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RESPONSES OF YOUNG TEA (*CAMELLIA SINENSIS*) CLONES TO DROUGHT AND TEMPERATURE. 3. SHOOT EXTENSION AND DEVELOPMENT

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SUMMARY

The effects of temperature (14–19°C) and mean soil water deficit (up to 90 mm) on the shoot extension and development rates of six contrasting tea clones in southern Tanzania were studied 10–28 months after field-planting. An exponential function with two constants, an initial shoot length and a relative extension rate (r), provided a reliable description of the length of axillary shoots for the period from the release of apical dominance to the unfurling of three true leaves. Apparent base temperatures (T_{be}) and thermal extension rates (ρ_e), derived from linear relations between r and the mean air temperature, were able to explain 85–92% of the seasonal variation in r for each fully irrigated clone. The mean soil water deficit was used to explain 80% of the remaining variation in r across three drought treatments.

Clonal differences in the values of T_{be} (8.9–11.3°C) and ρ_e ($7.8–11.8 \times 10^{-3}$ mm mm^{-1} (°Cd)$^{-1}$) can be used to explain differences in the seasonal distributions of yield. The apparent base temperatures for development (T_{bd}) were consistently 1.7–3.4°C below those for extension; an observation supported by the effects of temperature on the length of shoot internodes. The results are compared with those obtained in other studies and are discussed in terms of clonal selection, the choice of harvest intervals and the prediction of green-leaf quality.

INTRODUCTION

Tea (*Camellia sinensis*) is a perennial evergreen shrub, from which tender shoots are normally harvested at intervals of one to three weeks throughout the year. Near the Equator, where there are only small seasonal changes in temperature, the crop distribution can be relatively smooth from month to month (Carr and Stephens, 1992), but at high latitudes, it can be very uneven as low temperatures and/or drought restrict shoot extension for part of the year (Tanton, 1982a; Carr *et al.*, 1987; Stephens and Carr, 1993). In addition the synchronized growth by shoots of varying ages, caused by rising temperatures or the removal of drought stress, can cause large peaks and troughs in yield during the main growing season (Fordham and Palmer-Jones, 1977). An understanding of how shoot extension and development are affected by the environment would allow growers to schedule their labour, transport and processing resources effectively. An ability to differentiate

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between tea clones in terms of the responses of shoot extension and development to temperature and drought would also provide objective criteria by which to select the most appropriate clone for a given environment.

Exponential (Tanton, 1982a; Squire *et al.*, 1993), logistic (Bond, 1945) and Gompertz (Smith *et al.*, 1990) functions have all been used to describe the length (L, mm) of a shoot from the time (t, measured in days) that it is released from apical dominance to when it reaches a harvestable size. The exponential model (Equation 1) uses only two variables: an initial shoot length (L_o, mm) and a constant relative extension rate (r, mm mm^{-1} d^{-1}).

$$L = L_o\, e^{rt} \tag{1}$$

The logistic (Equation 2) and Gompertz (Equation 3) models use three variables: a factor (b) related to the relative extension rate, the time interval (c) from the date of release from apical dominance to the date when the maximum shoot extension rate is reached, and the final shoot length (L_f, mm).

$$L = L_f/(1 + e^{-b(t-c)}) \tag{2}$$

$$L = L_f\, e^{-e^{-b(t-c)}} \tag{3}$$

Tanton (1982a) reported that the relative extension rates of the shoots of field-grown Clone SFS204 in Malawi were linearly related to the weekly mean temperature above a base temperature of 12.8°C. Subsequently it has been reported that the base temperature for extension (T_{be}) ranges from 10.0°C for Clone 6/8 in southern Tanzania (Stephens and Carr, 1993) to 14.9°C for the same clone in Malawi (Cannell *et al.*, 1990). Differences have also been reported in the change of r with incremental increases in the mean temperature (termed the thermal extension rate, ρ_e), with values ranging from 9 to 23 × 10^{-3} mm mm^{-1} (°Cd)$^{-1}$ (Tanton, 1982a; Smith *et al.*, 1993).

Shoot development can be quantified in terms of the number and type of unfurled leaves. When an axillary bud is released from apical dominance, the shoot starts to extend and the two 'scale' leaves which surround the bud eventually fall away. The apex then unfurls a small unserrated 'fish' leaf and a series of 'true' leaves until the apex becomes dormant (Bond, 1945). A shoot is often considered ready for harvest when it unfurls the third true leaf, and so the time from the release of apical dominance to the unfurling of this leaf has been termed the shoot replacement cycle (SRC, d) (Clowes, 1986; Stephens and Carr, 1990). The inverse of the SRC is a development rate, which can be related to temperature by estimating a base temperature for development (T_{bd}, °C) and a thermal development rate (ρ_d, (°Cd)$^{-1}$) (Squire *et al.*, 1993).

In accompanying papers, Burgess and Carr (1996a) have reported how the ranking of contrasting clones in terms of yield, dry matter production and partitioning varied during the year in Southern Tanzania. For example, the yields from fully irrigated Clone SFS150 were greater than those from Clone 1 during the cool-dry periods but the ranking was reversed during the main warm-wet growing season. In this paper, the shoot extension and development rates of the six clones are examined with respect to temperature and drought, and the implications of the results are discussed in terms of clonal selection, the choice of harvest intervals and the prediction of green-leaf quality.

