 1989, thirty days after the imposition of drought treatments. On this date the SWD was about 70 mm in the unirrigated treatments, compared to 18 mm in the fully irrigated sub-plots; the maximum VPD was about 2.3 kPa. However measurements taken eleven days later on 17 November showed no significant drought effects. On this date the corresponding SWDs were 75 mm and 11 mm, but the maximum VPD was only 1.4 kPa.

The daily mean stomatal conductances (10.00 to 16.00 h) of the fully irrigated clones varied from 240 to 422 mmol m⁻² s⁻¹ during the 1990 dry season (Figure 12.1). Drought significantly ($P \leq 0.05$) reduced stomatal conductance on 4 September, about 40 days after the imposition of drought treatments, when the mean SWD in the unirrigated sub-plots was about 105 mm. At this time the SWD within the fully irrigated treatments was only 11 mm. The mean stomatal conductances of the unirrigated clones continued to decline after this date reaching 95 mmol m⁻² s⁻¹ by 1 November when the SWD had increased to about 137 mm (Figure 12.2).

Clone x drought interactions

In both years, once an effect of drought was established, there were clone x drought interactions ($P \leq 0.05$) on the stomatal conductance. On 6 November 1989 the stomatal conductance of fully irrigated clone 1 was lower ($P \leq 0.05$) than those of clones S15/10, 207, 6/8 and K35, but within the unirrigated treatments they were similar (Table 12.3). In 1990 the conductance of fully irrigated clone S15/10 was greater ($P \leq 0.05$) than those of the other fully irrigated clones, whereas in the unirrigated treatments the stomatal conductance of clone S15/10 was similar to those of clones 1 and SFS150.

The clone x drought interactions on stomatal conductance in 1990 were also examined by determining the slope of the best fit linear regression of the mean conductances of each unirrigated clone against the corresponding mean values of all the unirrigated clones. There were no significant clonal differences in the slope, but the estimated y-axis intercept for clone 207 was less ($P \leq 0.05$) than those for the other clones. The intercepts of clones 1, 6/8, SFS150 and S15/10 were similar (Table 12.4).

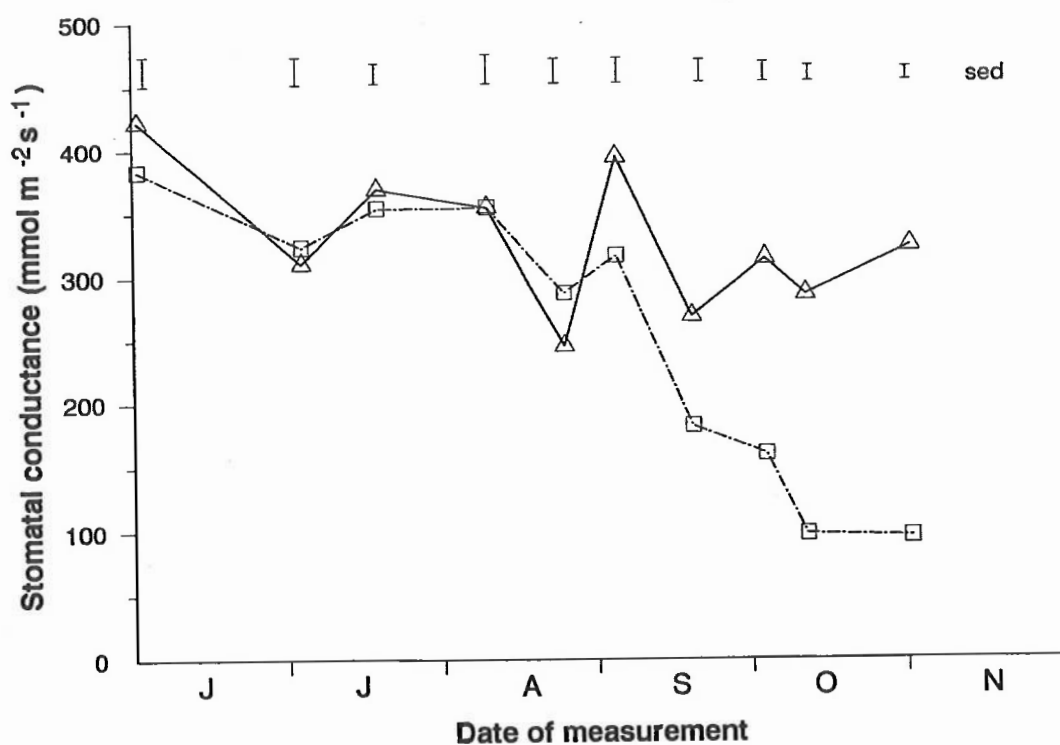


Figure 12.1.

Seasonal changes in the mean stomatal conductances (10.00 to 16.00 h) of six fully irrigated: —△— and unirrigated: —□— clones, measured using an AP3 porometer during the 1990 dry season.

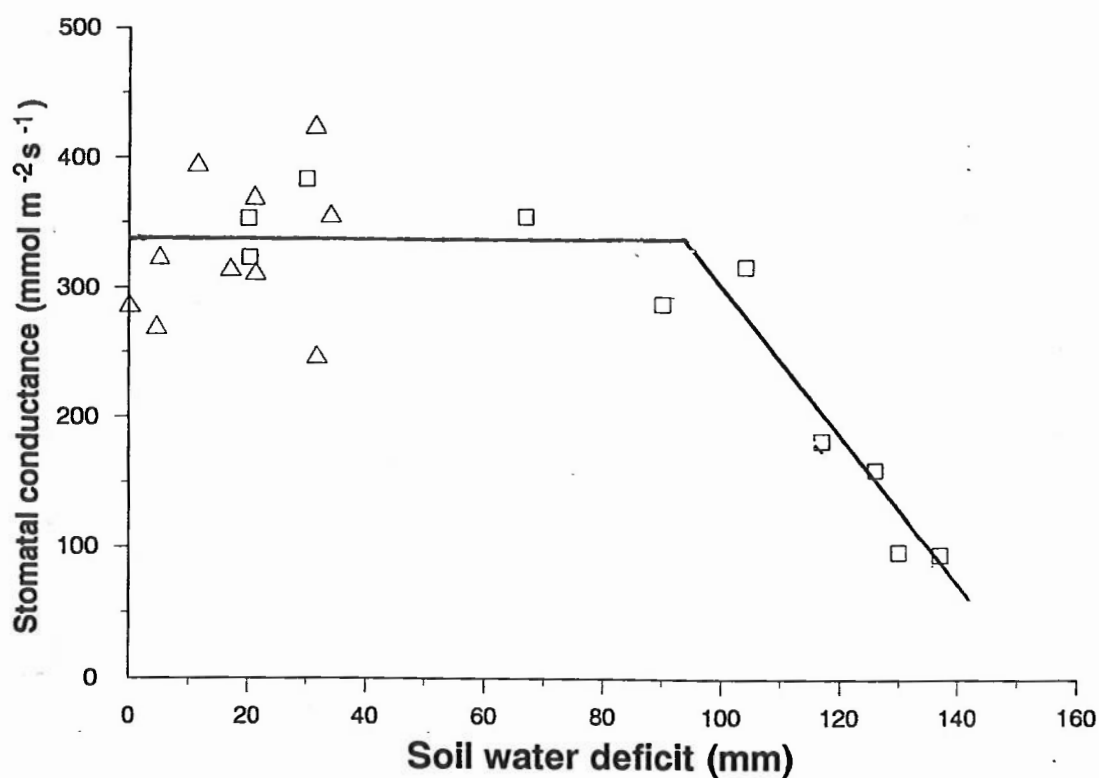


Figure 12.2.

Relationship between the mean stomatal conductance (10.00 to 16.00 h) of six clones measured using an AP3 porometer and the corresponding soil water deficit. Lines drawn by eye.

Table 12.3. Effects of drought on the mean stomatal conductance (10.00 to 16.00 h) for each of six clones measured using an AP3 porometer during the warm dry season in 1989 and 1990 ^a.

		Stomatal conductance (mmol m ⁻² s ⁻¹)							
		1989				1990			
		Fully irrigated		Unirrigated		Fully irrigated		Unirrigated	
		I ₅		I ₀		I ₅		I ₀	
Clone	1	171	z	169	a	292		213	a
	6/8	276	a	183	a	330		184	
	SFS150	238	az	166	a	251		199	a
	S15/10	330	a	188	a	400	a	234	a
	207	309	a	129	a	210	z	85	z
	K35	278	a	175	a	269		140	
sed (n)		40 (15)				20 (90)			

^a: Values taken when there were significant effects of drought on stomatal conductance in 1989 (6 November) and 1990 (4 September to 1 November).

Table 12.4. Y-axis intercepts of the best fit linear regressions of the stomatal conductances for each of six unirrigated clones against the corresponding mean values during the 1990 dry season (1 June to 1 November) (n = 54, r² = 83%).

