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RESPONSES OF YOUNG TEA (*CAMELLIA SINENSIS*) CLONES TO DROUGHT AND TEMPERATURE. II. DRY MATTER PRODUCTION AND PARTITIONING

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SUMMARY

The physiological basis for differences in yields from well-watered and droughted plants of four contrasting clones of tea were studied in terms of light interception, dry matter production and partitioning at a high altitude site in Southern Tanzania where there are marked seasonal variations in rainfall and temperature. The plant dry weights, including roots, were measured eight months after field planting and subsequently at intervals of three to four months, corresponding to the different seasons, during the following two years. Fully irrigated plants of one clone (S15/10) were also harvested after four years in the field. Clones differed in the rates of canopy spread and hence in their capacity to intercept solar radiation. The 'radiation use efficiency' (the net total dry matter production per unit of intercepted short-wave solar radiation) was similar for the four well-watered clones and ranged from 0.40 to 0.66 g MJ^{-1}, which corresponds closely to values reported for other woody tropical plants. A 16-week drought treatment imposed two years after planting reduced the mean light interception of the four clones by about 25% and the mean radiation use efficiency by 78% to 0.09 g MJ^{-1}. Clone S15/10, a cultivar from Kenya which produces large yields, partitioned a greater proportion of dry matter to leaves and harvested shoots than the other clones, and correspondingly less to large structural roots. This resulted in a maximum harvest index of 24%, substantially greater than other values reported in the literature. There were seasonal differences in partitioning with more dry matter being diverted to roots and less to shoots during the cool season. Although the drought treatments had no significant effect on root growth, the amount of dry matter partitioned to leaves, stems and harvested shoots declined by 80-95%. The roots of all four clones extended in depth at similar rates (about 2 mm d^{-1}), those of Clone S15/10 reaching 2.8 m after four years. The results are discussed in terms of appropriate field cultural practices and possible selection criteria for high yielding clones.

INTRODUCTION

The yield (Y; g m^{-2}) of a crop can be expressed by:

$$Y = S \, . \, f_S \, . \, \varepsilon_S . \, HI \qquad (1)$$

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where S is the short-wave solar radiation (MJ m^{-2}) incident during the measurement period, f_S is the proportion of this radiation intercepted by the crop canopy, ε_S is the ratio of total dry matter production to intercepted radiation, or radiation use efficiency (g MJ^{-1}), and HI is the harvest index, or that proportion of the total dry matter which forms the economic yield. Extensive studies of dry matter production and partitioning have been made on many annual crops, but similar research on perennial crops is limited. Corley (1983) has reported that the annual above ground dry matter production of crops such as cocoa, oil palm, coconut and rubber is between 20 and 29 t ha^{-1}. Assuming complete interception of annual short-wave radiation receipts of 6000 to 7500 MJ m^{-2} for the tropics, this is equivalent to a radiation use efficiency for above-ground dry matter of 0.27-0.48 g MJ^{-1}. By contrast Magambo and Cannell (1981) found that the annual dry matter production of harvested tea (Clone 6/8) with complete canopy cover grown at an altitude of 2178 m in Kenya was only 16.9 and 12.7 t ha^{-1}, with and without roots respectively. Using the same figures for annual short-wave radiation of 6000-7500 MJ m^{-2}, the values for ε_S of 0.22-0.28 g MJ^{-1} including roots (or 0.17-0.21 g MJ^{-1} without roots) are less than those estimated for other tropical perennial crops.

The productivity of tea is also limited by a low harvest index (Squire, 1985). The economic yield, which comprises shoots with a terminal bud and up to three unfurled leaves, can be increased by harvesting shoots with more leaves, but this reduces the quality and value of the processed product (Cloughley *et al.*, 1983). The harvest index can also be increased through clonal selection: for example Murty and Sharma (1986) reported indices of 7 and 16% for two tea clones in Southern India.

The yield development of six contrasting clones from Kenya, Malawi and Tanzania under a range of drought regimes have been described in Part I of this series (Burgess and Carr, 1996a). During the second year after planting harvested yields of dry tea under well watered conditions ranged from 2320-2510 kg ha^{-1} for Clones 1, 6/8 and SFS150 to 3590 kg ha^{-1} for Clone S15/10. This paper reports an investigation into the physiological basis of these clonal differences using the framework summarised by Equation 1, the overall aim being to quantify how the different parameters vary in their responses to drought and temperature, so that possible selection criterion might be identified.

METHODOLOGY

Site and climate

The Ngwazi Tea Research Unit (8°32'S, 35°10'E, altitude 1840 m) is situated next to the 500 ha fresh water Lake Ngwazi in the Mufindi District of the Southern Highlands of Tanzania. The year can be divided into three main seasons on the basis of rainfall and temperature. Over 95% of the 800-1100 mm annual rainfall occurs during the warm-wet season from the end of November to May, when the monthly mean air temperature (T_{mean}) is 16-19°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 annual incident short-wave radiation (S), measured using a Gunn Bellani pyranometer which was calibrated against a Kipp solarimeter in 1989, varies from 5950 to 6400 MJ m^{-2}. Mean daily values are at a maximum (23 MJ m^{-2}) in October when it is dry and at a minimum (15 MJ m^{-2}) during the rainy season from November to May when there is substantial cloud (Figure 1).

A gently sloping (< 3%) area close the lake and adjacent to an area of mature tea was selected as an experimental site. The soil is a Xanthic ferralsol with the particle size distribution of a sandy clay above 0.15 m and that of a clay below. Despite the high proportion of clay the soil remains friable because of the low effective cation exchange capacity (< 16 mmol 100g^{-1} of clay). The available water content held at matric potentials between -10 kPa and -1500 kPa ranges from 110 to 122 mm m^{-1} in the top 2 m of soil.

