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EFFECT OF SATURATION VAPOUR PRESSURE DEFICIT OF AIR ON SHOOT GROWTH OF CLONAL TEA *(CAMELLIA SINENSIS L.)* UNDER CONTROLLED ENVIRONMENTAL CONDITIONS

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Shoot extension and development measured on clones, ATK, B6/61 , B5/63 and 12/49 at 1.6, 2.1 and 2.6 kPa of saturation vapour pressure deficit (SVPD) of air at constant day (28°C) and night (18°C) temperatures of air and night-time humidity of 95% revealed significant ($p<0.001$) clone x saturation deficit interactions. Compared to shoot extension, development was less affected by the two higher levels of SVPD of air. Clone ATK was the least and B5/63 was the most affected by dry air, while the former maintained a fast rate of shoot extension and development compared to the other three clones under all levels of SVPD. Shoots of clone 12/49 were the slowest growing of all clones but had shown tolerance of dry air. The reduction in shoot extension and development of the clones were observed when SVPD was increased from 1.6 to 2.1 kPa (at 28°C). The response of shoot growth to SVPD is discussed in relation to harvesting, yield and identification of selection criteria.

INTRODUCTION

Environment influences the yield of tea through its effects on shoot growth. The genotype x environment (G x E) interactions in the yield of clonal tea in Sri Lanka reported by Wickramaratne (1981) could be the result of the differing responses of shoot growth to the environment of the four agro-ecological zones. This same study also revealed the existence of highly sensitive to relatively insensitive clones to the differing environments. Although tea is cultivated as a rainfed crop in Sri Lanka, a distinct dry period of not more than 3 to 4 months is a general characteristic feature of the annual weather in the eastern parts of up and mid country which is associated with low yields. The weather during this period is characterized by high day and low night time air temperatures, low relative humidity (<40%) and low rainfall (50 mm $month^{-1}$).

Closely associated with high air temperatures (>30-35°C) are the large saturation vapour pressure deficits of air which possibly suppressed the shoot growth of tea during dry weather in N. E. India, reported by Hadfield (1968). Therefore, either large SVPDs of air or soil moisture deficits or both can be constraint(s) to yields of clones during dry weather.Williams (1971) and Carr, Dale and Stephens (1987) linked low yields of tea in the dry season of Malawi to large saturation vapour pressure deficits of air (SVPD) above 2.0 kPa, while

Squire (1979) and Tanton (1982) demonstrated that dry air (SVPD)≥ 2.0 kPa suppressed shoot growth.

Although soil moisture deficits are controlled by irrigation in places like Malawi and Tanzania, the mitigation of SVPD of air on a plantation is not feasible.

However, Lebedev (1961) in Georgia (USSR) and Tanton (1982) in Malawi showed that mist irrigation could lower the adverse effects of dry air on shoot growth. Since mist irrigation of tea fields in large plantations is impracticable, the best alternatives appears to be the selection of tolerant/resistant clones by identifying the physiological attributes which are less affected by large SVPDs of air. Therefore, G x E interactions can become an useful attribute in solving agronomic problems of tea in the field.

MATERIALS AND METHODS

Saturation vapour pressure deficit of air

The experiment was carried out in the growth rooms (System Weiss, Walk-in type) of the Plant Breeding International (PBI), Cambridge. Three growth rooms were kept under constant day (28°C) and night (18°C) air temperatures throughout the experiment while the day time relative humidity (RH) varied: 65, 46 and 28%. The night RH was constant at 95% in each growth room. These conditions provided three levels of saturation vapour pressure deficit of air (SVPD) in the three growth rooms during the day, 1.6, 2.1 and 2.6 kPa respectively. The selected SVPD levels were the critical level at which the linear response of shoot growth to temperature was reported to have obscured (around 2.0 kPa) and two other levels which were about 0.5 kPa above and below this critical level. The duration of the day and night period in each growth room was 11.5 h.

The day and night time air temperatures inside each growth room were checked daily with a mercury-in-glass thermometer (dry bulb) and the RH with an Assman (aspirated) hygrometer. These values were used to check the SVPD of air in each growth room.