		Y-axis intercept (mmol m ⁻² s ⁻¹)	
Clone	1	16	±2.3 a
	6/8	16	±2.3 a
	SFS150	8	±2.3 a
	S15/10	72	±2.3 a
	207	-98	±2.3 z
	K35	-24	±2.3

Differences between clones in the ratio of stomatal conductance in the unirrigated sub-plots to that in the fully irrigated treatments were examined using the mean daily conductances recorded once there was a significant effect of drought. Although only significant at the 20% level these relative conductances ranged from 0.77 for clone SFS150 to 0.35 for clone 207 (Table 12.5). This ranking is similar to that determined for drought resistance in Chapter 5.

Table 12.5. Ratios of the stomatal conductances within the unirrigated treatment to those within the fully irrigated treatments for each of six clones between 4 September and 1 November 1990.

Ratio of conductance in the unirrigated treatments to that in the fully irrigated		
Clone	1	0.60 a
	6/8	0.46 a
	SFS150	0.77 a
	S15/10	0.47 a
	207	0.35 a
	K35	0.43 a
sed = 0.15 (n=5)		

Xylem water potential

Diurnal changes

The values of ψ_x for fully irrigated and unirrigated clones SFS150 and K35 measured on 3 October 1990 are shown in Figure 12.3. At 08.00 h the values of ψ_x were already lower in the unirrigated sub-plots than those within the fully treatments, indicating that they had remained lower during the night. This was confirmed by measurements taken between 05.30 and 07.40 h on 26 October 1990 which showed that values around dawn were lower ($P \leq 0.001$) in the unirrigated than the fully irrigated treatments.

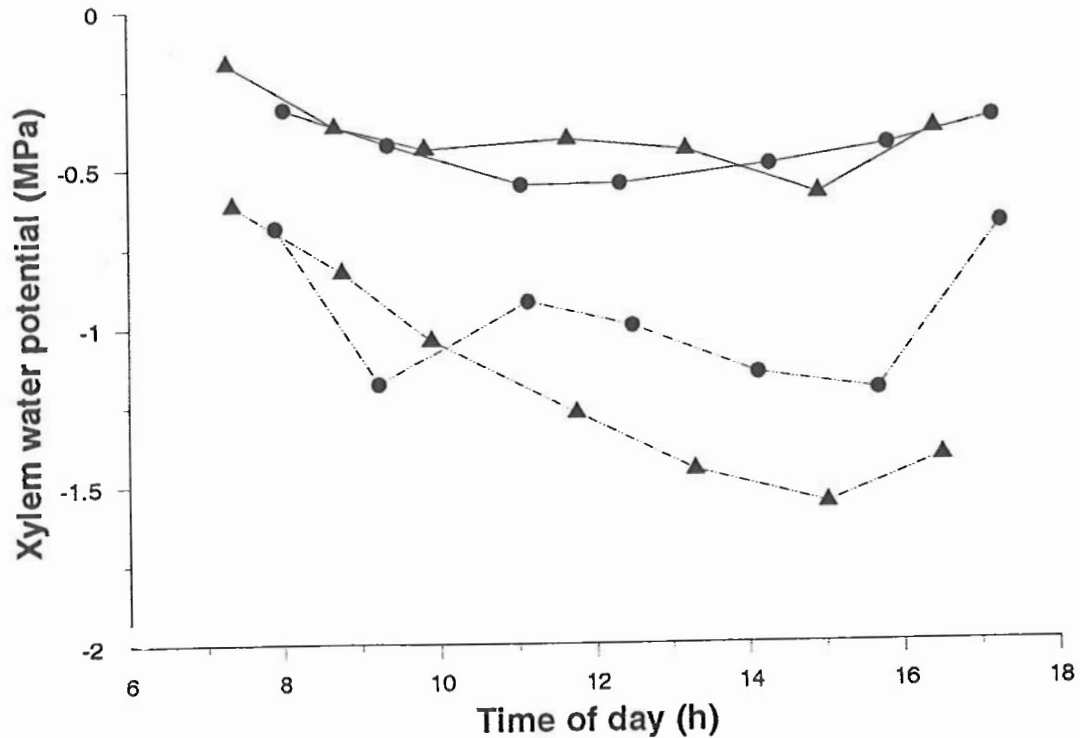


Figure 12.3. Diurnal changes in the xylem water potential for fully irrigated and unirrigated clones SFS150 and K35, measured on 3 October 1990. Fully irrigated clones SFS150: —●—, and K35: —▲—. Unirrigated clones SFS150: - -●- - and K35: - -▲- -.

As the incident solar radiation, the air temperatures and the VPD increased during the morning (cf Figure 11.4), the values of ψ_x started to fall reaching minimum values between midday and 16.00 h, before increasing again (Figure 12.3). Over 73% of this daily variation in ψ_x (MPa) for the unirrigated and the fully irrigated clones could be explained by a straight line relationship with the VPD (kPa) (Equations 12.1 and 12.2). The reduction in ψ_x per unit increase in VPD was greater ($P \leq 0.05$) in the unirrigated than the fully irrigated treatments as shown by the slope of these relationships:

$$\psi_x I_5 = -0.13(\pm 0.043) \cdot \text{VPD} - 0.26(\pm 0.060) \quad 12.1$$

$$\psi_x I_0 = -0.27(\pm 0.030) \cdot \text{VPD} - 0.74(\pm 0.041) \quad 12.2$$

Clonal differences (fully irrigated treatments)

In 1989 although the ψ_x of fully irrigated clone 6/8 was lower ($P \leq 0.05$) than that of clone 207, there were no significant differences between the values for the other clones. In 1990 there were no significant differences in the values ψ_x between any of the fully irrigated clones. (Table 12.6)

Table 12.6. Mean xylem water potentials (10.00 to 16.00 h) for each of six fully irrigated clones during the warm dry seasons in 1989 and 1990.

		Xylem water potential (MPa)	
		1989	1990
Clone	1	-0.55 az	-0.53 a
	6/8	-0.60 z	-0.55 a
	SFS150	-0.56 az	-0.51 a
	S15/10	-0.59 az	-0.54 a
	207	-0.53 a	-0.54 a
	K35	-0.58 az	-0.51 a
sed (n)		-0.030 (69)	-0.055 (60)

Effects of drought

In 1989 the first reduction ($P \leq 0.05$) in ψ_x due to drought was measured on 12 October, five days after the imposition of drought treatments. On this date the SWD in the unirrigated sub-plots had reached 36 mm compared to only 10 mm in the fully irrigated treatments.

The mean values of ψ_x for the fully irrigated clones were relatively consistent during the 1990 dry season ranging from only -0.32 to -0.57 MPa (Figure 12.4). The mean value of ψ_x within the unirrigated sub-plots was reduced ($P \leq 0.05$) by drought from -0.32 to -0.35 MPa on 9 August, thirteen days after the imposition of treatments. The mean SWD in the unirrigated treatments on this date had reached about 67 mm compared to 34 mm in the fully irrigated sub-plots. The mean value of ψ_x of the unirrigated clones then continued to decline reaching -1.69 MPa on 1 November when the SWD was 137 mm (Figure 12.5).

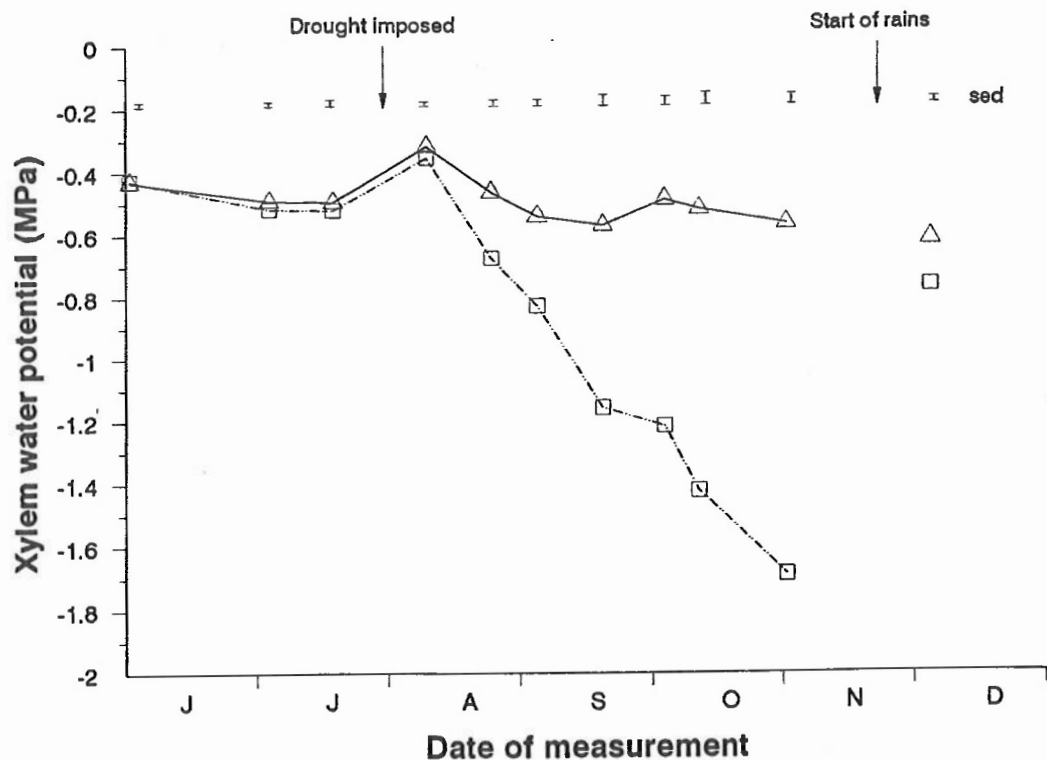


Figure 12.4. Seasonal changes in the mean xylem water potentials (10.00 to 16.00 h) of six fully irrigated: $\triangle$ and unirrigated: $\square$ clones during the 1990 dry season.