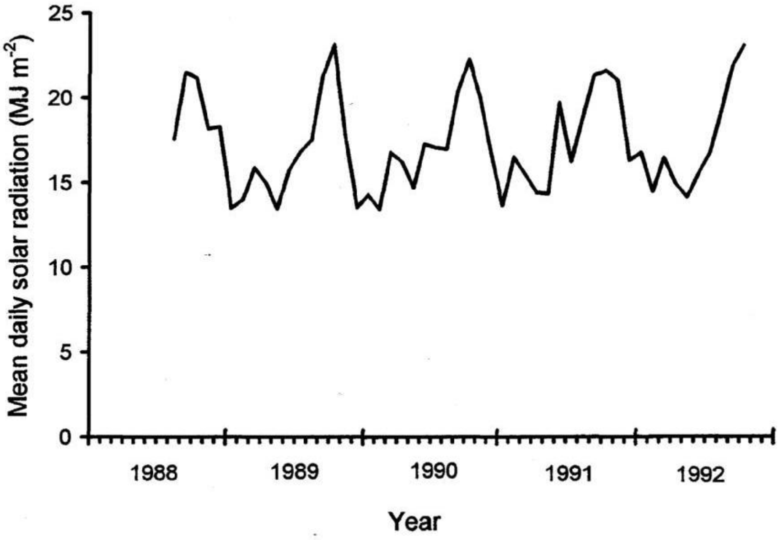

Figure 1. Measured mean daily total short-wave solar radiation at Ngwazi Tea Research Unit from August 1988 to October 1992.

Experimental treatments

Dry matter production and partitioning were studied in four contrasting tea clones of commercial and/or scientific importance in eastern Africa. These ranged from small-leaf Clone 1, to intermediate-leaf Clone 6/8 and large-leaf Clones SFS150 and S15/10. Clone S15/10, selected by the African Highlands Produce Company Ltd in Kericho, Kenya, produces the highest yield of the four clones under well-watered conditions (Burgess and Carr, 1996a), but when droughted the yield can be similar to those from Clones 1 and SFS150. Clone 1, selected in Tanzania, has a large shoot population density (Stephens and Carr, 1990), but the small fibrous shoots can be difficult to harvest by hand. It also has a high base temperature for shoot extension which results in small yields during the cool part of the dry season (Burgess and Carr, 1996b). By contrast Clone SFS150 (from Malawi) has a low base temperature for extension and as a consequence it produces relatively large yields at this time. Despite these contrasting responses to temperature Clones 1 and SFS150 have produced the same annual yields. Clone 6/8 is a high quality clone from Kenya which produces similar yields to Clones 1 and SFS150 when irrigated, but less than these clones when droughted.

Unreplicated 96 m^2 blocks of each of these four clones were planted in August 1988 at spacings of 1.2 x 0.8 m at one end of the line-source experiment described by Burgess and Carr (1996a), so that individual plants could be destructively sampled. Each clonal block was divided into three sub-plots, parallel to the irrigation lateral, labelled ‘wet’, ‘intermediate’ and ‘dry’. All of the tea was uniformly irrigated after planting in 1988 and during the initial part of each subsequent dry season. Differential drought treatments were imposed for seven weeks in 1989 (9 October to 27 November) and for sixteen weeks in 1990 (27 July to 18 November), when the plants in the ‘wet’ sub-plots continued to receive their full water requirements, those in the ‘dry’ sub-plots received no irrigation water and those in the ‘intermediate’ treatment were partially irrigated.

Crop management

The crop was mulched with Napier grass (*Pennisetum pupureum*) at planting in August 1988 and again in April 1989, and with Guatemala grass (*Tripsacum laxum*) in October 1990. Fertiliser rates were set to minimise nutrient deficiency and have been fully described in Paper I (Burgess and Carr, 1996a). The tea was brought into production by spreading the young branches and then 'pegging' them into position at intervals between April and October 1989. Shoots above a height of 0.45 m from the ground were removed in early November 1989, 15 months after planting, to produce a level plucking surface. The first routine harvest (in which protruding shoots, with two or more unfurled leaves or those with dormant buds, were removed by hand) followed one month later and subsequently at 13-15 day intervals extending up to 24 days during the cool seasons.

Plant harvests

During 1989 and 1990 whole plants, including roots, were harvested at the end of the rains in April/May, the end of the cool-dry season in August/September and the end of the warm-dry season in November/December (Table 1). One plant of each of Clones 1, 6/8, SFS150 and S15/10 was harvested from each of the 'wet', 'intermediate' and 'dry' sub-plots for the first time in April 1989, six months before the imposition of drought treatments. For the next four harvests from August 1989 (also before differential irrigation began) to August 1990 one plant from each of the four clones was selected from the 'wet' and 'dry' sub-plots only. In November 1990, to improve the precision of measurement, three plants of each clone were selected from the 'wet' and 'dry' sub-plots. In September 1992, four years after field planting, a further three plants of fully irrigated Clone S15/10 were harvested. The sampled plants were always surrounded on each side by bushes of the same clone and age, and from December 1989 the selected plants had the median ground cover of a pre-determined group of ten adjacent plants. The periods between harvests and the corresponding maximum actual soil water deficits in the selected drought treatments are shown in Table 1.

Table 1. *The dates of plant harvests, the corresponding seasons, mean air temperatures (°C), and maximum actual soil water deficits (SWD; mm) within each drought treatment for each of six sample periods.*

Sample period	Dates of harvests	Season and mean air temperature		Maximum SWD Drought treatment wet	intermediate	dry
1	15 Apr 89 - 6 Aug 89	Cool-dry	15.0	45	45	45
2	6 Aug 89 - 12 Dec 89	Warm-dry	16.9	58	-	84
3	12 Dec 89 - 5 May 90	Warm-wet	18.3	30	-	30
4	5 May 90 - 15 Aug 90	Cool-dry	14.7	45	-	70
5	15 Aug 90 - 26 Nov 90	Warm-dry	16.8	46	-	117
6	26 Nov 90 - 22 Sept 92	-	16.9	60	-	-

The canopy of each harvested plant was separated into woody stem, green stem and leaves. To retrieve the roots 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. The excavated soil was sieved through a 10 mm^2 wire mesh to remove the fine soil particles, before being sorted over a second sieve where the roots were removed by hand and classified visually as being either thick (diameter greater than 1 mm) or fine (diameter less than 1 mm). The roots, stems and leaves of each plant were then oven dried at 85-90°C for 48 hours, or until there was no further loss in mass. When the volume of a plant component was too large for the oven, the dry mass was estimated from the total fresh mass and the mean dry/fresh mass ratio of two to four randomly selected samples (range: 30-240 g).