Clones

The four clones used in this study were 1.5 to 2.0 years of age and raised from cuttings inside the glasshouses of PBI. Clones ATK, B6/61 and 5/63 were South Indian while 12/49 was Kenyan in origin. Four plants of each clone were used in each growth room thus allowing a total of 16 plants potted in plastic pots per room. The pots used were of two sizes 4617 and 7289 m^3 depending on the size of the plants, arranged randomly on perforated benches and irrigated daily by a drip system with the onset of the night-time conditions. The excess water was drained into a plastic pan kept beneath each pot and removed from the growth rooms just before the day-time conditions began.

The surface of each pot was covered by black polythene to prevent evaporation of water from the planting medium during day time and the growth of algae.Clones B6/61 and ATK had dark green, narrow leaves while that of B5/63 were thick, broad and soft. The shoots of clone B5/63 were the largest. Clone 12/49 had light green broad leaves which were larger

than the leaves of the others and was known to have drought tolerance (B.G.Smith, personal communication).

Shoot extension

From each clone, 15 shoots, each carrying an active terminal bud and two fully opened leaves, were plucked and the axillary bud of the third leaf was tagged and allowed to grow into a shoot. The length of the stalk of the expanding bud was measured when it was first visible using a Vernier caliper. The length was measured from the base of the bud to the leaf axil, twice a week until the shoot entered the rapid growth phase with the unfurling of fish leaf and thereafter more frequently, every two days. The measurements were continued until the new shoot completed its periodic growth cycle and became dormant. The **shoot extension rate** was determined by plotting the shoot length against the time (days from the time of shoot initiation until the shoot developed three true leaves). The **shoot length at harvest** of each shoot was measured when three leaves were unfurled. The **final shoot length** was measured when a shoot completed a periodic growth cycle with the terminal bud becoming dormant (banji).

Shoot development

The unfurling of the new leaves were observed until each shoot became dormant (banji). The duration of this process is called the **periodic growth cycle** (PGC). The **shoot replacement cycle** (SRC) is the time taken for unfurling of the third true leaf of a shoot from the time of the removal of apical dominance (shoot initiation) and the shoots of this stage are ready to be harvested.The **shoot development rate** (SDR) was calculated as the reciprocal of the shoot replacement cycle (1/SRC).The ***phyllochron*** is the time interval between the unfurling of two successive leaves on a shoot and this was measured for each shoot during a SRC thus obtaining two phyllochrons per shoot. These were the phyllochrons between the unfurling of the first and the second leaves and second and the third leaves.

RESULTS

Effect of dry air on shoots during the periodic shoot growth cycle

Duration of the periodic growth cycle

Although the duration of the periodic growth cycle (PGC) was prolonged at the two high levels of SVPD of air there were distinct clonal differences ($p<0.001$) at each of the three levels (Table 1).

At the lowest level of SVPD, shoots of the other three clones took an extra 6 to 7 days ($p<0.001$) than those of clone ATK, to complete the periodic growth cycle. However, when the SVPD was increased from 1.6 to 2.1 kPa the shoot development of clone B5/63 was further delayed, increasing the duration of PGC by 4 days ($p<0.001$) but remained unchanged thereafter. The shoots of clone B6/61 on other hand were more susceptible to the dryness of air at 2.6 kPa than at 2.1 kPa. None of the three levels of SVPD affected the duration of PGC of the shoots of clone ATK.

The response of the shoots of clone 12/49 to the increased dryness of air from 1.6 to 2.6 kPa was not clear. However, the shoots of this clone responded similarly to both the highest and the lowest levels of SVPD.

TABLE 1 - *Effect of saturation vapour pressure deficit of air on final shoot length and the duration of the periodic shoot growth cycle (PGC) of each of the four clones*

	Clone									
	PGC (days)					*Length (mm)*				
SD (kPa)	*ATK*	*B6/61*	*B5/63*	*12/49*	*Mean*	*ATK*	*B6/61*	*B5/63*	*12/49*	*Mean*
1.6	45	51	52	52	50	138	91	129	66	106
2.1	45	53	56	60	54	83	67	70	48	67
2.6	45	57	58	53	55	89	58	78	82	77
Mean	45	54	55	58		103	72	92	65	

		PGC				*Length*			
	df	ms	P	s.e.d.	LSD	ms	p	s.e.d.	LSD
Clone	3	1356.9	0.001	0.80	2.6	13781.8	<0.001	1.80	6.0
Saturation deficit	2	504.6	0.001	0.45	1.5	23806.4	<0.001	1.60	5.1
Clone x Satura tion deficit	6	155.6	0.001	1.30	4.0	4118.4	<0.001	3.10	10.3
Residual	168	13.4				72.9			
CV		6.9%				10.3%			

Final length of the shoot

The largest reduction in shoot length of 46% was observed in clone B5/63 ($p<0.001$) when SVPD of air increased from 1.6 to 2.1 kPa. However, when SVPD was further increased from 2.1 to 2.6 kPa, the effect of the dryness of air was less marked in the clones (Table 1).