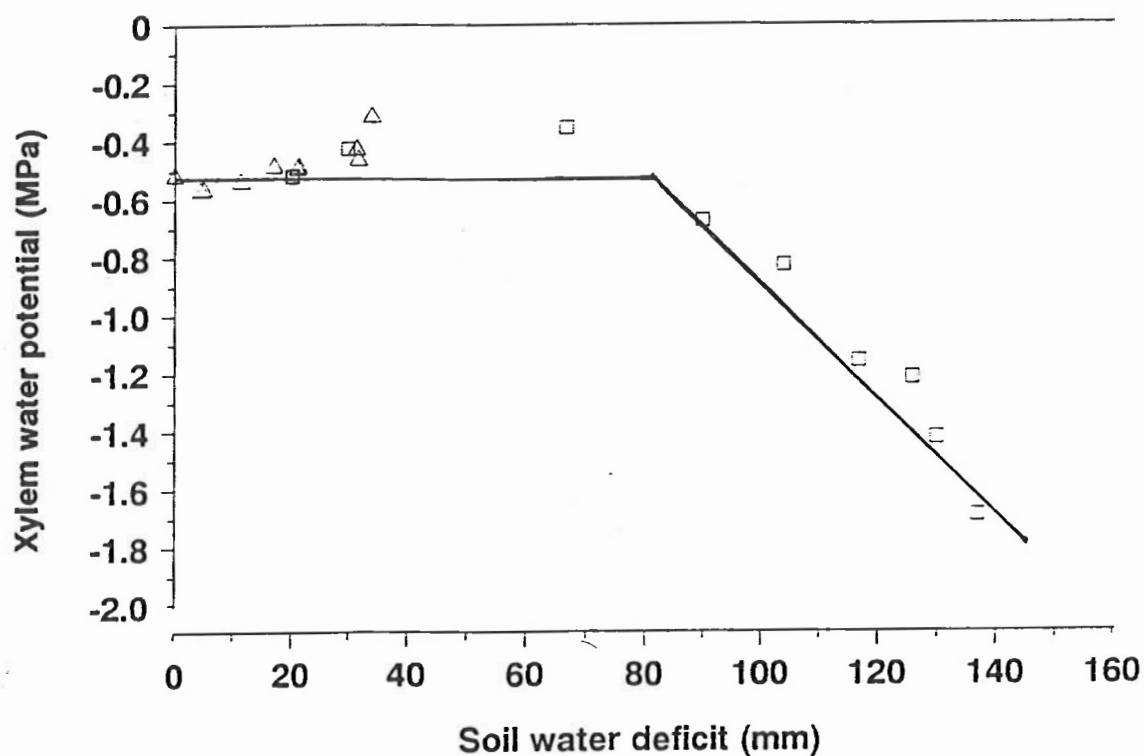


Figure 12.5. Relationships between the mean xylem water potential (10.00 to 16.00 h) of six clones and the corresponding soil water deficit. Lines drawn by eye.

Clone x drought interactions

Although the values of ψ_x for the fully irrigated clones were generally similar, in both years there were differences ($P \leq 0.001$) in the values of ψ_x of the six unirrigated clones. In November 1989 the values of ψ_x for clones 1, SFS150 and 207 within the unirrigated sub-plots were higher ($P \leq 0.05$) than that for clone K35 (Table 12.7). Within the unirrigated treatments in 1990, clones K35 and 207 had lower ($P \leq 0.05$) values of ψ_x than the other clones.

Table 12.7. Effects of drought on the mean xylem water potential (10.00 to 16.00 h) for each of six clones during the period when drought treatments were imposed in 1989 (6 to 17 November) and 1990 (4 August to 1 November).

		Xylem water potential (MPa)			
		1989		1990	
		Fully irrigated	Unirrigated	Fully irrigated	Unirrigated
		I ₅	I ₀	I ₅	I ₀
Clone	1	-0.51 a	-0.75 a	-0.52 a	-1.05 a
	6/8	-0.52 a	-0.85	-0.55 a	-1.15
	SFS150	-0.50 a	-0.74 a	-0.51 a	-1.01 a
	S15/10	-0.51 a	-0.86	-0.54 a	-1.07 a
	207	-0.46 a	-0.81 a	-0.52 a	-1.29 z
	K35	-0.48 a	-0.97 z	-0.48 a	-1.35 z
sed (n)		0.049 (18)		0.049 (75)	

The clone x drought interactions in 1990 were examined by determining the slope of the best fit linear regression between the daily mean values of ψ_x for each of the six unirrigated clones and the corresponding mean values of the group (Figure 12.6). The slopes for clones SFS150 and 1 were the most shallow ($P \leq 0.05$), suggesting that these clones were the most drought resistant (Table 12.8). The slopes estimated for clones K35 and 207 were the steepest ($P \leq 0.05$), suggesting that these clones were sensitive to drought.

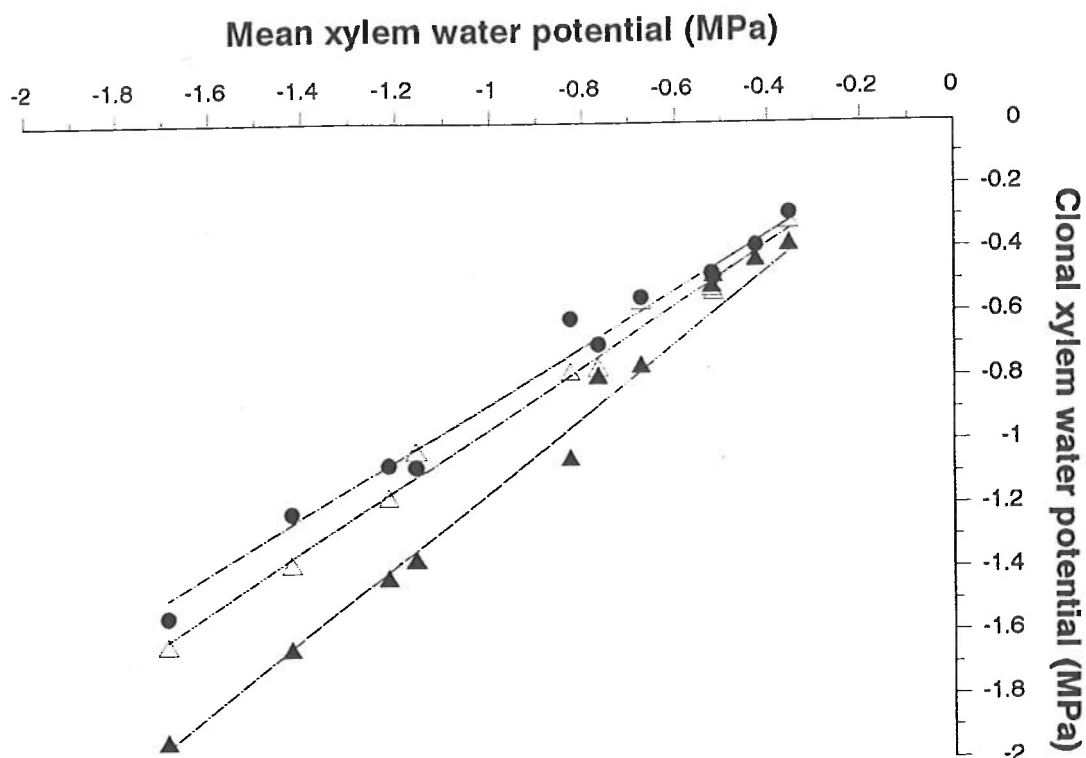


Figure 12.6. Relationships between the xylem water potentials for unirrigated clones SFS150:—●—, S15/10: —△— and K35:—▲— and the corresponding values for all six unirrigated clones.

Table 12.8. Slopes of the linear relationship between the mean xylem water potentials (10.00 to 16.00 h) for each of six unirrigated clones and the corresponding mean values of the group during the 1990 dry season (1 June to 1 November). The lines were constrained to pass through the origin ($n = 60$, $r^2 = 99\%$).