The dry mass of shoots harvested from each bush was estimated using the yields obtained from the corresponding treatments within the adjacent main experiment (Burgess and Carr, 1996a). In both November 1990 and September 1992 the dry mass of dead leaves which had collected at the base of each plant was also included in the estimate of total dry matter production. For the first harvest it was possible to complete everything within three days. The harvest starting in November 1990 (24 plants) took a total of 38 days, with root excavation, separation and weighing taking a further 18 days. To minimise possible confounding effects of changes in plant weight during this time, one plant was harvested within each treatment before proceeding to a second and a third replicate block. The reported harvest date was taken as that midway between the start and end of the harvesting period. The final harvest of three plants in September 1992, including roots to depths of 2.8 m, took 29 days.

Light interception

From December 1989 to September 1992 the crop cover of each harvested plant was measured using a 1.2 x 0.8 m grid, divided into 0.1 x 0.1 m squares, held horizontally above the bush. The proportion of each square (0-25, 25-75 or 75-100%) which included leaf, when examined individually from overhead, was recorded to provide an estimate of the ground covered by each plant. The total quantity of light intercepted by the plants between harvests ($S.\ f_S$; MJ m^{-2}) within selected treatments was then calculated using Equation 2 (Jackson and Palmer, 1979).

$$S.\ f_S. = S.\ C.\ (1 - e^{-k\,LAI'}) \qquad (2)$$

where S is the total incident short-wave solar radiation (MJ m^{-2}), C is the mean proportion of ground covered by the crop, k is the light extinction coefficient within the bush canopy and LAI' is the mean leaf area per unit area of crop cover. Measurements using a Decagon ceptometer (Delta-T Devices) on four contrasting clones, including Clones 6/8 and S15/10, in Kenya indicated a consistent extinction coefficient of 0.6 for photosynthetically active radiation (PAR) in a canopy of young tea (Ng'etich, 1995). In the absence of other information, the same value of k was assumed for short-wave radiation. The total leaf area of each plant was determined by measuring each leaf with a calibrated card (Pethiyagoda and Ragendram, 1965). For the last three harvests, leaf areas were calculated from the total fresh mass of leaf multiplied by the mean leaf area/fresh mass ratio determined from three randomly selected 100 g samples.

RESULTS

Light interception

The mean daily interception of solar radiation by the four fully irrigated clones increased from 3.8 MJ m^{-2} during the 1989/90 warm-wet season (16 to 21 months after field planting) to 9.4 MJ m^{-2} during the 1990 warm-dry season (24 to 27 months after planting) (Table 2). This was primarily a result of an increase in the proportion of intercepted radiation (f_S) from 25 to 45%, caused by an expansion in the crop cover (C) from 27 to 48%. Throughout this period the mean values of LAI' ranged from 4.7 to 5.1.

Table 2. *The mean daily light interception (*S.f$_{S;}$*; MJ m^{-2} d^{-1}) for all four fully irrigated clones and the corresponding total short-wave radiation (*S*; MJ m^{-2} d^{-1}), crop cover (*C*; %), leaf area per unit area of crop cover (*LAI'*), and proportion of radiation intercepted (*f$_S$*; %) for each of three sample periods from December 1989 to November 1990.* S.f$_S$ = S. C *(1-e $^{-0.6\ LAI'}$) (n=4).*

Sample period	Season	S	C	LAI'	f$_S$	S.f$_S$
3	Warm-wet	15.2	27	4.7	25	3.8± 0.5
4	Cool-dry	15.6	40	4.7	38	5.9± 0.7
5	Warm-dry	20.7	48	5.1	45	9.4± 0.6

There were differences between clones in light interception: for example in the period August to November 1990 (24-27 months after planting), fully irrigated Clones 1 and S15/10 intercepted more light (10.5-11.1 MJ m^{-2} d^{-1}) than Clone 6/8 (7.2 MJ m^{-2} d^{-1}). This again reflected differences in crop cover, 54-58% compared with 35% respectively (Table 3), rather than LAI' since Clone 6/8 had a larger value (6.4) than Clone S15/10 (4.4). These values of LAI' corresponded with visual observations that fully irrigated Clone 6/8 had a more upright and dense canopy than Clone S15/10. During the same period, the mean solar radiation intercepted by plants within the droughted treatments was 26% lower than that within the fully irrigated plots, mainly caused by a restriction of crop cover development. The observation that Clone 6/8 was particularly prone to defoliation when water stressed was substantiated by a reduction in the value of LAI’ to 4.8 in the droughted plots, similar to the values for the other clones (4.1-5.1).

Table 3. *Effects of drought on the mean light interception (*S.f$_{S;}$*; MJ m^{-2} d^{-1}) for each of four clones and the corresponding crop cover (*C*; %), leaf area per unit area of crop cover (*LAI'*), and proportion of radiation intercepted (*f$_S$*; %) for sample period 5 between August and November 1990. The mean incident total short-wave radiation (S) was 20.7 MJ m^{-2} d^{-1}.* S.f$_S$ = S. C (1-e$^{-0.6\ LAI'}$).

Drought treatment	Clone	C	LAI'	f$_S$	S.f$_S$
Wet	1	54	4.6	51	10.5
	6/8	35	6.4	35	7.2
	SFS150	45	4.9	43	8.9
	S15/10	58	4.4	54	11.1
	Mean	48	5.1	45	9.4
Dry	1	46	5.1	44	9.0
	6/8	23	4.8	22	4.6
	SFS150	35	5.0	33	6.9
	S15/10	38	4.1	35	7.3
	Mean	36	4.7	34	7.0
standard error of difference between:					
clone x drought treatments (n=3)		5.7	0.32	5.4	1.12
drought treatments	(n=12)	2.8	0.16	2.7	0.56

Dry matter production

In April 1989, eight months after field planting, the mean dry mass of a single plant at 30 ± 2 g was similar for each of the four clones. By November 1990, the net dry matter produced by the same clones had increased to a mean of 1165 ± 59 g for the fully irrigated plants (Table 4), with values ranging from a low of 1060 g for Clone 6/8 to a high of 1275 g for Clone 1, a difference which was not statistically significant (P=0.05). By September 1992, 49 months after field planting, the mean net dry matter produced by a fully irrigated Clone S15/10 plant had reached 4770 ± 597 g.