The response of clone 12/49 to the three levels of SVPD was inconsistent. However, the longest shoots were observed at the highest level of SVPD ($p<0.001$). The response of both the duration of PGC and the final length of shoots to the increased dryness of air from 1.6 to 2.6 kPa indicated that shoots of clone 12/49 were not adversely affected by the SVPD of air in the test range.

Shoots reaching the harvestable stage
Shoot replacement cycle

Clonal variations in the response of the duration of the shoot replacement cycle (SRC) to the three levels of SVPD of air were found highly significant ($p<0.001$). Clone ATK had the shortest duration of SRC, which remained stable at all three SVPD levels tested (Fig. 1). Although the shoots of clones B6/61 and B5/63 reached the harvestable stage at the same time at 1.6 kPa, the increased dryness of air from 1.6 to 2.1 kPa, prolonged the duration of SRC (by 18%) only in clone B5/63 ($p<0.001$). Whereas in clone B6/61, the largest change

occurred only when SVPD was increased from 2.1 to 2.6 kPa, indicating a 13% increase in the duration of SRC ($p<0.001$).

Once again, clone 12/49 demonstrated an anomalous behaviour at 2.1 kPa. On the contrary, at the highest and lowest SVPD levels the shoots of clone 12/49 showed no response, when the duration of SRC is considered.

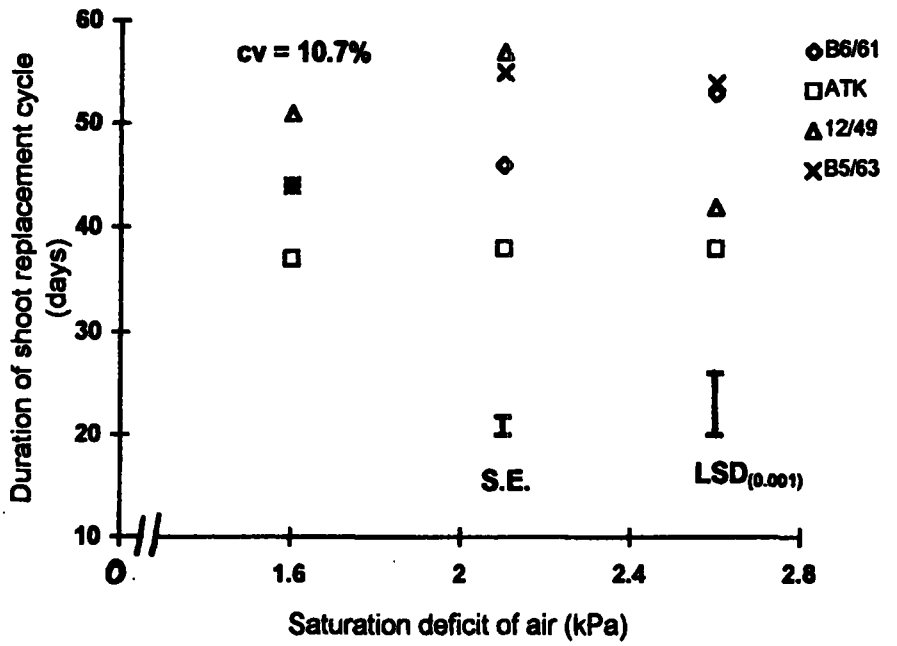

Fig. 1 - *Effect of saturation vapour pressure deficit of air at constant day and night temperatures of 28 and 18°C on shoot replacement cycle of each clone*
(The standard error (S.E.) and LSD are presented for clone x SVPD interaction)

Phyllochron

Although the duration of SRC was prolonged by the dryness of air the minimum number of leaves unfurled on a shoot (released from apical dominance) did not fall below three in any of the clones. Also, it was observed that the clonal mean of the third phyllochron was generally larger than that of the second (Table 2).