		Slope (MPa MPa ⁻¹)	
Clone	1	0.923 ± 0.018	a
	6/8	0.987 ± 0.025	
	SFS150	0.879 ± 0.025	a
	S15/10	0.956 ± 0.025	
	207	1.107 ± 0.025	z
	K35	1.154 ± 0.025	

Relationships between conductance and xylem water potential

The relationships between stomatal conductance and ψ_x were examined using the mean daily (10.00 to 16.00 h) data collected during the dry season in 1990. There were no significant relationships between the two variables when only the fully irrigated data were examined. However within the unirrigated treatments high stomatal conductances were associated with high values of ψ_x . There were differences ($P \leq 0.01$) in the value of the y-axis intercept of the best fit linear relationships between ψ_x and stomatal conductance for each of the clones, but the slopes were similar (Table 12.9).

Table 12.9. Y-axis intercepts of the linear relationship between daily values of xylem water potential and stomatal conductance for each of six unirrigated clones during the 1990 dry season from 1 June to 1 November. (slope = $3.40 \text{ MPa mol}^{-1} \text{ m}^2 \text{ s}$, $n=60$, $r^2 = 75\%$).

		Y-axis intercept (MPa)		
Clone	1	-1.75	± 0.10	az
	6/8	-1.81	± 0.10	a
	SFS150	-1.66	± 0.10	az
	S15/10	-1.95	± 0.10	a
	207	-1.49	± 0.11	z
	K35	-1.78	± 0.10	az

DISCUSSION

Stomatal conductance

Within the fully irrigated treatments the mean stomatal conductances were highest for clones 6/8 and S15/10 and lowest for clone 207 in both 1989 and 1990. The high stomatal conductance of clone 6/8 has been identified before by infiltration score measurements (Othieno, 1978b) and porometry (Renard *et al.*, 1979). In 1990 the mean conductance of irrigated clone 207, estimated with an AP3 porometer, was $233 \text{ mmol m}^{-2} \text{ s}^{-1}$. This was about 55% of the corresponding value of clone S15/10. Although this relative difference was dependent upon the porometer used (cf Chapter 11), clonal differences in stomatal conductance of the same magnitude have been reported by Sandanam *et al.* (1981).

Stomatal conductances were reduced when the actual SWD reached about 70 mm in 1989 and 105 mm in 1990. Although conductance measurements were only taken at 8 to 22 day intervals, these results suggest that the critical SWD for stomatal closure had increased in the second year. The available water within the estimated maximum rooting depth of these plants in September was about 90 mm in 1989 and 155 mm in 1990 (cf Chapter 3). The critical SWD for stomatal closure was therefore equivalent to about 65-80% of the available water content within the rooting depth of the crop. This is substantially higher than the 12-18% value reported by Stephens and Carr (1990b), beyond which the water use of a mature stand of clone 6/8 was reduced. However their results were based on daily estimates of soil water use rather than conductance.

There were significant clone x drought interactions on the value of stomatal conductance. For example: in 1990 the conductance of clone S15/10 was higher than clone 1 and SFS150 when fully irrigated, but under conditions of drought stress the conductances were similar. This relationship corresponds to that reported for annual yield in Chapter 5 (cf Table 5.5). Clone S15/10 had the highest yield within the fully irrigated (I_5) sub-plots, but a similar yield to those of clones 1 and SFS150 within the unirrigated (I_0) treatments. The low stomatal conductances recorded for unirrigated clones 207 and K35 also corresponded to their low annual yields when unirrigated.

The clonal differences in the response of stomatal conductance to drought were also analysed by regressing the daily conductances of each of the six unirrigated clones against the corresponding values for the group. This analysis indicated significant clonal differences in the intercept, but was unable to identify the clone x drought interactions. The stomatal conductances of each of the six unirrigated clones were also expressed relative to the corresponding values within the fully irrigated treatments. Although only significant at the 20% level this identified clones 1 and SFS150 as the most drought resistant and clone 207 as the most sensitive. These results correspond to the relative yield responses to drought shown by the same clones (cf Table 5.5).

Xylem water potential

The values of ψ_x were highest at dawn, declined during the day and rose again in the late afternoon. This diurnal change was linearly related to the VPD. The day-time ψ_x was reduced when the SWD exceeded about 40 mm in 1989 and about 70 mm in 1990. Assuming the same available water contents (AWC) used

to determine the critical SWD for stomatal conductance, the critical SWD for ψ_x was approximately 40% of the AWC within the maximum rooting depth of the crop. Due to the infrequency of measurements the actual value could be lower than this. In both years the critical SWD for ψ_x was less than that for stomatal opening. This supports the suggestion of Stephens and Carr (1991b) that the critical SWD for yield during the dry season is less than that for transpiration.

The xylem water potentials of the six clones were generally similar within the fully irrigated treatments. Therefore it was not possible to test the proposal of Squire (1976) that the yields of well watered clones are positively related to low values of ψ_x . A possible reason for the lack of difference is that the VPD at Ngwazi rarely exceeds 2.3 kPa, whereas it can exceed 3.5 kPa in Malawi (Tanton, 1982b). Under the relatively low VPDs of Tanzania the reduction in the ψ_x of well watered tea will be smaller and therefore the expression of clonal differences in the value of ψ_x is also reduced.

The drought resistances of the clones were examined using a technique proposed by Carr (1977b) which related drought susceptibility to the slope of the best fit linear relationship between the daily ψ_x of each unirrigated clone and the corresponding mean ψ_x of all six clones. This technique indicated that clones 1 and SFS150 were drought resistant and that clones 207 and K35 were drought susceptible. This ranking corresponds with the annual yields of the unirrigated clones (Table 5.5). Since the values of ψ_x were similar for each clone within the fully irrigated treatments, the same results can also be determined more simply and quickly from direct measurements of the ψ_x of the unirrigated clones.

Whilst both measurement of stomatal conductance and ψ_x were able to rank clones in terms of drought resistance, there were fewer problems with the ψ_x measurements particularly with regard to calibration (cf Chapter 11). Secondly, with the measurement of ψ_x , the difference between the drought resistant and susceptible clones became larger as drought stress increased. By contrast the separation of the stomatal conductances of drought resistant and susceptible clones decreased with drought stress making identification of drought resistance more difficult.

It is also of interest to note that both the stomatal conductance and ψ_x measurements during the 1990 dry season classified clone 1 as drought resistant. However the drought resistance of this clone was only evident from an analysis of the annual yield data, and not from the dry season yields (cf Chapter 5).

Therefore these two physiological measurements provided a better index of annual drought resistance of this clone than yield during the dry season.

Relationships between conductance and xylem water potential

There was no evidence of low stomatal conductances resulting in higher xylem water potentials, as suggested by Othieno (1978b). Instead those droughted clones with low stomatal conductances, such as clone 207, also had low xylem water potentials. For example in the unirrigated treatments during 1990 clone SFS150 and S15/10 had higher ground covers (cf Table 6.1) and stomatal conductances (Table 12.3) than clone 207, but clone 207 had the lowest xylem water potential. In determining the reasons for this, three possible causes for the weak link between stomatal conductance and ψ_x are suggested, followed by an analysis of why low conductances were related to low values of ψ_x .

The transpiration rate not only depends upon the stomatal conductance and leaf area, but can be affected by the aerodynamic conductance of the air and the boundary layer of the leaf. Whereas the greater ground cover of clones S15/10 and SFS150 would have increased transpiration, the effect was probably moderated by a decrease in aerodynamic conductance as the movement of air through the canopy was reduced (Jones, 1987). There may also be differences in boundary conductances at the leaf level. For example there are small hairs on the abaxial surface of the leaves of clone S15/10 which could decrease the boundary conductance and therefore transpiration. The greater size of the leaves of clone S15/10 may also decrease the boundary conductance relative to the small leaves of clone 207 (Monteith, 1965).

The reported stomatal conductances were only measured from a selected sample of healthy mature leaves at the upper surface of the canopy. However the leaf area index, within the area of ground cover, for this tea was typically three to six. Clonal differences in the conductances of these unmeasured leaves due to age or health (Sandanam *et al.*, 1981; Smith *et al.*, 1991) could also have affected transpiration.

Lastly the effective control of transpiration by the stomata can be moderated by negative feedback loops. For example a decrease in stomatal conductance causing a reduction in transpiration can also increase leaf temperature. This can raise the VPD between the leaf and the atmosphere which tends to increase transpiration (McNaughton and Jarvis, 1991).

Whilst these differences can explain why low conductances were not correlated with high xylem water potentials, they do not explain why drought resistant clones had high conductances and high xylem water potentials. Such a relationship could be apparent if the root distribution of the drought resistant clones enabled greater access to soil water. There was some indication of this: clone SFS150, which was drought resistant, had a larger proportion of thin roots at depth than three of the other clones and clone 207, which was drought susceptible, had a shallow maximum rooting depth (cf Chapter 8). However deep root distribution did not distinguish clone 1 as drought resistant.