The mean daily growth rate of the four clones increased from 0.4 g plant^{-1} between April and August 1989, to 3.6 g plant^{-1} from August to November 1990, and to 5.4 g plant^{-1} for fully irrigated Clone S15/10 between November 1990 and September 1992. These differences were associated with an increase in light interception from 3.8 to 13.6 MJ m^{-2} d^{-1} rather than changes in the radiation use efficiency which was usually in the range of 0.40 to 0.46 g MJ^{-1}, except during the warm-wet season from December 1989 to May 1990 when it was as high as 0.66 g MJ^{-1}. It is not possible to assess whether this difference was related to the quite small changes in the mid-afternoon vapour pressure deficit of the air between the warm-wet (0.7-0.9 kPa) and warm-dry months (0.9-1.5 kPa) although this could have been the case. There were no consistent differences between the radiation use efficiency of the four clones within the well-watered treatments.

Table 4. *The initial and final mean plant dry mass (g) together with the corresponding light interception* (S. f_S; *MJ m^{-2} d^{-1}*), *radiation use efficiency* (ε_S; g MJ^{-1}) *and growth rate* (g plant^{-1} d^{-1}) *for all four fully irrigated clones for each of five seasons between April 1989 and November 1990 (sample periods 1-5), and for Clone S15/10 between November 1990 and September 1992 (sample period 6). The plant spacing was 0.96 m^2. The values of the final mass in some periods are not the same as the initial mass in the next because the number of replicates (indicated in brackets) is different.*

Sample period	Season	Initial mass	Final mass	S. f_S	ε_S	Growth rate
1	Cool-dry	30 ± 2 (12)	80 ± 6 (12)	-	-	0.4 ± 0.1 (12)
2	Warm-dry	82 ± 7 (4)	183 ± 31 (4)	-	-	0.8 ± 0.2 (4)
3	Warm-wet	183 ± 31 (4)	529 ± 30 (4)	3.8 ± 0.5 (4)	0.66 ± 0.03 (4)	2.4 ± 0.2 (4)
4	Cool-dry	529 ± 30 (4)	793 ± 80 (4)	5.9 ± 0.7 (4)	0.46 ± 0.09 (4)	2.6 ± 0.6 (4)
5	Warm-dry	793 ± 80 (4)	1165 ± 59 (12)	9.4 ± 0.6 (12)	0.40 ± 0.05 (12)	3.6 ± 0.6 (12)
6	-	1230 ± 118 (3)	4770 ± 597 (3)	13.6 ± 2.2 (3)	0.42 ± 0.05 (3)	5.4 ± 0.7 (3)

By August 1990, two years after field planting and following the short drought treatment in 1989, the mean total dry mass of a fully irrigated plant (793 g), including harvested shoots, was only 12% greater than that of an unirrigated plant (710 g). However three months later, immediately following the second period of drought, the mean dry mass of the fully irrigated plants had increased by 47% to 1165 g, whereas that of the droughted plants had risen by only 13% to 804 g (Table 5). The reduced daily growth rate of the unirrigated plants was associated with a 26% decrease in the amount of intercepted light from 9.3 to 6.9 MJ m^{-2} d^{-1}, and a 78% reduction in radiation use efficiency from 0.40 to 0.09 g MJ^{-1}. There were also indications of differences between clones in the drought sensitivity of the radiation use efficiency index ($P \leq 0.05$), with Clone 6/8 being more susceptible to water stress than Clones 1 and SFS150.

Table 5. *Effects of drought on the initial and final dry mass (g) of each of four clones on 15 August and 26 November 1990 respectively and the intervening light interception (*$S.f_S$*;* MJ m^{-2} d^{-1}*), radiation use efficiency (*ε_S; g MJ^{-1}*) and growth rate* (g $plant^{-1}$ d^{-1}). *The plant spacing was 0.96 m^2.*

Drought treatment	Clone	Initial mass	Final mass	$S.f_S$	ε_S	Growth rate
Wet	1	1007	1275	10.5	0.23	2.6
	6/8	641	1059	7.2	0.58	4.0
	SFS150	816	1099	8.9	0.32	2.8
	S15/10	706	1226	11.1	0.45	5.1
	Mean	793	1165	9.4	0.40	3.6
Dry	1	985	1116	9.0	0.14	1.3
	6/8	564	514	4.6	-0.11	-0.5
	SFS150	696	958	6.9	0.37	2.6
	S15/10	595	627	7.3	-0.03	0.3
	Mean	710	804	7.0	0.09	0.9
standard error of difference between:						
clone x drought treatments (n=3)[a]		-	162	1.12	0.169	1.57
drought treatments (n=12)[a]		22	81	0.56	0.085	0.787

[a]: Except for the values of initial plant mass where the mean value for each drought treatment is based on four, rather than twelve, replicates.

Dry matter partitioning

There were important seasonal effects on the partitioning of dry matter by well watered plants as the proportion diverted to leaves and harvested shoots declined from 43-49% during the warm-dry and warm-wet weather to 13-28% during the cool seasons (Figure 2). This was matched by increased partitioning to the roots from 14-22% during the warm weather to 43-46% during the cool periods.

To minimise any interactions between clone and season, clonal differences were compared from December 1989 to November 1990, a period of one year beginning 16 months after planting. The mean daily increment in the dry mass of shoots harvested from fully irrigated Clone S15/10 (0.50 g $plant^{-1}$) was greater ($P \leq 0.01$) than those from Clones 1, 6/8 and SFS150 (0.32-0.38 g $plant^{-1}$) (Table 6a). These values are equivalent to dried tea yields of 1940 and 1210-1440 kg ha^{-1}respectively.