METHODOLOGY

Site and climate

Measurements were made at the Ngwazi Tea Research Unit (lat 8°32′S, long 35°10′E, altitude 1840 m) in the Mufindi district of southern Tanzania, where the climate can be divided into three main seasons on the basis of rainfall and temperature. Over 95% of the 800–1100 mm annual rainfall occurs between the end of November and May, when the monthly mean air temperature (T_{mean}) is 16 to 19°C. The dry season can be divided into two: being cool (13–16°C) from June to August and warm (16–19°C) from September to November. The mid-afternoon vapour pressure deficit (VPD) reaches a monthly maximum of 1.5 kPa in October, which is below the level that has been reported to affect shoot extension (Tanton, 1982b). A full site description is provided by Burgess and Carr (1996a).

Experimental design and treatments

Six clones were planted at a spacing of 1.2 × 0.8 m in August 1988 within the line-source irrigation experiment described by Burgess and Carr (1996a). The clones were chosen because of their scientific and/or commercial importance in eastern Africa. They comprised small-leaved Clones 1 and 207, intermediate-size leaf Clone 6/8 and large-leaved Clones SFS150, S15/10 and K35. The clones varied in their relative yields during the cool-dry and the warm-wet seasons, and in their countries of selection (Table 1).

The experiment comprised four replicate blocks, two either side of a central

Table 1. *Leaf size, yields of dry tea (kg ha^{-1}) during the cool-dry (June to August 1990) and warm-wet seasons (December 1990 to May 1991) from fully irrigated plants during the third year after planting, together with the site of original selection (latitude and approximate altitude above sea level) for each of six clones*

		Yield			
Clone	Leaf size	cool-dry season	warm-wet season	Site of original selection	
1	small	170	1840	Tanzania	(8°33′S, 1900 m)
207	small	220	1860	Tanzania	(8°33′S, 1900 m)
6/8	intermediate	220	1540	Kenya	(0°, 1900 m)
SFS150	large	330	1610	Malawi	(16°5′S, 650 m)
S15/10	large	280	2510	Kenya	(0°22′S, 2000 m)
K35	large	180	1530	Kenya	(0°22′S, 2000 m)
S.e.d. (n = 4)		26	137		

irrigation lateral, containing six 24 × 6.4 m plots (running perpendicular to the lateral) which were randomly allocated to each clone. The clonal plots were subdivided into six contiguous drought treatments labelled from I_5 (full irrigation), closest to the central lateral, to I_0 (most drought stressed) at the extreme sides of the experiment. From planting until the start of the rains in November 1988, until early October 1989 and late July 1990, the plants were irrigated uniformly before the potential soil water deficit reached 60 mm. Differential drought treatments were imposed during seven weeks towards the end of the 1989 dry season (9 October to 27 November) and for sixteen weeks (27 July to 18 November) in 1990. The mean maximum soil water deficit, calculated using a validated soil water balance model (Burgess and Carr, 1996a), within the unirrigated (I_0), partially irrigated (I_2) and fully irrigated (I_5) sub-plots in 1989 were 84, 70 and 58 mm respectively. The corresponding deficits in 1990 were 117, 104 and 46 mm.

Between April and October 1989 the young branches were 'pegged' horizontally to encourage the rapid establishment of full ground cover and at all times fertilizer rates were sufficiently high to prevent nutrient deficiency. The first routine harvest of shoots took place in early December 1989, and subsequently at intervals ranging from 13 days during the warmest months to 24 days during the coolest period.

Measurements

Shoot extension and development were studied on selected generations of axillary buds that were released from apical dominance on the same day by plucking apical shoots with two unfurled leaves. The lengths (± 0.1 mm) of those buds, in the axils of the uppermost leaves, were measured using Vernier callipers at two-week intervals until the scale leaves fell away. Afterwards, the length (± 1 mm) from the axil to the base of the exposed apex of each growing shoot, and the number and type of unfurled leaves, were recorded at weekly intervals until four true leaves had unfurled.

For the first three generations, selected between May and July 1989, two shoots were monitored on each of three bushes within each of the four replicate blocks of each clone making a total of 144 shoots per generation. In order to analyse the effects of drought, three shoots were monitored on each of two bushes in each of the four fully irrigated (I_5), partially irrigated (I_2) and unirrigated (I_0) sub-plots of each clone between August 1989 and October 1990, a total of 14 generations with 432 shoots per generation.

The shoot is initially concealed by the scale leaves and so a relationship was derived in order that the length of the enclosed shoot could be calculated from the bud length. The length of ten buds (range: 5–44 mm) and enclosed shoots (range: 1–15 mm) were measured on three dates during 1990 within one fully irrigated (I_5) and one unirrigated (I_0) sub-plot of each clone. The best fit linear relation between bud and shoot length ($n = 360$, $R^2 = 73\%$), constrained to pass through the origin, showed that the ratio of shoot length to bud length was greater

($p \leqslant 0.05$) for the small-leaved Clones 1 and 207 (0.33–0.34) than for the large-leaved Clone K35 (0.29); the ratios for Clones 6/8, SFS150 and S15/10 (0.30–0.32) were intermediate. The effects of drought on this ratio were negligible and therefore ignored.

Selection of a shoot extension model

The choice of the most appropriate equation to model shoot extension was based on an analysis of the growth of six shoots released from apical dominance during the warm-dry (September 1989), the warm-wet (January 1990) and the cool-dry (June 1990) seasons from each of the six fully irrigated clones. The exponential model using only two parameters explained 94–95% of the variation in shoot length with time in each of the seasons. Although the inclusion of a third parameter with the logistic or Gompertz model increased the proportion of explained variation to 96–99%, the estimates of the final length (L_f) were inaccurate because few measurements were made after the period of maximum extension rate. This problem was most acute towards the end of the cool season when temperatures were rising. By contrast the values of L_o and r calculated with the exponential model were consistently realistic and they appeared to be normally distributed within each treatment. For these reasons the exponential model was chosen to quantify the clonal differences in shoot extension responses to temperature and drought.