As reported in Chapter 7, clones 1 and SFS150 also had high ratios of CO_2 uptake (A) to stomatal conductance for water vapour (g). The possible effects of clonal differences in the ratio A/g on stomatal conductance and ψ_x are examined in Figure 12.7.

Stomatal conductance decreases when a clone is drought stressed and this tends to reduce photosynthesis. However for a given conductance, a clone with a high A/g ratio can maintain a higher assimilation rate than a clone with a low ratio. By using these assimilates to decrease the osmotic potential, such a clone can maintain the turgidity of the cells of the roots and leaves (Ludlow and Muchow, 1990). By maintaining the turgidity of the roots, root expansion can continue to increase the soil water available to the plant which reduces the drought stress and thereby maintains the ψ_x . By maintaining the leaves turgid the clone may also maintain stomatal conductance, which in turn will enable photosynthesis to continue.

By contrast if the ratio of A/g is low, then the assimilates available for growth and osmotic adjustment will be reduced. This can cause reduced root extension and thereby exacerbate the initial drought stress. Reduced osmotic adjustment within the leaf can cause lower leaf turgor. This, or the effects of low root turgor affecting the production of phytohormones (Turner, 1991) such as abscisic acid (Raschke, 1987) and cytokinins (Davis and Mansfield, 1987), can increase leaf abscission and can reduce stomatal conductance. These may further decrease the level of photosynthesis. Figure 12.7 therefore provides a possible mechanism for relating available water and high values of A/g , with high values of ψ_x and stomatal conductance.

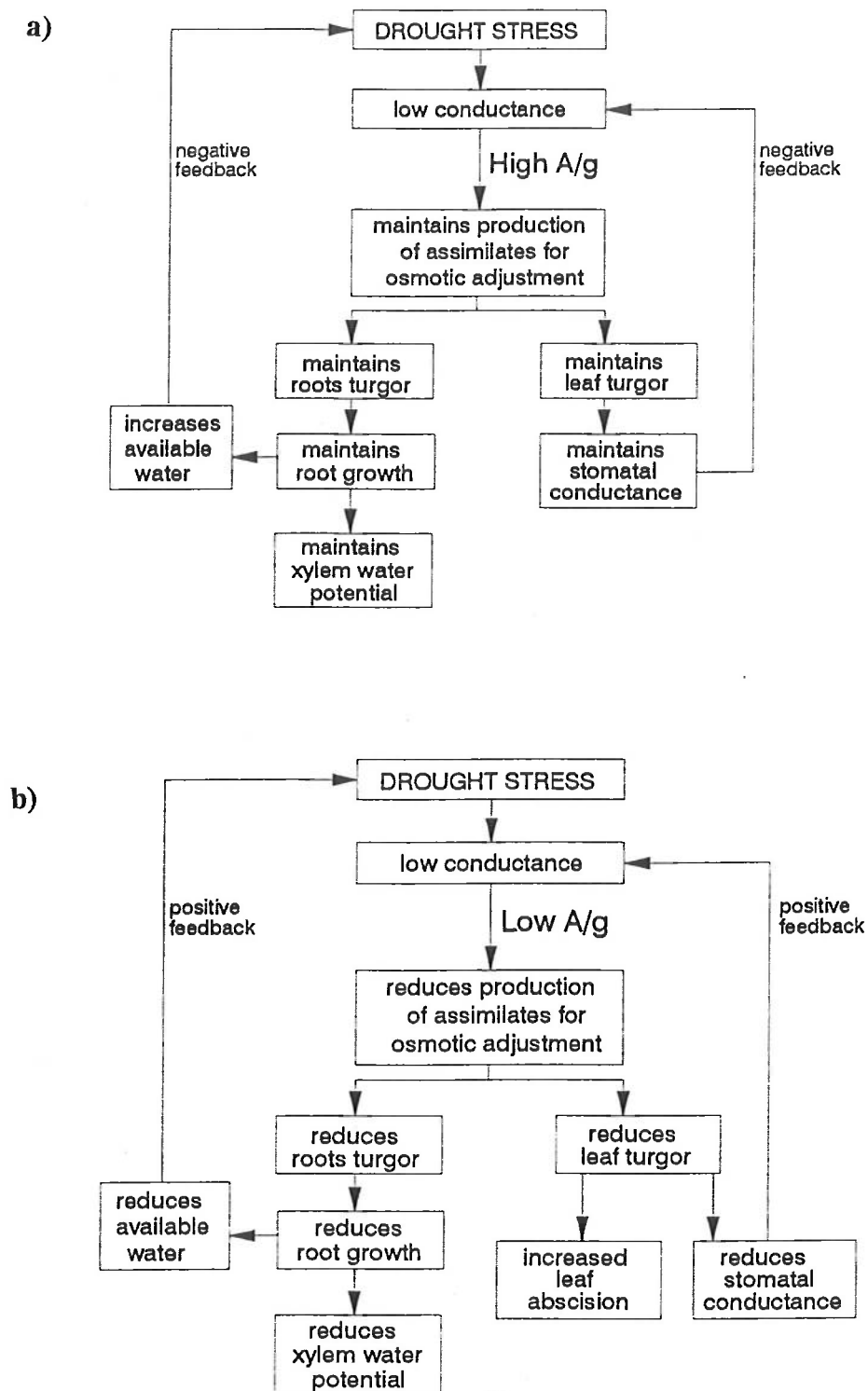


Figure 12.7.

Diagram showing the possible consequences of a) a high and b) a low ratio of assimilation rate (A) to stomatal conductance on the xylem water potentials and stomatal conductances of droughted plants (modified from Ludlow and Muchow, 1990).

CONCLUSIONS

Xylem water potentials were lowest in those droughted clones which gave the lowest annual yield of tea. Because there were no significant differences in the xylem water potentials of the fully irrigated clones, drought responses could be determined as effectively from direct measurement of ψ_x in the unirrigated plots as from the regression analysis proposed by Carr (1977b). Each of these techniques classified clone 1 as drought resistant, an attribute which was apparent over the whole year, but not from an analysis of yields over the dry season.

Stomatal conductances were also lowest in those droughted clones which gave the lowest annual yield. The use of a regression technique was not successful because stomatal conductances tended to converge as drought stress increased making clone x drought interactions difficult to establish.

There were no significant relationships between the stomatal conductance and the ψ_x of the fully irrigated clones. However in dry soil conditions, clones with low stomatal conductances also had low values of ψ_x . This indicates that the causal link between stomatal conductance and ψ_x was weak. Instead clonal differences in the available water due to deeper roots and in transpiration efficiency, indicated by the ratio A/g , could explain why some clones had high values of ψ_x and high values of stomatal conductance when droughted.

CHAPTER 13

SYNTHESIS: CLONAL SELECTION CRITERIA

In this chapter the results from the experimental work are synthesised in order to recommend selection criteria which can be used to identify high yielding and drought resistant clones. The annual yield of a clone under drought stress is determined both by its potential yield and its drought resistance (ie, the capacity to sustain that high yield when drought stressed). Those traits which are not necessarily linked to total yield, but are still important in the commercial production of tea are also considered.

HIGH POTENTIAL YIELD

The clonal traits determining potential yield were investigated using a framework (cf Figure 2.1) that related yield to dry matter production and the harvest index. Clone S15/10 gave a yield of made tea of 3760 kg ha⁻¹ in the third year of planting. This was over 1100 kg ha⁻¹ higher than each of the other five clones. Whilst clone S15/10 had the second highest rate of dry matter production, the high yield was primarily a result of increased partitioning of dry matter to leaves and harvested shoots (Table 13.1).

Table 13.1. Rankings of six fully irrigated clones in terms of their annual yield and corresponding physiological traits.

	Measurements where fully irrigated						
	Annual yield	Ground cover	Leaf photo-synthesis (Smith, 1991)	Dry matter production	Proportion of dry mass to leaves and shoots	Proportion of stem growth that is green	Proportion of shoots that are active
	Table 5.5	Table 6.1	Table 6.4	Table 7.3	Figure 8.3	Table 8.2	Table 10.6
Clone							
1	4	1	1	1	5	5	4
6/8	2	5	4	=3	2	3	3
SFS150	3	3	3	=3	4	4	5
S15/10	1	2	2	2	1	1	1
207	5	4	6	5	6	6	2
K35	6	6	5	6	3	2	6

The high yield of clone S15/10 could have been determined by the following techniques:

- 1: The high partitioning to leaves and harvested shoots can be measured relatively easily by the complete harvest of plants up to about a year after field planting. However after this age the excavation of roots becomes labour intensive.
2. A year after field planting a higher proportion of the stem of clone S15/10 was green than that of more woody clones such as clones 1 and 207. In practice this variable could probably be measured by the harvest of selected branches.
3. Clone S15/10 also had a higher proportion of active shoots on the bush than the other clones. These measurements should be taken over a period of a few months to minimise the effects of seasonal peaks and troughs in yield on the proportion of active shoots.