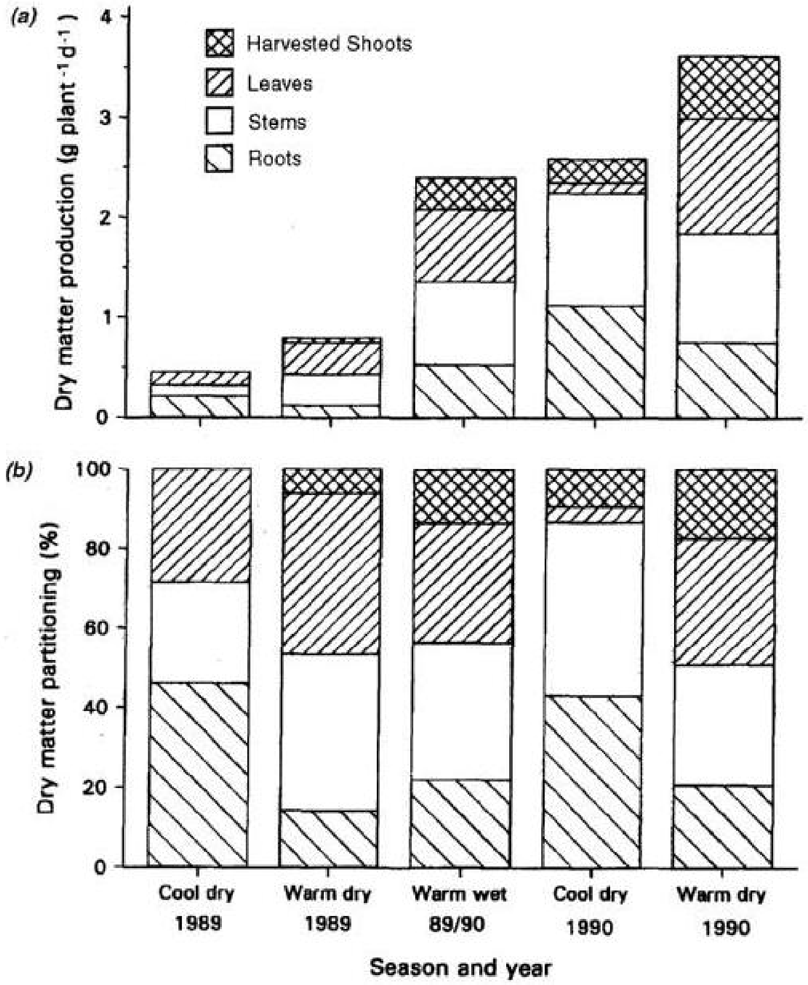

Figure 2. Changes in (a) the rate of dry matter production and (b) the partitioning of that dry matter to harvested shoots, leaves, stems and roots, averaged for all four well-watered clones (1, 6/8, SFS150 and S15/10) in each of five seasons from April 1989 to November 1990.

Although the high yields from Clone S15/10 were partly a result of a large total dry matter production, the harvest index of this clone reached 16%, between December 1989 and November 1990, compared to 11-15% for the other three clones. In addition Clone S15/10 partitioned a greater proportion of dry matter to leaves (29%) and green stem (8%) than Clones 1, 6/8 and SFS150 (Figure 3). By contrast only 11% of its dry matter was partitioned to thick structural roots compared to 23-29% for the other clones. There were no significant differences between clones in the amount of dry matter partitioned to woody stems, or to fine roots. During the 22 months from November 1990 to September 1992, the daily yield increment from fully irrigated Clone S15/10 increased to 1.31 g plant^{-1} (equivalent to an annual yield of about 5000 kg dried tea ha^{-1}) and the harvest index reached a value of 24% (Table 6b).

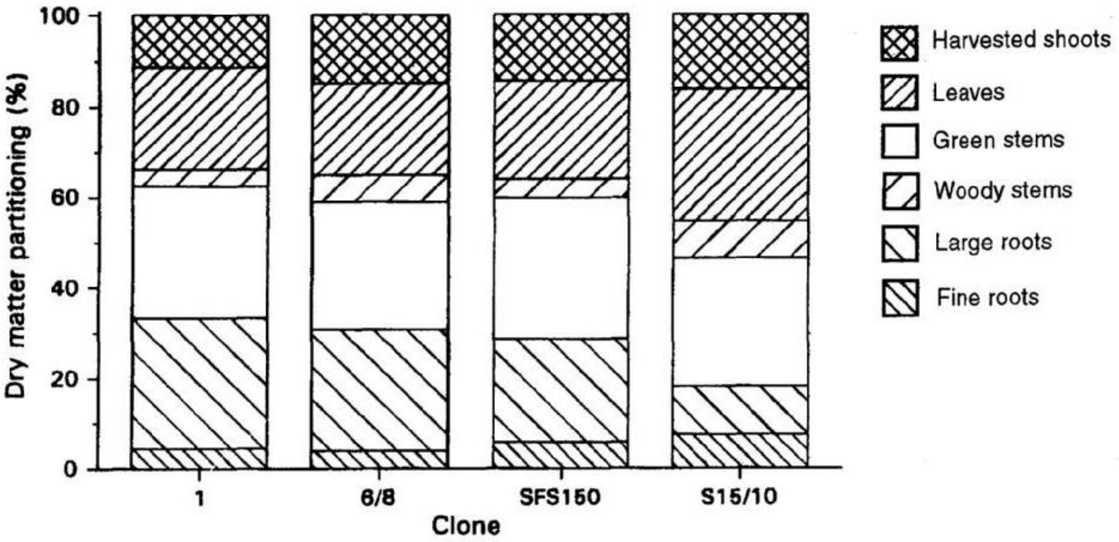

Figure 3. The proportion of dry matter partitioned to harvested shoots, leaves, green stems, woody stems, large roots and fine roots for each of four fully irrigated clones between December 1989 and November 1990. The absolute values for dry matter are given in Table 6.