Values for L_o, r and the development rate (1/SRC) were calculated for each shoot using the data collected between the release from apical dominance and the unfurling of the third true leaf. The mean internode length (i, mm) of each shoot was determined from the slope of the best fit linear relation between shoot length and the number of expanded leaves (above the fish leaf). For each fully irrigated clone, the mean values for r, 1/SRC and i from each generation were then used to establish the best-fit linear relation with the corresponding mean air temperature (T_{mean}). The values of T_{mean}, derived from daily maximum and minimum temperatures recorded in a Stevenson screen sited about 800 m from the experiment, were calculated from the date of selection to the mean day when the shoots in that treatment had unfurled three true leaves. The x-axis intercepts of the linear relations were then used to establish the apparent base temperature for the relative extension rate (T_{be}), development rate (T_{bd}) and shoot length per internode (T_{bi}, °C), whilst the slopes corresponded to the thermal extension rate (ρ_e), the thermal development rate (ρ_d) and the thermal response of internode length (ρ_i, mm $°C^{-1}$).

The effects of drought were first examined by comparing the values of L_o, r and 1/SRC for shoots in the unirrigated (I_0) and partially irrigated (I_2) treatments with those in the fully irrigated (I_5) sub-plots. Then, to remove any confounding effect of temperature, the mean actual values of r and 1/SRC within each drought treatment were expressed as a ratio of those predicted using the temperature relations established for the fully irrigated tea. These ratios were then related to the corresponding mean soil water deficit (SWD_{mean}, mm) determined for the period from the date of selection to the unfurling of the third true leaf.

RESULTS

Initial shoot length

Although the initial lengths are often ignored in descriptions of shoot extension, they are critical because the consistency of their determination can highlight the reliability, or otherwise, of the model. Reassuringly, the mean value for L_o for fully irrigated tea, derived using the exponential equation, was only 0.15 mm greater than the mean measured value; a difference which is similar to the precision of the initial measurement (± 0.1 mm) (Table 2). The fitted and measured values of L_o also ranked the clones in a similar order, with the initial lengths for Clones 1, 207 and S15/10 being greater ($p \leqslant 0.001$) than those for Clone K35. Although the measured and the fitted data showed no consistent seasonal variation during April, at the end of the warm-wet season, the mean fitted value of 1.3 mm was particularly high. This increase, which was not apparent in the measured values, was probably an artefact caused by assuming a constant r over a period when T_{mean} was declining. Although this effect could be minimized by examining extension within a shorter time period, the resultant value for r would only be appropriate for part of the shoot replacement cycle.

Relative extension rate

The relative extension rates showed distinct seasonal changes with maxima of $60–94 \times 10^{-3}$ mm mm^{-1} d^{-1} for those shoots which were released from apical dominance during the warm weather from October 1989 to March 1990, and minima ($29–49 \times 10^{-3}$ mm mm^{-1} d^{-1}) for shoots selected at the beginning of the cool season in May and June 1990. The relationship between r and season varied

Table 2. *The measured and fitted (using an exponential equation) initial lengths (mm) of shoots at the time of release from apical dominance for each of six fully irrigated clones between August 1989 and October 1990*

	Initial shoot length	
Clone	Measured	Fitted
1	1.06	0.98
207	1.05	0.83
S15/10	1.02	0.89
SFS150	0.86	0.65
6/8	0.85	0.72
K35	0.75	0.60
Mean	0.93	0.78
S.e.d. (n = 14)	0.04	0.09

with clone: from October 1989 to March 1990 the shoots of Clone 1 (80–90 × 10^{-3} mm mm^{-1} d^{-1}) had consistently higher values of r than those of Clone 6/8 (63–74 × 10^{-3} mm mm^{-1} d^{-1}), but shoots of Clone 1 released from apical dominance in May and June (29–40 × 10^{-3} mm mm^{-1} d^{-1}) had extension rates that were lower than or similar to those for Clone 6/8 (38 × 10^{-3} mm mm^{-1} d^{-1}) (Fig. 1a). Between 85 and 92% of this seasonal variation in r, for the fully irrigated clones, could be explained by straight line relations with the corresponding mean air temperature ranging from 14 to 19°C (Table 3; Fig. 2).