Both the second and the third phyllochrons of clone ATK remained remarkably constant at all levels of SVPD, although in the other three clones the two phyllochrons varied widely. Only in clone B6/61 both phyllochrons increased consistently with the increase in the dryness of air within the test range. The two phyllochrons of clone B5/63 did not respond to SVPD of air beyond the level of 2.1 kPa. Probably the prolonged duration of the SRC of this clone at 2.1 kPa could largely be attributed to the increased duration of the two phyllochrons.

However, clone 12/49 showed no distinct pattern in the response of both phyllochrons to the varying degree of dryness of air. The results suggest that the clone x SVPD interactions were more distinct in the third phyllochron than that of the second.

TABLE 2 - *Effect of saturation vapour pressure deficit of air on the duration of second and third phyllochrons of each of the four clones*

SVPD (kPa)	*Phyllochron (days) Clone*									
	Second leaf					*Third leaf*				
	ATK	*B6/61*	*B5/63*	*12/49*	*Mean*	*ATK*	*B6/61*	*B5/63*	*12/49*	*Mean*
1.6	5.0	5.0	5.3	5.3	5.2	5.0	5.5	6.4	8.6	6.4
2.1	5.0	6.1	7.4	7.3	6.5	5.2	7.2	7.4	7.9	6.9
2.6	5.2	7.1	7.2	6.1	7.2	5.2	8.3	7.1	6.1	6.7
Mean	5.1	6.1	6.0	6.1		5.1	7.0	7.0	7.5	

	df	ms	p	s.e.d.	LSD	ms	p	s.e.d	.LSD
Clone	3	13.7	<0.001	0.08	0.3	34.5	<0.001	0.13	0.4
SVPD	2	27.7	<0.001	0.07	0.2	12.3	<0.001	0.12	0.4
Clone x SVPD	6	07.1	<0.001	0.13	0.4	18.3	<0.001	0.23	0.8
Residual	168	0.25				0.80			
CV		10.3%				8.5%			

Shoot length

Except in clone 12/49 the shoot length at harvest reduced with the increase in SVPD from 1.6 to 2.1 kPa ($p<0.001$) and remained unchanged thereafter (Fig. 2). However, there were distinct clonal differences in the degree of response of the shoot length to dry air.

Clone B5/63 which produced the longest shoots at harvest at the lowest level of SVPD was more affected than the other clones by the increased dryness of air from 1.6 to 2.1 kPa showing a 31% reduction in the shoot length. In clones ATK and B6/61, the shoot length was reduced by only 14 and 28% respectively.

Although clone 12/49 had the shortest shoots at harvest, among the four clones tested at the lowest level of SVPD (1.6 kPa), the shoot length was not affected by the increase in the dryness of air. However, the short shoots observed in the middle level of SVPD (2.1 kPa) were unusual.

Rate of shoot growth
Shoot extension rate

The degree of response of the rate of shoot extension (SER) to the three levels of SVPD varied in the four clones. The SER which was measured up to the stage of harvest was reduced by 21 to 52 % ($p<0.001$) by the increase in the dryness of air from 1.6 to 2.1 kPa (Fig. 3). However, there was no further reduction in the SER when SVPD of air was increased from 2.1 to 2.6 kPa.