Table 6. *The net dry matter partitioned (g plant^{-1} d^{-1}) to harvested shoots, leaves, stems, large and fine roots for (a) each of four fully irrigated clones between December 1989 and November 1990, and (b) for Clone S15/10 from November 1990 to September 1992.*

(a)

Clone	Component					
	Harvested shoots	Leaves	Stems	Roots large	Roots fine	Total
1	0.32	0.67	0.99	0.86	0.12	2.96
6/8	0.35	0.49	0.82	0.65	0.09	2.40
SFS150	0.38	0.58	0.95	0.61	0.15	2.67
S15/10	0.50	0.94	1.20	0.33	0.24	3.22
Sed	0.03	0.14	0.25	0.13	0.07	0.41
n	4	3	3	3	3	3

(b)

	Harvested shoots	Leaves	Stems	Roots large	Roots fine	Total
Clone S15/10	1.31	1.41	1.96	0.60	0.14	5.43
Se	0.23	0.25	0.44	0.10	0.02	0.71
n	4	3	3	3	3	3

Sed = standard error of the differences; se = standard error of the mean; n = number of observations on which each value is based.

The reduced partitioning of dry matter to structural roots by fully irrigated Clone S15/10 did not result in shallow rooting. In November 1990, 27 months after planting, the mean maximum rooting depth of this clone (1.46 m) was intermediate between those of Clones 1 (1.37 m) and 6/8 (1.66 m); these values were not significantly different (P=0.05). Assuming that Clone S15/10 was representative of the four clones the mean increase in maximum rooting depth, from the end of the first year to the fourth year after planting, appeared to be consistent ranging from 2.1 ± 0.12 mm d^{-1} (df = 26, R^2 = 92%), from August 1989 to November 1990, to 2.0 ± 0.11 mm d^{-1} (df = 4, R^2 = 99%) from November 1990 to September 1992 (Figure 4). By then the maximum rooting depth of Clone S15/10, four years after field planting, had reached 2.8 m.

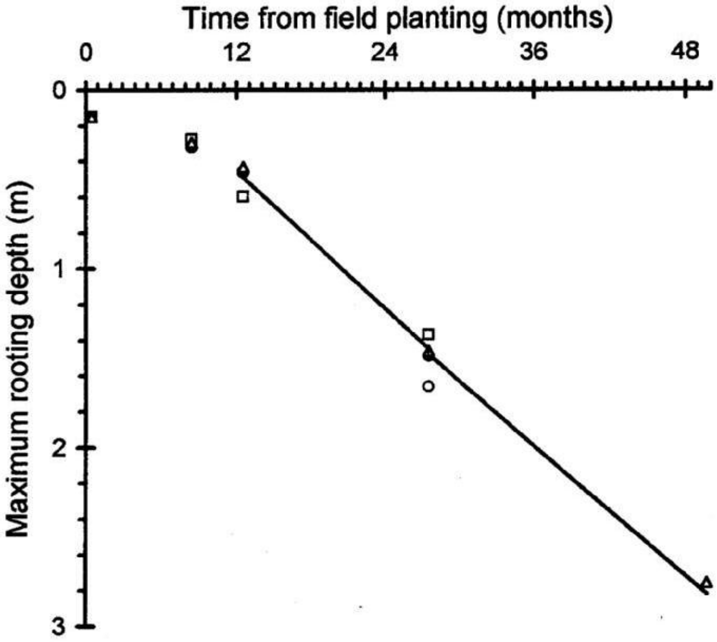

Figure 4. Increase in the mean maximum rooting depth of four irrigated clones (1, 6/8, SFS150 and S15/10) with time from field planting in August 1988 to November 1990 and for Clone S15/10 (△) only until September 1992. The slopes of the fitted lines are 2.10 ± 0.116 mm d^{-1} between August 1989 and November 1990 (all clones), and 2.00 ± 0.112 mm d^{-1} from November 1990 to September 1992 (Clone S15/10).

In November 1990, although drought treatments had been imposed during the preceding 16 weeks, the maximum root depths of the four clones in the ‘dry’ plots were similar to those in the ‘wet’ treatments. The relative insensitivity of root growth to drought was also demonstrated by the observation that droughted bushes partitioned a similar amount of dry matter to roots as the well-watered plants (Table 7). Because the net production of total dry matter was reduced by drought, the proportion of the total that was partitioned to roots increased from 21% in the ‘wet’ plots, to 65% where the plants were droughted. By contrast drought substantially reduced both the amount and the proportion of dry matter partitioned to leaves, stems and harvested shoots. For example: the amount of dry matter partitioned to above-ground components declined by between 80 and 95%, with the result that the harvest index fell from a mean value of 17% in the ‘wet’ treatments to only 8% in the ‘dry’ plots.

Table 7. *The effects of drought on the net dry matter partitioning (g plant^{-1} d^{-1}) to harvested shoots, leaf, stem, large roots and small roots for four clones between August and November 1990. The values in brackets are proportions (%) of the total partitioned to each component.*

Drought treatment	Harvested shoots	Leaves	Stems	Roots large	Roots fine	Total
Wet	0.63 (17)	1.15 (32)	1.09 (30)	0.36 (10)	0.38 (11)	3.62
Dry	0.07 (8)	0.07 (8)	0.17 (19)	0.38 (42)	0.21 (23)	0.91
sed (n=4)	0.026	0.26	0.04	0.21	0.11	0.41

DISCUSSION

The results are discussed in relation to the effects of genotype and the environment on the key variables determining yield shown in Equation 1, namely light interception, radiation use efficiency and dry matter partitioning. The practical opportunities which exist to identify new high yielding clones and the need to modify cultural practices to exploit these relations are also considered.

Light interception

The use of Jackson and Palmer's (1979) model for light interception in a discontinuous canopy highlighted the importance of crop cover, relative to the values of LAI’ and k, in determining the solar radiation intercepted by young tea. Since the normal growth habit of a tea bush is upright, the leaf area index tends to be high within the canopy. Even at the lowest calculated value for LAI’ of 4.1, the tea plants intercepted 91% of the incident light within the area of the bush. Because additional leaf growth at the centre of the bush leads to greater shading of the existing leaves, increased light interception in young tea at a fixed spacing depends primarily on promoting the lateral spread of the bush. Tea growers have developed many practical ways of doing this including pruning and ‘pegging’.