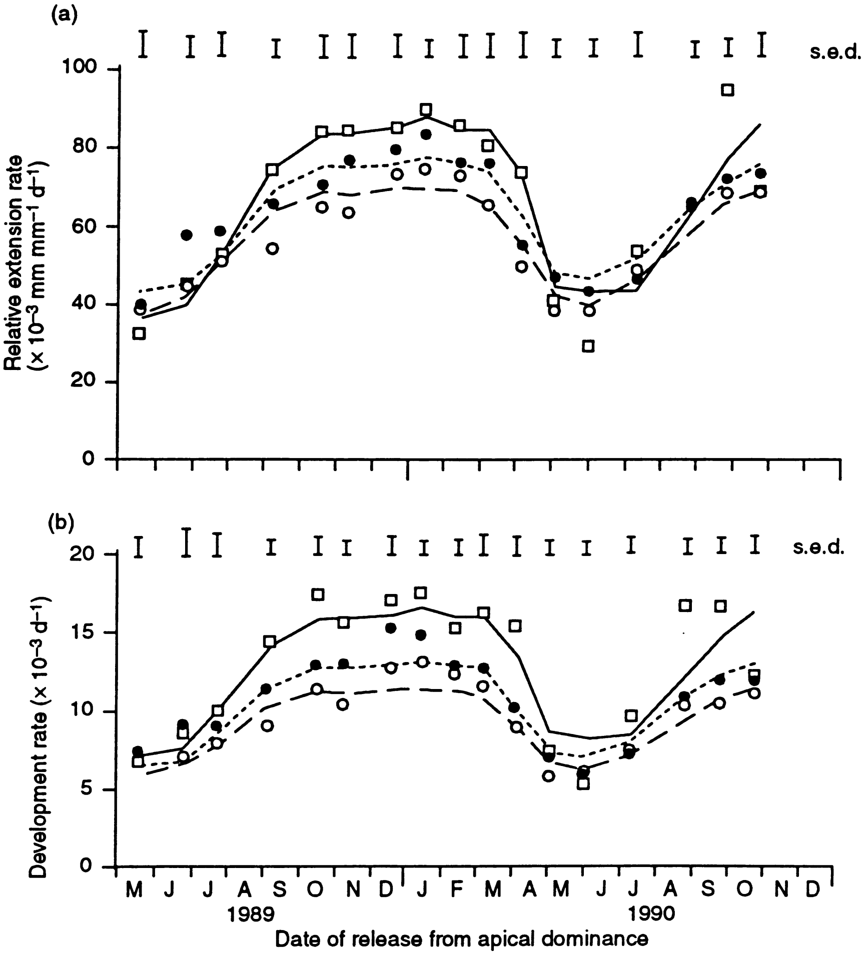

Fig. 1. Seasonal changes in (a) the mean relative extension rate and (b) the mean development rate (from the time of release from apical dominance to the unfurling of the third true leaf) for shoots released from apical dominance between May 1989 and October 1990 for fully irrigated Clone 1 (□——□) Clone SFS150 (●·····●) and Clone 6/8 (○– – –○) (n = 24). Lines show the estimated rates derived from measurements of air temperature.

Table 3. *Shoot extension: the slope* (ρ_e, 10^{-3} *mm mm*$^{-1}$ *(°Cd)*$^{-1}$)*, the y-axis intercept* (*a*, × 10^{-3} *mm mm*$^{-1}$ *d*$^{-1}$)*, correlation coefficient* (R^2*, %*)*, and corresponding base temperature* (T_{be}*, °C*) *with 95% confidence intervals, as derived from the best fit linear relation between the relative shoot extension rate (r) and the corresponding mean air temperature* (T_{mean}*, °C*) *for each of six fully irrigated clones. The equations are of the form:* $r = \rho_e T_{mean} + a$ *(n = 17). The last column reports an equivalent base temperature* (T_{be}'*, °C*) *after allowing for diurnal changes in air temperature*

Clone	Slope ρ_e	Y-axis intercept a	R^2	Base temperature T_{be}	Base temperature T_{be}'
1	11.8 ± 1.2	−132 ± 21	85	11.1 (9.4–12.1)	12.1
K35	11.1 ± 0.9	−126 ± 15	92	11.3 (10.2–12.1)	12.5
207	10.9 ± 0.8	−112 ± 14	92	10.3 (9.1–11.1)	10.8
S15/10	8.6 ± 0.9	−87 ± 15	85	10.1 (8.2–11.3)	10.6
6/8	7.8 ± 0.7	−74 ± 12	87	9.5 (7.5–10.7)	9.7
SFS150	8.0 ± 0.8	−70 ± 14	86	8.9 (6.7–10.2)	8.9

Clones 1 and K35 had the highest base temperatures (11.1–11.3°C) and thermal extension rates (11.1–11.8 × 10^{-3} mm mm^{-1} (°Cd)$^{-1}$). By comparison Clones 6/8 and SFS150 had the lowest values: 8.9–9.5°C and 7.8–8.0 × 10^{-3} mm mm^{-1} (°Cd)$^{-1}$ respectively.

The air temperature at night often fell below the base temperatures indicated in Table 3 and so a relation based on mean daily air temperature is likely to

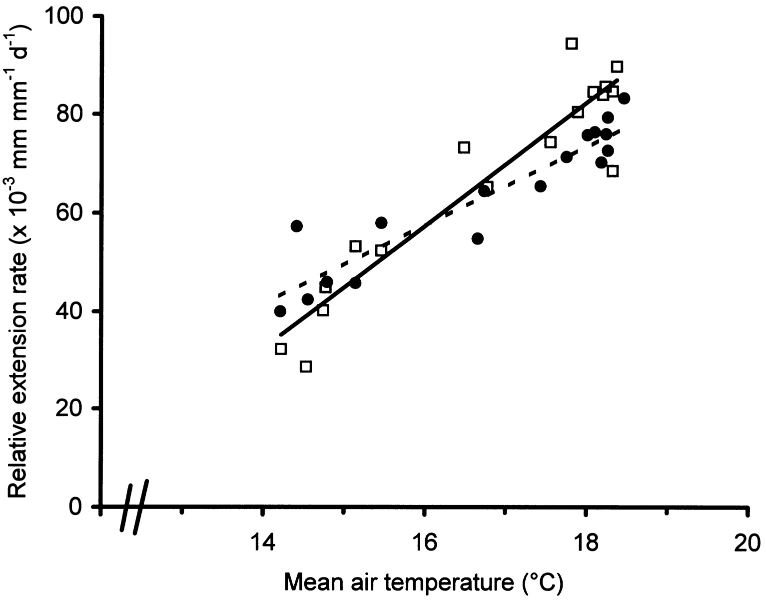

Fig. 2. Effects of mean air temperature (T_{mean}) on the relative extension rates (r) of shoots of fully irrigated Clone 1 (□——□) (r = 0.0118 (T_{mean} − 11.1); R^2 = 85%), and Clone SFS150 (●·····●) (r = 0.0080 (T_{mean} −8.9); R^2 = 86%).

underestimate the true base temperature for extension. An alternative estimate of T_{be} can be obtained 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 is chosen, the best fit linear relationship between the relative extension rate and the mean daily thermal time will pass through the origin. This analysis, whilst indicating a consistent value for T_{be} of 8.9°C for Clone SFS150, increased the values for Clones 1 and K35 by about 1°C to 12.1 and 12.5°C respectively.