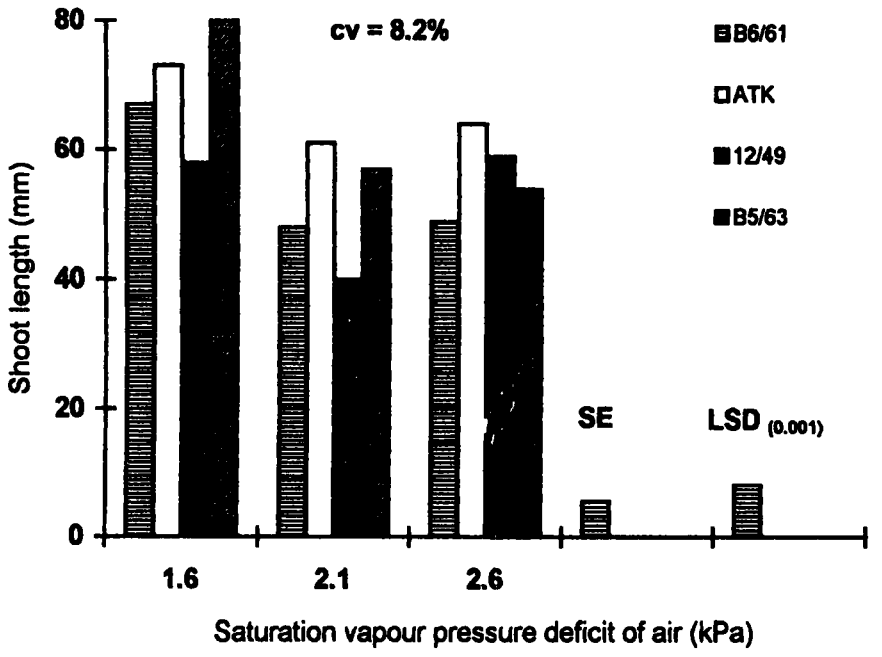

Fig. 2 -*Effect of saturation vapour pressure deficit of air at constant day and night temperatures of 28 and 18°C on shoot length at harvest of each of the four clones (The standard error (S.E.) and LSD are presented for clone x SVPD interaction)*

The shoots of clone ATK grew faster than those of the other three clones ($p<0.001$) and were relatively less affected by the increase in the dryness of air. The shoots elongated at a rate of 3.6 to 4.9 mm d^{-1} from dry to moist air respectively. Shoots of clone 12/49 grew slowly under all three levels of SVPD with an average SER of 2.4 mm d^{-1}.

Shoot development rate

In comparison to SER shoot development rate (SDR) was less affected by the increase in SVPD of air from 1.6 to 2.6 kPa (Fig. 4). However, the response of SDR to the increase in SVPD of air in clones B6/61 and B5/63 showed similar trends to that of SER though to a lesser degree.

Although the shoots of clone 12/49 developed faster at the highest level of SVPD (2.6 kPa) than at the lowest level (1.6 kPa), the SDR was still lower than that of clone ATK ($p<0.001$) at the highest level of SVPD.

DISCUSSION

Although the increased dryness of air from 1.6 to 2.6 kPa did not arrest shoot growth in any of the four clones, the two higher levels of SVPD tested in this study reduced shoot length and rate of shoot extension (SER), increased the time taken by shoots to reach harvestable stage (SRC) and prolonged the duration of time between the unfolding of two successive leaves (phyllochron). Therefore, according to the results, the occurrence of the

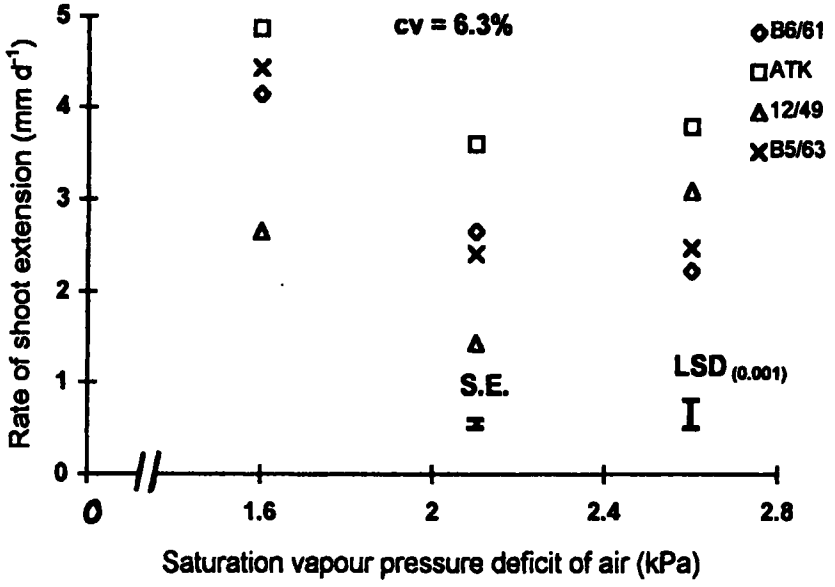

Fig. 3 -*Effect of saturation vapour pressure deficit of air at constant day (28°C) and night (18°C) temperatures on shoot extension rate of each of the four clones. (The standard error (S.E.) and LSD are presented for clone x SVPD interaction)*