Although the tea bushes in this experiment were pegged during 1989, there were still important clonal differences in light interception. For example Clone S15/10, which tends to spread naturally was able to intercept more solar radiation than Clone 6/8 (which has a more erect habit) and this characteristic can explain, in part, the particularly large yields obtained from Clone S15/10 during the initial three years of this experiment (Burgess and Carr, 1996a). The capacity of a clone to establish rapid full-crop cover is also beneficial because it minimises weed growth and soil erosion, and encourages the build-up of leaf litter beneath the canopy.

The results also highlight the importance of minimising water stress to maximise light interception by young tea plants. Whereas mature bushes of some clones may be able to maintain a full crop canopy after six months without rain or irrigation (Stephens and Carr, 1991), the young plants in this experiment showed a mean reduction of 26% in light interception *during* four months of drought. As reported in Part I (Burgess and Carr, 1996a), such reductions in canopy cover will reduce yields during the subsequent wet season.

Radiation use efficiency

The observation that there were no consistent differences between the radiation use efficiency of the four clones under well-watered conditions corresponds with measurements made during 1990 (Smith *et al.*, 1994) which showed that the fully illuminated leaves of these clones had similar photosynthetic rates (3.96-4.22 μmol m^{-2} s^{-1}). Although the same authors reported that a fifth clone, labelled 207, had a low photosynthetic rate (3.35 μmol m^{-2} s^{-1}) the radiation use efficiency of this clone was not measured.

The mean ε_S values of 0.40-0.66 g MJ^{-1} for the four fully irrigated clones are higher than the estimate (0.25 g MJ^{-1}) inferred for six year old harvested Clone 6/8 grown at high altitude (2178 m) in Kenya (Magambo and Cannell, 1981). Although the mean annual air temperature at Ngwazi (16.7°C) is marginally higher than that at the Kenyan site (16.2°C), there are seasonal differences in temperature which may be important. Secondly although it was reported that the plants in Kenya had 'complete' canopy cover, the first measurements were taken only four months after the bushes had been pruned and during a period when hail damage occurred. In such circumstances, it is improbable that light interception was 100% and therefore the actual radiation use efficiency could have been higher than the values indicated. An additional explanation is that the tea bushes sampled in Kenya, which were older and larger than those monitored in Tanzania, had correspondingly greater respiration losses. If the level of respiration, relative to photosynthesis, increases as a plant grows (Charles-Edwards, 1982) then this would also reduce the value of ε_S. This may also explain the observation that the radiation use efficiency fell from 0.66 to 0.42 g MJ^{-1} over the experimental period described here.

The possible effects of biases in the reported values of ε_S, caused by the selection of particularly large or small plants at the start or the end of each period, were minimised by measuring at least three plants at each harvest. A larger sample than this was precluded because of the limited plot sizes and the need to excavate roots to depths below 1.5 m in the final two harvests. The precision of the values also depends on the validity of the assumption that the turnover of fine roots or the breakdown of leaf litter were minimal. If either of these assumptions is incorrect then ε_S will have been underestimated.

The values of 0.40-0.66 g MJ^{-1} are similar to those reported for other tropical woody crops such as oil palm (0.70 g MJ^{-1}; Corley *et al.*, 1971 calculated by Squire, 1990). However they are lower than those, including roots, for well-watered tropical annual crops such as groundnut (1.09 g MJ^{-1}; Azam-Ali *et al.* 1989). A possible reason for the apparent low radiation use efficiency of tea is that a high proportion, between 67% (Tanton, 1979) and 85% (Hadfield, 1974), of the total dry matter produced by photosynthesis is estimated to be lost by respiration compared with 30-50%, for example, by a grass crop (Charles-Edwards, 1982). A second explanation, is that the individual leaves of tea bushes have a relatively slow rate of carbon assimilation (Smith *et al.*, 1993). This could be due partly to environmental factors, such as the vapour pressure deficit of the air, limiting stomatal conductance. However Squire (1985) and Cannell (1985) have suggested that the removal of the shoots which form important sinks for assimilates could also feed back to reduce photosynthetic rates.

The values established for the radiation use efficiency of tea in Tanzania are also lower than those for crops, including roots, grown in temperate areas such as sugar beet (1.6 g MJ^{-1}; Scott *et al.*, 1994) and willow cuttings (1.58 g MJ^{-1}; Cannell *et al.*, 1987). Whereas canopies in Britain are seldom light saturated for prolonged periods, the day-time light intensities at the experimental site in Tanzania are often above the level (1000 μmol m^{-2} s^{-1} photosynthetically active radiation (PAR) or about 480 W m^{-2} total short-wave radiation) where photosynthetic rates are insensitive to changes in illuminance (Smith *et al.*, 1993). In addition because most leaves of commercially harvested tea are concentrated in a narrow layer near the surface of the canopy, they will tend to be exposed to the full intensity of the incident radiation. By contrast if the same bushes are left unharvested for many months an uneven canopy is produced with fewer, but larger individual shoots with erect leaves at the top and horizontal leaves lower down. Light penetration will be deeper within such a canopy and a greater number of leaves will intercept light at intensities where photosynthesis per unit of radiation is more efficient than in a conventionally harvested bush. This may also explain why Magambo and Cannell (1981) found that dry matter production was less in harvested tea than in unharvested plants even though the canopy cover was ‘complete’ in both cases.

Whereas the imposition of water stress caused a 26% reduction in light interception from August to November 1990 (24 to 27 months after planting), the value of ε_S was reduced by 78%. This sensitivity of radiation use efficiency to drought is also substantiated by measurements reported by Smith *et al.* (1994). These showed that the mean leaf photosynthetic rate (at illuminances greater than 1000 μmol m^{-2} s^{-1} PAR) for the same four clones at this time was halved from 4.1 μmol m^{-2} s^{-1} in the well-watered treatments to 2.0 μmol m^{-2} s^{-1} where the plants were most stressed.