Shoot development

The development rates of shoots from the fully irrigated clones showed similar seasonal changes to those for shoot extension, being highest for those released from apical dominance during the warm weather from October to March. At this time values ranged from $14–16 \times 10^{-3}$ d^{-1} for Clone 6/8 to $18–20 \times 10^{-3}$ d^{-1} for Clone 1, corresponding to shoot replacement cycles of 62–71 and 50–55 days respectively (Fig. 1b). Shoots released from apical dominance in June at the beginning of the cool season had the slowest development rates ($9–10 \times 10^{-3}$ d^{-1}), corresponding to shoot replacement cycles of 100–110 days.

Between 75 and 89% of the seasonal variation in the shoot development rate of each fully irrigated clone could be explained by a straight line relationship with the mean air temperature (Table 4). The base temperatures for development showed similar clonal rankings to those for extension, being lowest for Clones 6/8 and SFS150 (6.1 and 7.0°C respectively) and highest for Clones 1 and K35 (8.7 and 9.2°C). Similarly the thermal development rates (ρ_d) were lower for Clones

Table 4. *Shoot development: the slope (ρ_d, 10^{-3} $(°Cd)^{-1}$), the y-axis intercept (a, 10^{-3} d^{-1}), correlation coefficient (R^2, %), and corresponding base temperature (T_{bd}, °C), with 95% confidence intervals, derived from the best fit linear relation between the shoot development rate (1/SRC, d^{-1}) and the corresponding mean air temperature (T_{mean}, °C) for each of six fully irrigated clones. The relationships are of the form: $1/SRC = \rho_d\ T_{mean} + a$ ($n = 17$). The last column reports an equivalent base temperature (T_{bd}', °C) after allowing for diurnal changes in air temperature*

Clone	Slope ρ_d	Y-axis intercept a	R^2	Base temperature T_{bd}		Base temperature T_{bd}'
1	1.9 ± 0.3	-17 ± 5	75	8.7	(5.1–10.6)	8.8
K35	1.7 ± 0.1	-15 ± 2	89	9.2	(7.4–10.5)	9.4
207	1.9 ± 0.2	-17 ± 4	81	8.6	(5.7–10.4)	8.7
15/10	1.4 ± 0.2	-11 ± 3	81	7.8	(4.7–9.7)	7.9
6/8	1.2 ± 0.1	-7 ± 2	84	6.1	(2.9–8.2)	6.2
SFS150	1.4 ± 0.1	-10 ± 2	86	7.0	(4.4–8.7)	7.1

6/8 and SFS150 ($1.2–1.4 \times 10^{-3}$ (°Cd)$^{-1}$) than for Clones 1 and K35 ($1.7–1.9 \times 10^{-3}$ (°Cd)$^{-1}$).

For each clone the apparent base temperature for shoot development (range: 6.1–9.2°C) was 1.7–3.4°C lower than that for extension (range: 8.9–11.3°C). The values of T_{bd} were below or close to the monthly minimum air temperature of 8°C and so the base temperatures, estimated using daily mean temperatures, were similar to those calculated with an allowance for diurnal changes.

Internode length

The seasonal changes in the mean length of the internode, from the fish leaf to the third true leaf, were similar to those for relative extension rates, being greatest (18–29 mm) for shoots released from apical dominance during the warm weather and least (8–16 mm) for those selected in June when it was cool. Although there were no differences between clones in the internode length of those shoots released from apical dominance when it was warm (between December 1989 and March 1990), shoots of Clone 1 had shorter internodes (8–14 mm) than those of other clones (10–25 mm) during the cool season (from June to August 1990).

Between 61 and 84% of the seasonal changes in internode length for each fully irrigated clone could be explained by a straight line relation with the corresponding mean air temperature (Table 5). The base temperature (T_{bi}) and the incremental increase in length per °C rise in temperature (ρ_i) were lowest for Clone SFS150 (8.0°C and 2.2 mm °C^{-1}) and highest for Clone 1 (12.8°C and 4.1 mm °C^{-1}). The air temperature at night often fell below the base temperatures reported for Clones 1, 207 and K35, and so the true base temperatures for internode length are increased by up to 3°C when allowance is made for diurnal changes.

Table 5. *Internode length: the slope (ρ_i, mm °C^{-1}), the y-axis intercept (a, mm), correlation coefficient (R^2, %), and corresponding base temperature (T_{bi}, °C) with 95% confidence intervals, derived from the best fit linear relation between the mean internode length (between the fish leaf and a third true leaf) (i, mm) and the mean air temperature (T_{mean}, °C) for each of six fully irrigated clones. The relationships are of the form: $i = \rho_i\ T_{mean} + a$ ($n = 17$). The last column reports an equivalent base temperature (T_{bi}', °C) after allowing for diurnal changes in air temperature*

				Base temperature	
Clone	Slope ρ_i	Y-axis intercept a	R^2	T_{bi}	T_{bi}'
1	4.1 ± 0.5	−53 ± 8	84	12.8 (11.5–13.6)	15.9
K35	3.5 ± 0.7	−39 ± 11	64	11.3 (7.4–13.1)	12.7
207	4.0 ± 0.6	−48 ± 10	75	11.8 (9.6–13.1)	13.8
S15/10	3.1 ± 0.6	−32 ± 9	65	10.4 (6.4–12.2)	10.9
6/8	2.8 ± 0.5	−29 ± 8	67	10.4 (6.6–12.2)	10.9
SFS150	2.2 ± 0.4	−17 ± 7	61	8.0 (1.4–10.6)	8.0