The greater partitioning of dry matter to leaves shown by S15/10 would also have helped the clone to establish a larger ground cover. Selection of clones with high photosynthetic rates at light saturation and reduced respiration losses should be long term objectives as the efficiency of dry matter production per unit of intercepted total solar radiation is lower for tea ($0.33\text{--}0.55 \text{ g MJ}^{-1}$) than many other crops.

DROUGHT RESISTANCE

Drought resistance was expressed as the relative yield response to drought. When drought resistance was determined using only the yields from the dry season, clone SFS150 was identified as drought resistant. When the yields for a full twelve months were considered then clone 1 also proved to be drought resistant. This variation was a result of the dry season including a period of relatively low temperatures, and the two clones showing different responses to temperature. This also highlights the need to consider carefully the time period studied.

The genotypic traits indicative of drought resistance can be separated into those that are evident from comparisons of well watered plants, and those that are only apparent when the clones are drought stressed (Table 13.2).

Table 13.2. Rankings of six clones in terms of their relative yield response to drought (drought resistance) and corresponding physiological traits. Also shown is the ranking of the clones in terms of yield in the unirrigated (I_0) treatment.

Clone	Relative yield response to drought	CO ₂ uptake per H ₂ O transpired (Smith, 1991a) ^a	Plant survival	Measurements where unirrigated			Yield
				Ground cover	Xylem water potential	Relative stomatal conduct- ance ^b	
	Table 5.5	Table 7.4	Table 5.4	Table 6.1	Table 12.7	Table 12.5	Table 5.5
Clone							
1	1	1	=1	1	2	2	2
6/8	4	=3	3	4	4	4	4
SFS150	2	2	=1	2	1	1	3
S15/10	5	5	5	3	3	3	1
207	6	6	6	5	5	6	6
K35	3	=3	4	6	6	5	5

^a: measurements taken with fully irrigated treatments

^b: ratio of stomatal conductance for each unirrigated clone relative to that when well watered.

In the well watered plants:

1. A high ratio of CO₂ fixed per unit H₂O transpired measured at a leaf level (Smith, 1991a) was positively correlated with the drought resistance of clones 1 and SFS150. This variable can be measured relatively quickly, but requires specialist equipment and maintenance.
2. A deeper distribution of thin roots could have been used to identify clone SFS150 as drought resistant, but not clone 1. This destructive technique, if used for plants more than a year after field planting, is also slow and labour intensive and therefore it is not recommended for the screening of large numbers of clones.

When drought stressed, the drought resistant clones showed the following traits in comparison to those that were drought susceptible:

1. less leaf abscission and therefore better maintenance of ground cover,
2. higher xylem water potentials,
3. higher stomatal conductances relative to those when well watered, and
4. greater resistance to *Phomopsis theae*.

The yield when droughted depends upon the potential yield and the drought resistance of the clone. In this experiment the high yield potential of clone S15/10 was sufficiently large that it enabled clone S15/10 to yield more than the other clones when drought stressed even though it was not drought resistant.

OTHER CONSIDERATIONS

Quality

It is essential that the selected clone is able to produce good quality tea. This was not specifically examined in this experiment, except by the composition of harvested shoots. In the future the quality of made tea produced by each of these clones in Southern Tanzania should be evaluated.

Base temperatures for shoot extension and development

Where there are seasonal changes in temperatures, clones with low, rather than high, base temperatures for shoot extension and development can produce a more even distribution of yield. This reduces fluctuations in labour, transport and factory requirements, and should also result in a more consistent quality of made tea. As already stated, differences between clones in temperature response can also affect the apparent response to drought when measured over individual seasons.

Number of shoots, shoot fresh mass and dry matter content

There was antagonism between the effects of shoot mass and shoot population density on yield. Therefore these two variables should be analysed together when used as selection criteria for yield. However, assuming that the shoots are of acceptable quality, clones with large shoots can enable greater labour productivity. This can be particularly important towards the end of a pruning cycle when shoot sizes are generally small.

The mean dry mass of harvested shoots varied from about 20.7% for clone SFS150 to 24.2% for clone 1. Such differences are ignored in clonal field trials where a constant conversion factor is used. Selection of clones with shoots that

have a high dry matter content could enable savings in transport and withering costs.

All these criteria are proposed from an evaluation of six contrasting clones between eight and thirty three months after planting in the field. They should be validated when the clones are mature.

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APPENDIX A**SOIL PROFILE AND ANALYSIS**

Location: Ngwazi Tea Research Unit (8°32'S, 35°10'E), below a mature stand of tea planted in 1971 adjacent to experiment N9.

Date: 16/6/90

Surveyor: R.W. Payton

Relief: Lake basin, gentle concave slope (<3%) about 200 m from lake shore.

Aspect: NW

Elevation: 1840 m

Parent material: Colluvium from deeply weathered granite and migmitites

Soil classification: Xanthic Ferralsol (FAO-UNESCO 1988)

Soil drainage class: Well drained

Land-use: mature tea planted in 1971

Profile description:

0 - 0.15 m Ah

Dark greyish brown (10YR 4/2) slightly moist, stoneless sandy clay; very weakly developed fine granular structure; very friable; very porous; low packing density; slightly sticky and moderately plastic when wet; abundant fine fibrous roots; gradual wavy boundary.

0.15-0.70 m AB

Brown (10YR 5/3) moist stoneless clay; massive breaking easily to a very fine granular structure; very porous; low packing density; moderately weak soil strength; very friable; slightly sticky and moderately plastic when wet; many fine fibrous roots; common fine and coarse woody roots; diffuse smooth boundary.

0.70-1.60 m Bw

Pale brown (10YR 6/3) moist clay; massive breaking easily to very fine granular structure; extremely porous; low packing density; very weak soil strength; very friable; slightly sticky and slightly plastic when wet; many fine fibrous roots; common fine and coarse woody roots.

1.60-2.00 m Bgl

Pale olive (5Y 6/3) with many prominent white (5Y 7/1) mottles; moist stoneless clay; moderately developed medium blocky structure; very porous; medium packing density; firm when moist; slightly sticky and moderately plastic when wet; common fine fibrous roots; few coarse woody roots; gradual smooth boundary.

2.00-2.60 m Bg2

Light grey (7.5GY 7/1) with common pale olive mottles; slightly moist stoneless clay; weakly developed coarse angular blocky structure; moderately porous; medium packing density; very firm when moist; common fine fibrous roots; clear smooth boundary.

3.20-5.00 m BC(g)

Plinthite horizon consisting of reddish yellow (7.5YR 6/6) slightly moist friable clay with a cellular network of very firm, brittle red (2.5YR 4/8) weakly cemented by iron oxides.

Comments: Soil is a friable clay classified as a Xanthic Ferralsol, i.e. dominated by activity clays with low effective cation exchange capacity ($< 16 \text{ mmol } 100 \text{ g}^{-1}$ of clay). The profile has been affected in the past by a fluctuating watertable at 1.60 m depth, but is now freely drained.

Soil samples collected:

Bulk samples: 0-0.15 m, 0.15-0.70 m, 0.70-1.60 m, 1.60-2.00 m, 2.00-2.60 m, 2.60-4.00 m.

Moisture tins: 1 x 0.15-0.20 m, 3 x 0.55-0.60 m, 3 x 1.80-1.85 m, 3 x 2.70-2.75 m

Soil analysis was completed following the methods cited in Weatherhead *et al.*, (1990)

Table A.1. Analytical data for soil samples collected at Ngwazi Tea Research Unit (8°32'S, 35°10'E),(R. Payton, personal communication)

Horizon	Ah	AB	Bw	Bg	1Bg	2BC(g
Depth (m)	0-0.15	0.15	0.70	1.60	2.00	2.60
		-0.70	-1.60	-2.00	-2.60	-4.00
Chemical analyses						
Soil pH (H ₂ O)	4.55	4.18	4.90	5.82	5.45	6.04
(KCl)	3.83	3.90	4.18	4.76	4.84	4.72
Organic carbon %w/w	1.46	0.76				
Exch. cations						
mmol 100 g ⁻¹ (0.1M BaCl ₂)						
Ca	1.17	0.82	1.09	0.79	0.77	0.81
Mg	0.30	0.21	0.40	0.21	0.19	0.20
K	0.55	0.15	0.01	0.02	0.06	0.01
Al (1M KCl)	1.66	1.31	0.71	0.15	0.10	0.15
Exch. acidity (1M KCl)						
mmol 100 g ⁻¹	2.06	1.61	0.91	0.25	0.15	0.30
CEC mmol 100 g ⁻¹						
ECBC (0.1M BaCl ₂)	4.08	2.79	2.41	1.27	1.17	1.32
CEC(NH ₄ OAc)	12.46		3.98			
Avail P ppm (Bray 1)	6.51	3.52	1.44	1.26	1.09	0.56
Dithionit ext. Fe (%)	0.20	0.26	0.21	0.12	0.10	1.69
Base saturation						
at soil pH (%)	49.5	42.3	62.2	80.3	87.2	77.3
Physical analyses						
Sand 600 µm-2 mm (%)	11	8	2	6	5	5
200-600 µm (%)	34	26	12	6	8	7
100-200 µm (%)	13	9	10	4	8	5
60-100 µm (%)	2	3	2	5	3	6
Silt 2-60 µm (%)	2	2	4	10	10	23
Clay <2 µm (%)	38	52	70	69	66	54
Bulk density g cm ⁻³	1.24	1.21	1.01			1.17
Total porosity (vol%)	51	53	61			55
Air capacity (vol%)	26	26	29			20
Available water						
10-1500 kPa (vol%)	11.78	12.18	11.08			9.29
mm m ⁻¹	118	122	111			93
Easily available water						
10-200 kPa (vol%)	12.04	12.37	8.97			9.29
mm m ⁻¹	120	104	90			93
Moisture retention						
5 kPa (vol%)	26.00	29.52	35.88			36.53
10 kPa (vol%)	24.71	26.83	32.54			34.88
40 kPa (vol%)	22.37	23.89	28.64			32.67
200 kPa (vol%)	12.67	16.48	21.08			27.36
1500 kPa (vol%)	12.93	14.65	21.46			25.59