There were also indications that the radiation use efficiency of Clone 6/8 was reduced more by water stress than those of Clones 1 and SFS150. Although this difference must be treated with caution because of the limited sample size, the results are again supported by the observations of Smith *et al.* (1994) who reported that the mean leaf photosynthetic rates for unirrigated plants of Clones 1 and SFS150 (2.1-2.2 μmol m^{-2} s^{-1}) were 30% greater than those for Clone 6/8 (1.6 μmol m^{-2} s^{-1}). These differences also correspond with the observation, reported in Part I (Burgess and Carr, 1996a), that the annual yields from Clones 1 and SFS150 were less sensitive to drought than those of Clone 6/8.

Dry matter partitioning

Effects of temperature: dry matter partitioning to harvested shoots and leaves was lower (both in absolute and relative terms) during the cool season (T_{mean} = 14-15°C), than during the warm months from September to April (T_{mean} = 16-19°C). This corresponds with concurrent measurements reported in Part III (Burgess and Carr, 1996b) which showed that shoot extension rates were closely related to air temperature. Because net dry matter production appears to be less sensitive to low temperatures than shoot extension, the reduced ‘demand’ for photosynthates by the shoots at low temperatures results in increased partitioning of dry matter to the roots. This translocation of photosynthates to the roots during cool weather has also been demonstrated for tea using radio-carbon tracing techniques in Assam (Manivel and Hussain, 1982), whilst active root growth during the cool season in Tanzania has been observed in underground root chambers by Carr (1971).

As air temperatures increase the processes are reversed. High temperatures lead to fast shoot extension rates and the resultant ‘demand’ of the shoots for photosynthates reduces the diversion of assimilates to the roots. Preferential translocation of dry matter to the canopy after a cool season has also been reported for tea in Malawi (Fordham, 1972; Herd and Squire, 1976), which explains, in part, the large peaks in yield observed from irrigated tea in Southern Tanzania during October (Stephens and Carr, 1991; Burgess and Carr, 1996a).

Effects of clone: in addition to rapid establishment of crop cover, the large initial yields from Clone S15/10 resulted from a high harvest index, which was associated with greater dry matter partitioning to other, non-harvested, leaves than for the other three clones. A similar positive relationship between the harvest index and the proportion of dry matter partitioned to the canopy has been reported by Othieno (1982) in Kenya. Of particular interest for clonal selection is that this physiological trait was apparent in plants less than eight months after field planting. Clonal differences in the proportion of dry mass partitioned to the leaves of young tea plants may therefore be a selection criterion for identifying high yielding clones at a relatively early stage.

The harvest index (24%) observed for Clone S15/10, for the period two to four years after field planting, is substantially greater than the value of 16% reported for Clone UPASI-3 in Southern India (Murty and Sharma, 1986) and the 8% reported for Clone 6/8 at high altitude in Kenya (Magambo and Cannell, 1981). This new target for the harvest index of tea highlights the potential opportunities for growers to increase yields through clonal selection, and Clone S15/10 in particular may provide a good base from which to breed and select further high yielding clones. Indeed African Highlands Produce Co. Ltd. is already using this clone within its breeding programme in Kenya.

The stems of Clone S15/10 were also less woody (they had a high proportion of green stem) than those of the other clones. Increases in the proportion of green stem should benefit yield since it increases both the photosynthetic area and the proportion of the bush that remains harvestable. This is also likely to reduce the ‘creep’ in the height of the canopy surface over time and hence extend the length of the pruning cycle. The proportion of the stem that is green may also provide a visible and easily determined criterion for selecting high yielding clones.

Although Clone S15/10 partitioned a relatively small proportion of dry matter to thick roots, it had a similar mass of fine roots to Clones 1, 6/8 and SFS150. It is these thin roots that are believed to be important in determining the uptake of water and nutrients from the soil. In Assam, high ratios of fine to thick roots in nine-month-old plants of a single clone were linked to rapid canopy growth (Chamuah, 1988), a characteristic also shown by Clone S15/10. By contrast Nyirenda (1990) in Malawi reported that high ratios of thick to thin roots were associated with vigorous clones. This may be true if vigour is defined as the capacity of a clone to develop a new canopy quickly after being pruned. Field experience in Kenya has indicated that Clone S15/10 produces less crop than expected in the year immediately after pruning. The small mass of structural roots in Clone S15/10 provides a physiological explanation for this observation, as these roots are an important source of the starch reserves utilised during refoliation. As a result some growers in Kenya have altered their pruning policy for this clone so that only a proportion, usually a half, of each plant is pruned at any one time to enhance the rate at which the bushes return to full productivity.

Effects of drought: the short periods of drought imposed had no observable effects on root depth, nor on the amount of dry matter partitioned to structural roots; instead drought severely reduced partitioning to harvested shoots and leaves. Similar results have been reported for very young tea plants five to twelve months after propagation (Kulasegaram and Kathiravetpillai, 1976) and for two to four year old field grown clones in Kenya (Othieno, 1982). This supports the view that root growth is less sensitive to low soil water potentials than the growth of leaves and shoots.

The rates of root extension with depth averaged about 2 mm d^{-1} from the first to the fourth year after field planting and there were relatively small differences between clones in root depth. Since the maximum rooting depth observed at this site for mature tea (Clone 6/8) is about 5.5 m, roots can be expected to reach this depth seven to eight years after planting. Treatment effects on root distribution with depth will be reported elsewhere.

In summary, although young well-watered tea plants can have a similar radiation use efficiency to other woody tropical crops, yields remain limited by a low harvest index. With some clones, such as S15/10, it is possible for growers to remove 24% of the net annual dry matter production as a saleable crop, although the relatively small mass of structural roots may necessitate a change in pruning practice. Because partitioning to the canopy and harvested shoots is also affected by temperature, harvest indices above this level should be achievable where mean annual air temperatures are greater than about 17°C. The trial has also highlighted the adverse effects on yield of even short periods of drought stress on young tea plants through reductions in light interception and, particularly, radiation use efficiency and harvest index.

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