Effects of drought

Relative to the fully irrigated treatments, the drought in the I_0 sub-plots reduced both the measured and fitted values of initial shoot length for those buds released from apical dominance from October to November 1989 and from August to September 1990 by between 18 and 35%. By contrast in September 1989 and June 1990, prior to the imposition of drought treatments, the mean values of L_o within the drought-stressed sub-plots (1.0–1.6 mm) were greater ($p \leqslant 0.05$) than those in the well-watered treatments (0.7–0.8 mm). This effect, which was not apparent in the measured values, was probably an artefact caused by assuming a constant relative extension rate over a period when growth was being reduced by drought.

The relative extension and development rates of shoots in the droughted plots were less than those of shoots within the fully irrigated plots during both dry periods, and between 70 and 80% of this reduction could be explained by linear relations with the mean soil water deficit (range: 15–90 mm) (Fig. 3a and b). The relative change in r (-0.72% mm SWD^{-1}) was greater ($p \leqslant 0.05$) than that shown by shoot development (-0.56% mm SWD^{-1}), and so the mean rates of relative extension and development at a mean soil water deficit of 80 mm were 50% and 64% respectively of those predicted from temperature alone. The relative responses of r and 1/SRC to SWD_{mean} did not vary between clones.

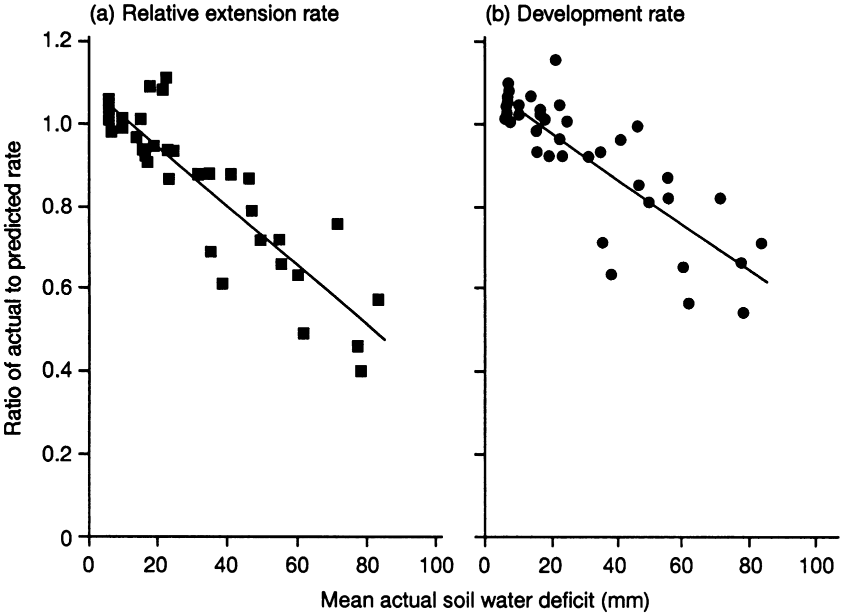

Fig. 3. Effects of mean soil water deficit (SWD_{mean}) on the ratio of actual to predicted rates of (a) relative extension (ratio = $1.08 - 0.0072\ \text{SWD}_{\text{mean}}$; $R^2 = 80$%) and (b) development (ratio = $1.09 - 0.0056\ \text{SWD}_{\text{mean}}$; $R^2 = 70$%).

DISCUSSION

Although previous studies of the responses of shoot extension and development to temperature have been conducted using individual clones (Tanton, 1982a; Stephens and Carr, 1993), this experiment allowed a direct comparison of the responses to temperature and drought for six of the most scientifically and/or commercially important clones in eastern Africa. These results are discussed in terms of their consistency with previous work, the relative sensitivity of shoot extension and development to temperature and drought, clonal selection, the choice of harvest intervals and the prediction of green-leaf quality.

Consistency with previous work

As in previous studies, an exponential equation was able to describe adequately shoot lengths, measured from the release of apical dominance to the unfurling of the third true leaf, for all six contrasting clones growing at mean air temperatures between 14 and 19°C. The values of r and L_o were found to be normally distributed and the results could be analysed statistically without the need for transformation. The fitted values of the initial shoot length corresponded closely to the measured values.

Within the fully irrigated treatments, the relations between r and T_{mean} for the young tea plants were relatively stable throughout the year and a single value of T_{be} could be calculated for each clone. By contrast it has been suggested in previous studies, involving mature plants of Clone 6/8 in southern Tanzania, that the relation between shoot extension rate and T_{mean} during a period of rising temperatures can be different from that during a cooling phase. The apparent lack of such seasonal changes in this experiment could have been the result of the relative extension rates being determined over a period of 50–110 days, rather than the shorter period of one month used by Stephens and Carr (1993).

The base temperature derived for the shoot extension of young plants of Clone 6/8 (9.5°C) is similar to the value (10°C) observed, during a period of cooling temperatures, for shoots of well-fertilized mature plants of the same clone at the same site (Stephens and Carr, 1993). However, both these values are substantially below that (14.9°C) derived from measurements on Clone 6/8 in Malawi (Cannell *et al.*, 1990). This apparent discrepancy could be caused by differences in the climate and/or the measuring procedure. The temperatures in Malawi (T_{mean} = 18–27°C) were higher than those (T_{mean} = 14–19°C) in Tanzania, making the extrapolation to T_{be} less precise. The observed responses of shoot extension to temperature in Malawi may also have been confounded by the adverse effects of drought stress (Cannell *et al.*, 1990), high vapour pressure deficits (Tanton, 1982b; Carr *et al.*, 1987), and short daylengths (Smith *et al.*, 1993). By contrast, in Tanzania T_{be} was derived from shoot measurements on fully irrigated tea with relatively low mid-afternoon vapour pressure deficits (0.6–1.5 kPa).