APPENDIX B**SUMMARY OF METEOROLOGICAL OBSERVATIONS****Table B.1. Summary of meteorological observations at Ngwazi Tea Research Unit (8°32'S, 35°10'E, altitude 1840 m) in 1989.**

Month	Monthly totals		Monthly means of daily values					
	Rain (mm)	E _{pan} (mm)	Air temperature			Solar radiation (MJ m ⁻²)	Wind run (km)	VPD 15.00 h (kPa)
			Max (°C)	Min (°C)	Mean (°C)			
Jan	161	94	21.5	14.3	17.9	13.5	-	0.54
Feb	234	97	22.5	13.2	17.9	13.9	120	0.74
Mar	164	100	22.6	13.5	18.1	15.9	102	0.67
Apr	86	82	21.1	13.7	17.4	14.9	123	0.75
May	39	73	19.1	13.0	16.0	13.5	144	0.60
Jun	2	81	18.7	10.1	14.4	15.7	148	0.76
Jul	2	86	18.1	9.2	13.6	16.8	145	0.85
Aug	0	98	18.5	10.0	14.3	17.5	149	0.92
Sept	2	127	22.2	11.0	16.6	21.3	151	1.22
Oct	1	149	23.3	11.6	17.5	23.1	153	1.46
Nov	75	122	23.6	13.1	18.3	17.5	128	1.14
Dec	174	95	22.5	14.0	18.2	13.5	96	0.71
Total	941	1205						
Mean			21.1	12.1	16.7	16.4	130	0.86

Table B.2. Summary of meteorological observations at Ngwazi Tea Research Unit (8°32'S, 35°10'E, altitude 1840 m) in 1990.

Month	Monthly totals		Monthly means of daily values					
	Rain (mm)	E _{pan} (mm)	Air temperature			Solar radiation (MJ m ⁻²)	Wind run (km)	VPD 15.00 h (kPa)
			Max (°C)	Min (°C)	Mean (°C)			
Jan	242	96	23.0	12.9	17.9	14.3	100	0.85
Feb	195	87	23.0	14.3	18.7	13.4	125	0.78
Mar	260	99	22.7	13.7	18.2	16.8	98	0.76
Apr	139	92	22.4	14.0	18.2	16.2	102	0.73
May	15	75	20.2	12.5	16.3	14.7	129	0.78
Jun	5	82	19.6	10.5	15.0	17.2	132	1.00
Jul	2	87	19.0	8.3	13.6	17.0	133	1.02
Aug	0	89	18.9	10.0	14.5	16.9	156	0.94
Sept	0	114	20.8	11.1	15.9	20.4	168	1.09
Oct	0	145	23.4	11.5	17.5	22.2	155	1.50
Nov	63	127	23.6	12.7	18.2	20.0	146	1.11
Dec	103	106	23.8	13.1	18.4	16.7	108	0.95
Total	1024	1198						
Mean			21.7	12.1	16.7	17.1	129	0.96

Table B.3. Summary of meteorological observations at Ngwazi Tea Research Unit (8°32'S, 35°10'E, altitude 1840 m) in 1991.

Month	Monthly totals		Monthly means of daily values					
	Rain (mm)	E _{pan} (mm)	Air temperature			Solar radiation (MJ m ⁻²)	Wind run (km)	VPD 15.00 h (kPa)
			Max (°C)	Min (°C)	Mean (°C)			
Jan	276	85	23.1	13.7	18.4	13.6	93	0.64
Feb	160	105	24.1	13.3	18.7	16.5	113	1.06
Mar	132	95	23.9	14.0	18.9	15.5	105	0.75
Apr	86	87	21.7	13.5	17.6	14.4	119	0.64
May	10	77	20.3	12.8	16.6	14.3	141	0.73

APPENDIX C

CALCULATION OF STOMATAL CONDUCTANCE FROM MEASUREMENTS TAKEN WITH A DELTA-T AP3 POROMETER

Equipment and theory

The AP3 produced by Delta-T Devices Ltd, Burwell is a non-ventilated transient or dynamic porometer. It consists of a sensor head which is attached to a console unit containing a pump, a humidity control and a digital display. The sensor head contains a narrow polypropylene chamber (6 mm deep x cross sectional area of 56 mm²) which has a humidity sensor and thermistor at one end between an inlet for dry air and a exhaust outlet (cf Figure 11.11). At the other end when a leaf is held in position by a clamp, water vapour starts to move by diffusion towards the humidity sensor. Once the humidity sensor detects a predetermined humidity, the transit time (dt) for the relative humidity to increase by another 5% points is recorded. When this is reached the temperature of the porometer cup and the temperature of the leaf, measured by a thermistor on the upper side of the clamp, are recorded and dry air is pumped into the chamber until the humidity is reduced by at least 10%. The process is then repeated.

Calibration procedure

Although Monteith *et al.* (1988) have described the theoretical basis of relating the value of dt to leaf conductance, in practice it is difficult to quantify the effects of the absorption of water by the sides of the chamber and the time response of the humidity sensor. It is therefore necessary to calibrate measurements of dt against a series 'known' resistances on a polypropylene calibrate plate which is backed by wet blotting paper.

The values recommended by the manufacturers for the resistances of these holes have recently been changed (Chris Nichol, personal communication, 1991). All the resistances measured at Ngwazi were based on the currently recommended values (cf Table 11.2), which were originally calculated for a temperature of 20°C and sea level atmospheric pressure P_o (100 kPa). At Ngwazi, where the altitude is 1800 m, the actual atmospheric pressure (P) was assumed to be 81.6 kPa (Doorenbos, 1976). To correct for the effect of this lower pressure the resistances in Table 11.2 ($r_{(P_o)}$) were corrected using Equation C.1.

$$r(P) = r(P_0) P/P_0 \quad \text{C.1}$$

A correction was also made to the recorded transit time (dt) when the cup temperature (T_c ; °C) was not 20°C. This correction is given by Equation C.2 (Monteith *et al.*, 1988)

$$dt_{(T=20^\circ\text{C})} = dt_{(T \neq 20^\circ\text{C})} [(T_c + 273)/293]^{1.7} \quad \text{C.2}$$

The full calibration procedure used is summarised in Figure C.1. The operating humidity was set first at the ambient humidity. A stable value of dt , the cup temperature (T_c) and the difference between the temperature of the cup and the calibration plate (dT) were recorded for each position on the calibration plate.

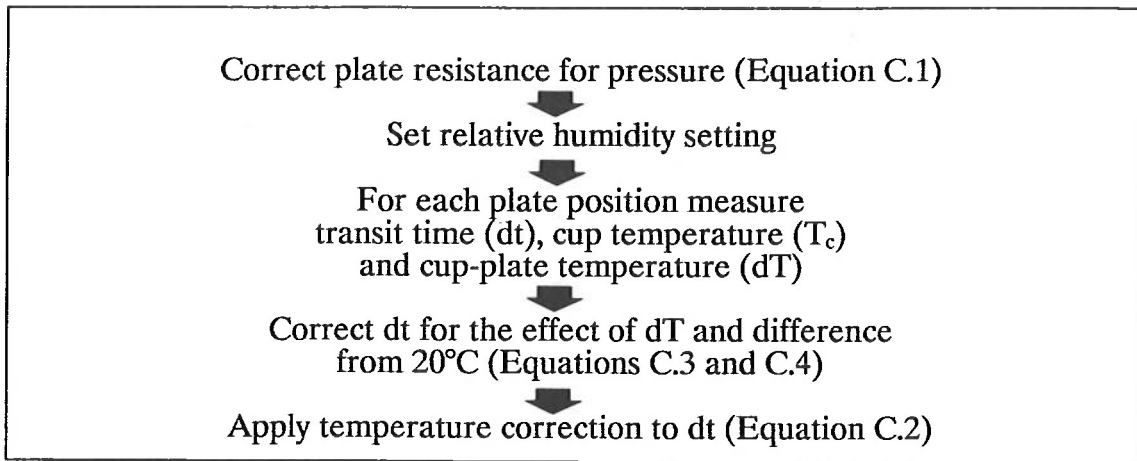


Figure C.1. Procedure for recording and correcting calibration transit times

When the temperature (T_p) of the calibration plate was higher than that of the cup (T_c) the increased vapour pressure in the plate reduced the transit time for each of the specified resistances. This effect was corrected by using Equation C.3 (Monteith *et al.*, 1988), where χ_c is the saturation vapour concentration at cup temperature.

$$dt_{(dT=0)} = dt_{(dT \neq 0)} \cdot \frac{(1 - 1/\chi_c \cdot d\chi_c / (T_c - T_p) \cdot (T_c - T_p))}{(1-h)} \quad \text{C.3}$$

The transit time was also corrected for the departure of the cup temperature from 20°C as recommended by Monteith *et al.* (1988) using Equation C.4.

$$dt_{(20^{\circ}\text{C})} = \frac{dt_{(T)} \cdot 0.037 + 1/17.14}{0.037 + 1/\chi_c} \quad \text{C.4}$$

Lastly the temperature correction (Equation C.2) was applied to the transit time.