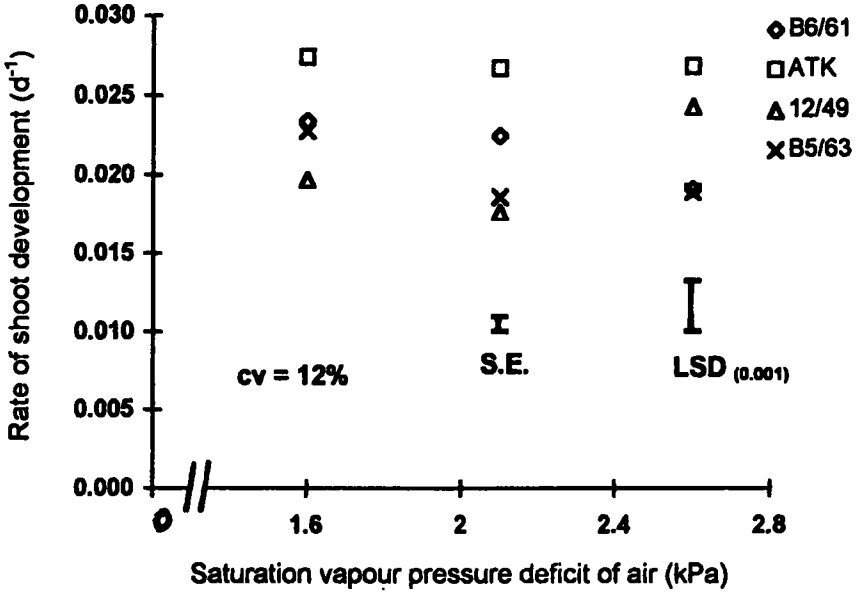

Fig. 4 -*Effect of saturation vapour pressure deficit of air at constant day (28°C) and night (18°C) temperatures on shoot development rate of each of the four clones. (The standard error (S.E.) and LSD are presented for clone x SVPD interaction)*

dryness of air during dry weather can affect the yield of clonal tea through its effect on shoot extension and development. However, the degree of dryness at which SVPD of air alone could affect shoot growth varied between clones and also within the same clone for the different physiological attributes of shoot growth studied.

The results have greater significance to tea grown under irrigation than under rainfed conditions. The suppressed yields of irrigated tea during dry weather reported elsewhere (Williams, 1971; Carr *et al.*, 1987) could therefore be attributed to the suppressed shoot growth due to high SVPD. Although Tanton (1982) and Squire (1979) in Malawi showed that shoot extension was adversely affected by saturation vapour pressure deficits of air above 2.0 kPa, the varying degree of response exhibited by the shoots of the four clones tested in this study suggest that the critical level of SVPD of air which affects shoot growth should differ between clones. Further, shoot extension was more sensitive to dry air than shoot development. Similar results were reported by Burgess (1992) too for fully irrigated clones in Tanzania. These two physiological attributes therefore, could be two independent growth processes which do not come under the same genetic control.

The reduced yields at high SVPDs of air can be explained by the suppressed shoot development as shown in this study, resulting in fewer number of shoot replacement cycles per year and prolonged harvesting intervals due to large phyllochrons. The large phyllochrons observed at high SVPDs can result in a small number of harvestable shoots if the harvesting interval is shorter than a phyllochron. Therefore, the results of this study indicate the necessity of increasing the length of harvesting interval, i.e. by reducing the frequency of harvesting, when large saturation vapour pressure deficits of air dominate the dry weather.

The results suggest that with the physiological maturity of the shoot the effect of SVPD on shoot development becomes less prominent as demonstrated by the third phyllochron (Table 2). To some extent, this fact explains the relatively low susceptibility of the shoot development to the dryness of air in the test range when compared to shoot extension.

The previous work on the effects of SVPD on tea which was mostly done on shoot extension and yield is not adequate to understand how dry air caused yield decline during dry weather in many parts of the world. Also, it is not yet completely understood how the SVPD of air affects the shoot dry weight and the density of harvestable shoots. In order to understand the yield decline of irrigated clones during the dry season the effect of SVPD on these two physiological attributes also have to be studied.