The extension rates in Malawi were determined from weekly measurements of shoots 30–50 mm in length for a period of nine months, whereas the shoots in

Tanzania were monitored from the release of apical dominance to harvest. In addition, because the extension rates in Malawi were initially monitored on bushes that had been pruned five months earlier, it is possible that the remobilization of starch reserves from the structural roots after pruning may have enhanced shoot growth rates for part of the year. Such effects were minimized in Tanzania because the young tea bushes had yet to be pruned and the measurements were taken over a period exceeding one year.

Relative sensitivity of shoot extension and development

Shoot extension was found to be more sensitive than shoot development to changes in temperature. This observation was supported by the effects of temperature on the lengths of internodes (Table 5) and the lengths of shoots with three unfurled leaves (Fig. 4). In addition the apparent base temperatures for shoot extension for all six contrasting clones were consistently 1.7–3.4°C greater than those for development, confirming similar observations reported by Stephens and Carr (1993) for mature plants of Clone 6/8. By contrast, Squire *et al.* (1993) reported no difference between the base temperatures for the shoot extension and development of Clone S15/10 at four elevations in Kenya. The lack of a difference in Kenya could be associated with site-related factors obscuring the responses to temperature or the imprecision resulting from the extrapolation of measurements taken within a relatively narrow T_{mean} range (15.8–18.5°C).

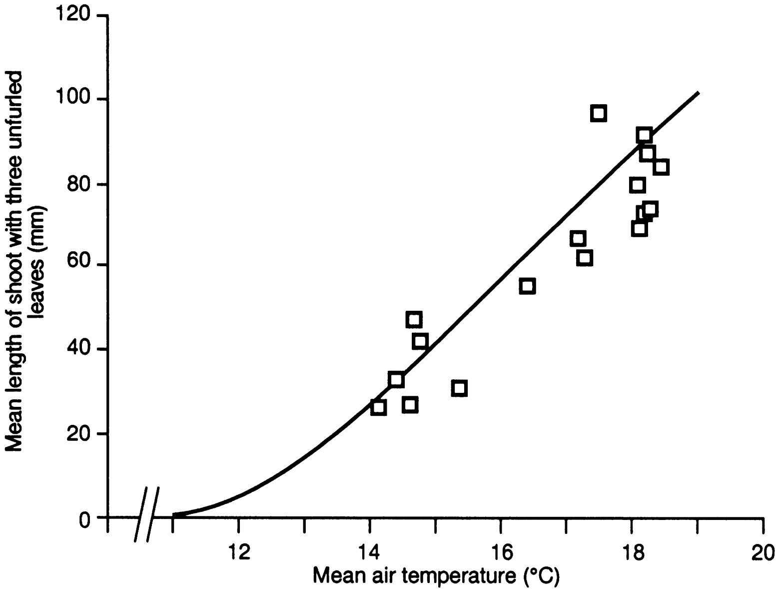

Fig. 4. Effects of mean air temperature (from the release of apical dominance to the unfurling of the third true leaf) on the mean length of a shoot with three unfurled leaves from fully irrigated Clone 1(□), together with a calculated length (——) based on the equation $L_{3bud} = L_o\, e^{\rho_e(T_{mean} - T_{be})/(\rho_d\,(T_{mean} - T_{bd}))}$. The values of L_o (0.98 mm), ρ_e (0.0118 mm mm^{-1} (°Cd)$^{-1}$), T_{be} (11.1°C), ρ_d (0.00195 (°C d)$^{-1}$), and T_{bd} (8.7°C) are derived from Tables 2, 3 and 4.

Differences in the relative sensitivity of the development and extension processes to temperature and drought have also been observed in field studies with other crops. For example, Milford *et al.* (1985) reported that the base temperature for the leaf appearance rate of sugar beet (1°C) was about 2°C lower than that for leaf expansion (3°C). Similar differences have also been reported for fibre hemp (Van der Werf *et al.*, 1995). In cereals, Ong and Baker (1985) reported that rates of leaf appearance tend to be less sensitive to environmental conditions than rates of leaf expansion. They related this, in part, to the relative positions of the sites of leaf emergence and leaf extension. Differences in the age of the cells at these sites could also be an explanation for the contrasting sensitivities to drought (Lawlor and Leach, 1985).

Clonal selection

The values of T_{be} ranged from 8.9°C for Clone SFS150 to 11.1–11.3°C for Clones 1 and K35. It is probably not accidental that the clone with the lowest base temperature was originally selected in Malawi where the response of shoot extension to temperature can be readily observed at a single site because of the relatively large seasonal changes in the mean monthly values of T_{mean} (18–25°C). By contrast the two clones from Tanzania (1 and 207) appear to have been selected despite, rather than because of slow rates of shoot extension during the cool season. However this could be advantageous in areas subject to frost, as in Mufindi, as low growth rates at this time can reduce the susceptibility of a crop to damage (Cooper, 1963).