Measurement of conductance

After completing the calibration the porometer was used to measure stomatal conductance using the procedure outlined in Figure C.2. When the sensor head was placed on the leaf the digital display was monitored until a stable value of dt was obtained. The stable value of dt was then recorded with the corresponding cup temperature and the difference between the cup and the leaf temperature.

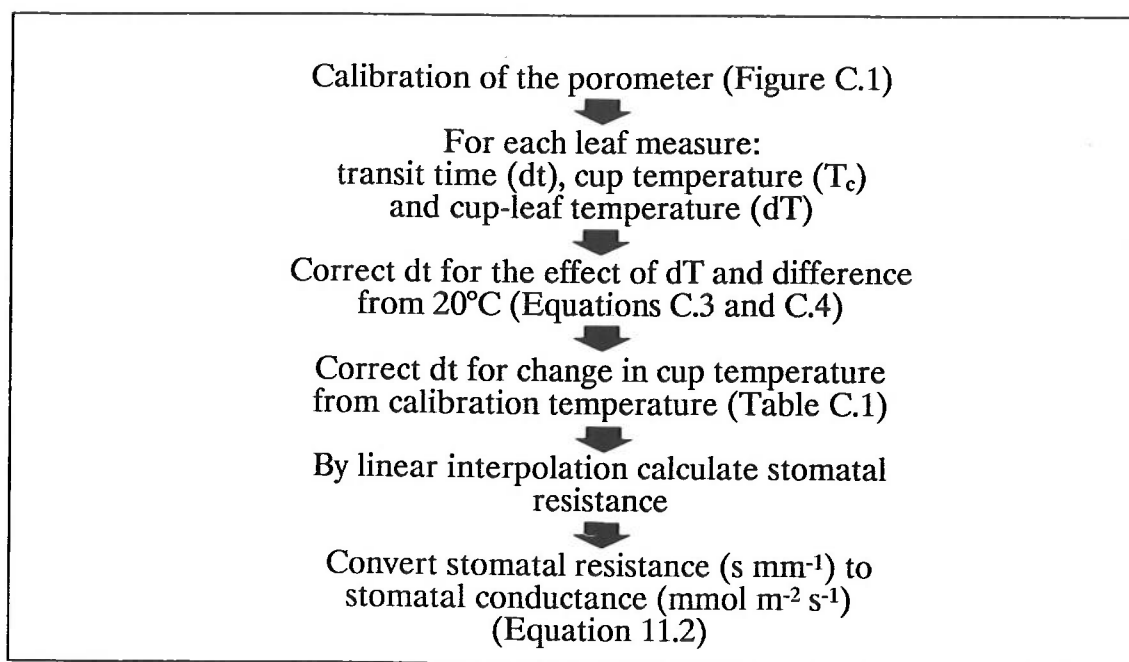


Figure C.2. Procedure for measuring stomatal conductance

In order to calculate stomatal conductance the measured value of dt was first corrected using Equations C.3 and C.4. This corrected transit time was then compared with the corrected calibration transit times obtained under the similar

humidity and temperature conditions to estimate the corresponding stomatal resistance. The process of interpolating the results was computerised using a spreadsheet program.

However it practice the operating temperature sometimes changed rapidly from the temperature at calibration, especially in the early morning or late afternoon. The effects of temperature on the corrected values of dt measured using the calibration plates relative to the corresponding values measured at 20°C are shown in Figure C.3. When the cup temperature was above 20°C, the correction factors described in Figure C.1 were generally successful. However when the cup temperature fell below 20°C the temperature corrections were not as effective. Because temperature changes between 10 and 20°C occurred rapidly at the beginning and the end of the day it was not feasible to carry out a calibration for each new temperature. Therefore empirical correction factors were developed using the values shown in Figure C.3 to correct the values of dt when the cup temperature at measurement was different from the temperature of the cup at calibration. These corrections were only needed when working at humidities of 50, 60 or 70% and are presented in Table C.1.

Table C.1. Empirical correction equations for changes in the cup temperature (T_c ; °C) from the corresponding temperature of the cup at calibration (T_{calib} ; °C) for three preselected levels of relative humidity.

Relative humidity (%)	Temperature range (°C)	Correction equation
50%	13-29	$dt_{cor} = dt \cdot (e^{13.3/T_{calib}}) / (e^{13.3/T_c})$
60%	12-22	$dt_{cor} = dt \cdot (e^{23.6/T_{calib}}) / (e^{23.6/T_c})$
70%	10-20	$dt_{cor} = dt \cdot (e^{35.8/T_{calib}}) / (e^{35.8/T_c})$

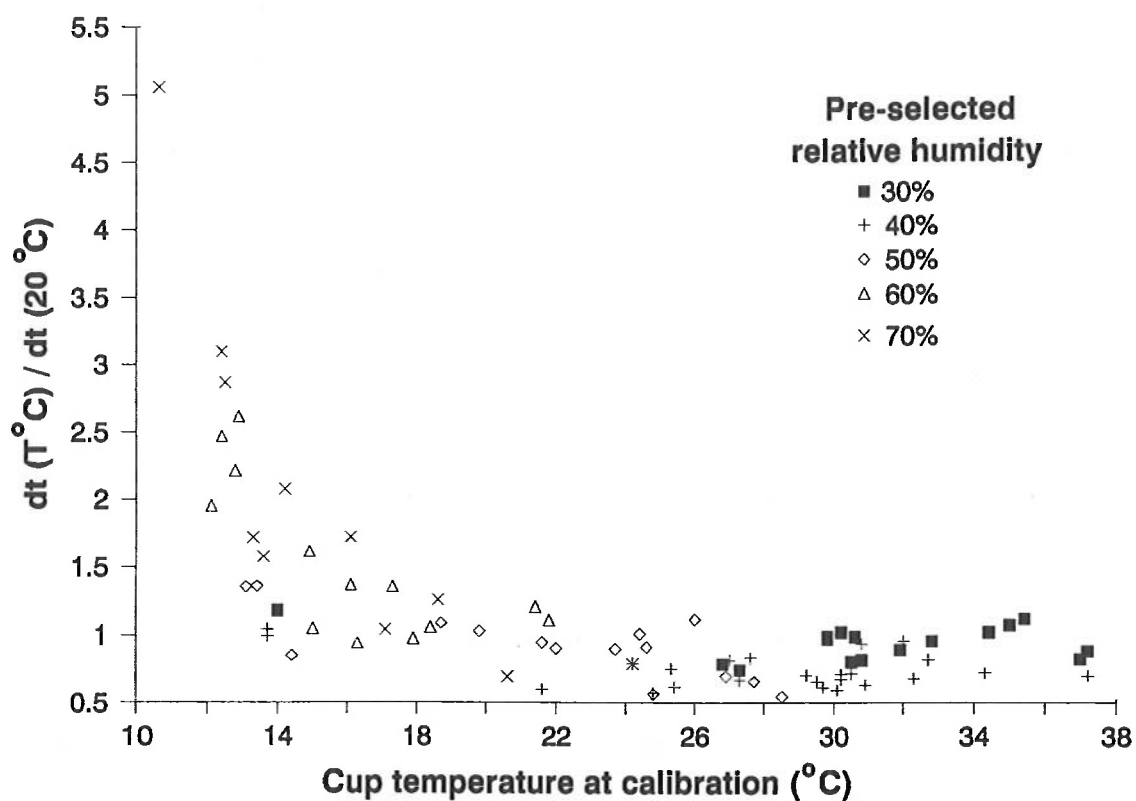


Figure C.3. Effects of cup temperature at calibration on the ratio of the corrected transit time (dt at $T^{\circ}\text{C}$) relative to the transit time measured at 20°C .