The anomalous behaviour of the shoots observed in clone 12/49 in the middle growth room (2.1 kPa) cannot be explained by the results. The plants which were raised inside the glasshouses of PBI may have undergone a physiological stress while remaining in them.

The shoot length at harvest of clones B6/61 and 12/49 remained unchanged at different levels of SVPD while SER and SDR changed due to changes in the duration of SRC. Therefore, shoot length at harvest alone will not be an ideal measure of the effects of environmental variables on shoot growth. To overcome this disadvantage, when the effects of environmental variables on shoot growth in relation to yield are investigated, both the duration of SRC and the harvested shoot length or shoot extension rate should be measured.

Thermal time calculated over a base temperature of 12.5°C for shoot development (up to harvestable stage of bud and three leaves)) of the susceptible clones, B6/61 and B5/63 showed an increase from 462d°C in moist air (1.6 kPa) to 567d°C in dry air (2.6 kPa) although the temperature was kept constant during day and night in all three growth rooms. Stephens and Carr (1992) suggested that thermal time could be affected by factors like nutritional status of the soil. It is also possible, that the two high SVPDs had changed either the thermal time or the base temperature of the two susceptible clones in this experiment.

Genotype x Environment interactions

The effects of genotype x environment interactions on shoot growth observed in this study could be summarized as follows.

(i) Clone B5/63 was the only clone which had both shoot extension and development adversely affected by SVPD of air at 2.1 kPa.

(ii) Shoot development in clone B6/61 was suppressed only at the highest level of SVPD of air (2.6 kPa) in the test range.

(iii) Compared to clones B6/61 and B5/63, the shoot length and rate of shoot extension were less affected by the SVPD of air at 2.1 kPa, in clone ATK while shoot development was totally unaffected.

(iv) Although, the shoot length of clone 12/49 remained stable at the highest and the lowest levels of SVPD of the test range, the reduced duration of SRC increased the rates of shoot extension and development up to the harvestable stage at the highest level of SVPD (2.6 kPa).

Shoots of clone ATK in this study were reasonably tolerant of dry air within the range tested while clone B5/63 was the most susceptible. Venkataramani and Sharma (1974) reported that clone B5/63 was drought sensitive. The adverse effects of drought on this clone therefore, could have been partly due to the high saturation vapour pressure deficits of air during the dry season.

On the other hand, shoots of clone 12/49 should either possess tolerance to dry air or favoured by the dryness of air within the test range. Similar observations were made for clones 31/8, 15/10 and 57/15 in Kenya by Odhiambo, Nyabundi and Chweya (1993), where shoot extension rate was increased by high SVPDs of air above 2.0 kPa during dry weather. Also, a stable shoot length at harvest irrespective of the changes in SER at different SVPD levels shown by clone 12/49 could be an advantage for mechanical harvesting. However, such clones should possess heavy shoots and a large shoot population density to compensate for the relatively slow shoot growth in order to have a reasonably good yield in dry weather.

Practical implications

The occurrence of short shoots during dry weather can cause difficulties in both manual and mechanical harvesting. A stable shoot length in both wet and dry weather is therefore, an advantage.

The shoots of clones with a stable shoot development rate and a phyllochron can be harvested at similar intervals in both moist and dry weather. In order to find whether such clones possess yield stability under both these situations, the sensitivity of the other yield components (density of harvested shoots and mean shoot dry weight) to dry air has to be investigated.

Clonal differences in the response of shoot growth to large saturation vapour pressure deficits of air indicate the necessity for selection of tolerant clones for areas prone to dry weather. Since mist irrigation is not practicable on plantations to moisten the air during dry weather, clones selected for tolerance/ resistance are the only possible answer for such conditions.

The shoot development rate, shoot length at harvest and the base temperature and thermal time required for shoot development could possibly be used as criteria for selecting clones for areas prone to prolonged durations of dry weather.

Also, it should be possible to reduce the dryness of air by growing suitable shade trees with deep root systems, which can increase the humidity and decrease the day-time air temperature of the micro-climate surrounding the tea bushes. Further, by lowering the ambient temperature in the micro-climate during dry weather, the shade trees can bring down the high leaf temperatures too which affect photosynthesis.

In order to obtain more economic benefits from irrigation of tea in dry weather, genotype x environment interactions need to be taken into consideration.

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