The values for ρ_e ranged from 7.8×10^{-3} mm mm^{-1} (°Cd)$^{-1}$ for Clone SFS150 to 11.8×10^{-3} mm mm^{-1} (°Cd)$^{-1}$ for Clone 1. The positive association between high values of T_{be} and ρ_e meant that the ranking of some of the clones in terms of shoot extension rate varied during the year. For example whereas shoots of Clone SFS150 extended faster than those of Clone 1 at low temperatures, the order was reversed during warm weather (Fig. 2). These changes can also explain the observed variations in seasonal yield distribution with Clone SFS150 yielding more than Clone 1 during the winter months but less than Clone 1 during the warm season (Burgess and Carr, 1996a). In frost-free areas where T_{mean} is close to T_{be} for part of the year, the selection of clones such as SFS150, which have low base temperatures, may have significant commercial benefits due to the evening out of the subsequent peaks and troughs in yield.

The positive relation between T_{be} and ρ_e is also evident in data from Malawi (Cannell *et al.*, 1990). One possible explanation is that during the cool season, clones with a high T_{be} may be able to store more assimilates in the structural roots than clones with a low value. These additional assimilates could then be used to maintain particularly fast growth rates during the subsequent warm season Ideally, for frost-free areas, clones need to be identified which combine a low base temperature with a high thermal extension rate.

An additional approach is to select those clones which have identical base temperatures for extension and development, so that the length of a shoot with, say, three unfurled leaves is independent of temperature. This would facilitate easy harvesting and could, assuming that harvest intervals were correctly adjusted, result in a relatively consistent quality of green leaf (in terms of shoot stage) throughout the year. The clonal differences in the sensitivity of the mean internode length to temperature (range: 2.2–4.1 mm $^{\circ}C^{-1}$) indicates that it would be possible to select for this trait in existing plant populations.

Choice of harvest interval

Most tea growers in Southern Tanzania aim to harvest a high proportion of shoots with three unfurled leaves. The harvest interval is therefore selected to ensure that pluckers are presented with shoots of the required standard, namely those that have just unfurled the third true leaf, rather than shoots which are more advanced (which could reduce the quality of the processed tea) or less developed (which could reduce yield).

Grice (1982) in Malawi, recommended that the optimal balance between yield, quality and labour productivity was achieved by maintaining an interval that was equivalent to one quarter of the shoot replacement cycle, and subsequent work has established that this interval is also appropriate in southern Tanzania (Stephens and Carr, 1993). By using the derived relations between development rate and temperature (Table 4), it is possible to estimate the appropriate harvest interval for individual clones at different mean air temperatures (T_{mean}). For example when T_{mean} is 17°C, Clones 1 and 207 have a shoot replacement cycle of 65 days ($1/SRC = 15.3 \times 10^{-3}\ d^{-1}$) which suggests a harvest interval of about 16 days. By contrast at the same temperature the SRC for the other four clones range from 71 to 78 days ($1/SRC = 12.8$–$13.9 \times 10^{-3}\ d^{-1}$) corresponding to an interval of 18–19 days.

The relative responses of shoot extension and development to mean soil water deficit (Fig. 3a and b) also allow the selection of an appropriate harvest interval for young drought-stressed tea bushes. For example, when T_{mean} is 17°C and SWD_{mean} is 57 mm (half of the total extractable water in the root zone), the calculated shoot replacement cycle of Clone S15/10 is 102 days ($1/SRC = 0.77 \times 12.8 \times 10^{-3}\ d^{-1}$) which suggests an interval of about 25 days. Although such calculations are possible when T_{mean} and SWD_{mean} can be averaged over a complete shoot replacement cycle, in practice temperature and soil water deficit change from day to day. To allow for this, a procedure to determine the appropriate harvest interval for individual clones, from the relatively short time period between a shoot unfurling the second and third true leaves, has been developed for use by commercial growers in southern Tanzania (Burgess, 1993).

Green leaf quality

The quality of green leaf sold to tea factories in east and central Africa is often assessed by determining the proportion of harvested shoots with three or fewer unfurled leaves and/or the number of shoots per kg green leaf (Clowes, 1986). This paper shows that much of the variation in the shoot size to shoot stage relationship for individual clones can be predicted from the responses of shoot extension and development to temperature and soil water deficit.

Within the stated temperature range (14–19°C), it has been shown that the value of r can be derived from $\rho_e\ (T_{mean} - T_{be})$. Similarly the value of t, the time from the release of apical dominance to the unfurling of the third true leaf, can be derived from $(\rho_d(T_{mean} - T_{bd}))^{-1}$. By incorporating these terms into the exponential function in Equation 1, it is possible to express the length of a shoot when it unfurls its third true leaf (L_{3bud}) as a function of the mean air temperature (Equation 4).

$$L_{3bud} = L_o\, e^{\rho_e(T_{mean} - T_{be})/(\rho_d\ (T_{mean} - T_{bd}))} \tag{4}$$

Using this equation and the values of L_o, ρ_e, T_{be}, ρ_d and T_{bd} obtained from shoots of fully irrigated Clone 1, the derived relation between L_{3bud} and T_{mean} corresponds closely to the measured values of L_{3bud} (Fig. 4). This relation is approximately linear for values of T_{mean} between 14 and 19°C and a linear extrapolation would suggest an apparent base temperature of about 12.3°C. This is within the range of T_{bi} values (11.5–13.6°C) estimated for Clone 1 from a linear regression of mean internode length and T_{mean} (Table 5). However Equation 4 also suggests that, for Clone 1, the actual response of L_{3bud} to T_{mean} is likely to be curvilinear at temperatures between 11 and 13°C.

By combining Equation 4 with those, for example, relating length to shoot weight (Smith *et al.*, 1990), it should be possible to estimate the effects of clone, drought and temperature on the mean fresh weight of a shoot at a given developmental stage. Such a procedure could provide tea growers with a systematic way of predicting the number of shoots per kg harvested leaf at different times during the year.

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