Tropical Agricultural Research and Extension. 1(2): 74-80, 1998

Water relations of clonal tea (*Camellia sinensis* L.) with reference to drought resistance: II. Effect of water stress

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Accepted 13 August 1998

ABSTRACT

Most of the tea (*Camellia sinensis*) plantations in Sri Lanka are subjected to drought damages during the first quarter of the year due to uneven distribution of rainfall. Hence, screening of clones for drought tolerance is important for introducing suitable clones for drought prone regions. A glass house experiment was conducted using young tea plants to study the clonal variation of water relations pertaining to drought tolerance. Soil moisture stress reduced relative water content and water potential, and increased diffusive resistance of tea leaves. The critical leaf water potential increasing diffusive resistance and reducing transpiration of drought tolerant clone (TRI 2025) is comparatively higher than that of drought susceptible clone (TRI 2023). The drought tolerant clone permanently wilted at a soil water potential lower than that for the drought susceptible clone. Results showed that the clones having efficient stomatal control for reducing water loss and osmotic adjustments for absorbing water from drier soils can withstand drought.

Key words: *Camellia sinensis,* drought, tea, transpiration, water potential

INTRODUCTION

Stomatal transpiration, diffusive resistance and plant water potentials greatly influence the water balance of plants. Therefore, the physiological functions of the leaf canopy play a decisive role in the water economy of plants which determines their growth and survival. Jones (1983) reported a functional relationship between root water potential and leaf water potential together with leaf conductances.

Plants withstand soil drying by lowering their water potentials to more negative values than that of soil. However, there is a limit that a plant can adjust its osmotic potential for the absorption of water from drying soil before it is permanently wilted. Accumulation of osmotically active solutes in the plant cells causes changes in the osmotic potential. Such osmotic adjustments are considered to be important properties of drought tolerant plant species (Munns *et al.* 1979; Hale and Orcutt 1987; Planchon 1987; Venkataraman *et al.* 1989; Brisson *et al.* 1993).

Soil moisture stress affects the stomatal conductance and transpiration of tea (*Camellia sinensis*) leaves (Fordham 1971; Callander and Woodhead 1981; Gee *et al.* 1982; Saikia and Dey 1984; Squire 1990). A greater reduction of evaporation has been observed in tea when soil moisture deficit exceeded a critical limit of about 60 mm in southern highlands of Tanzania (Stephens and Carr 1991). Depending on the soil type, growth of tea is reduced when available water falls below a critical limit. At the high end of the soil moisture range, problems may occur due to poor aeration. Plant growth often appears to be optimal within the range of 60-70% of the total moisture content although this may vary with environmental conditions (Tkebuchava 1989; Hasan *et al.* 1968). Willatt (1971) reported that poor growth of tea occurred when the soil moisture content was below 40% of the available range. Even with the presence of ample moisture in the soil, water potential of the tea plant can be affected if the surrounding environment is dry (Williams 1971). However, Squire (1978) suggested that the stomatal conductance of tea leaves was independent of the saturation vapour pressure deficit. Some clonal differences in the stomatal conductance of tea have also been reported (Squire 1976).

Experimental results have shown that the relative water content has a close relationship with leaf water potential (Burrows and Milthorpe 1976). This relationship, illustrated by the pressure volume curve, could be used as a key factor for screening plant species for drought tolerance (Jarvis and Jarvis 1963; Jones *et al.* 1981; Sandanam *et al.* 1981). The effects of soil moisture stress on plant growth are

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Abbreviations: DR - Diffusive resistance, LWP - Leaf water potential, OP- Osmotic potential, RWC - Relative water content, RWP - Root water potential, TR - Transpiration.

well known (Mansfield and Wilson 1981; Gee *et al.* 1982; Saikia and Dey 1984; Squire 1990; and Burgess 1992a).

The clonal variation in the water relation characteristics of tea provide a basis for selection of clones for drought prone regions. The present experiment was conducted to uncover the clonal differences of water relations with reference to soil moisture stress.

MATERIALS AND METHODS

Treatments

The details of the experimental layout and materials and methods were presented in the previous paper (Wijeratne *et al.* 1998). Potted plants of TRI 2025 (drought tolerant) and TRI 2023 (drought susceptible) clones were used for the study. Two moisture regimes, i.e. Well watered and water stressed, were maintained throughout the experimental period. Four treatment combinations i.e. 2 clones x 2 moisture regimes, were arranged factorially in three replicates, each having 80 plants. Plants receiving well watered treatment were watered daily and the other set of plants were kept without watering until they were permanently wilted. Bare soil evaporation was measured using pots without plants.

Measurements

Transpiration (TR) was measured gravimetrically by weighing pots as well as using the Steady State Porometer (Li-1600, Li-Cor Inc. Ltd. USA). Diffusive resistance (DR) was also recorded using the porometer. Relative water content (RWC) (Sandanam *et al.* 1981) and leaf water potential (LWP) (Scholander *et al.* 1965) were also measured using mature tea leaves. Water potential of the drying soil (SWP) was estimated from a calibration curve of water potential versus moisture content (Reeve and Carter 1991). Root water potential of water stressed plants (RWP) was estimated using the method described by Jones (1983).

To study the water relation characteristics of the two clones in detail, relative water content and leaf water potential at the turgor loss point were estimated from the pressure volume curves as described by Doley (1981) and Jones (1992). In order to draw these two curves, daily averages of leaf water potential and relative water content from well watered and moisture stressed plants were used. Using the pressure volume curve it is possible to determine the osmotic potential at full turgor and turgor loss point. The difference between these two points gives the range of osmotic adjustment inherited by the plant.

RESULTS

The patterns of variation of plant and soil water potentials *viz.* For leaf, root and the soil during a complete drying cycle are shown in Fig. 1 The soil water potential of the root zone at permanent wilting point estimated from soil samples collected from permanently wilted plants, was - 1.47 (±0.19) Mpa for TRI 2023 and -2.78 (±0.16) for TRI 2025. The percentages of soil moisture at these soil water potentials were 5.89 (±0.17) and 5.08 (±0.07), respectively. At the beginning of the drying cycle, the pre-dawn water potentials of plants were near zero. Subsequently it decreased towards mid-day when a larger gradient between soil and plant occurred. The gradual reduction of soil water potential in drying pots reduced the gradient between leaf and root water potentials which were found to be close to each other at permanent wilting point when there was no available water for plant growth. The soil, root and leaf water potentials reduced consistently with soil drying. This pattern was

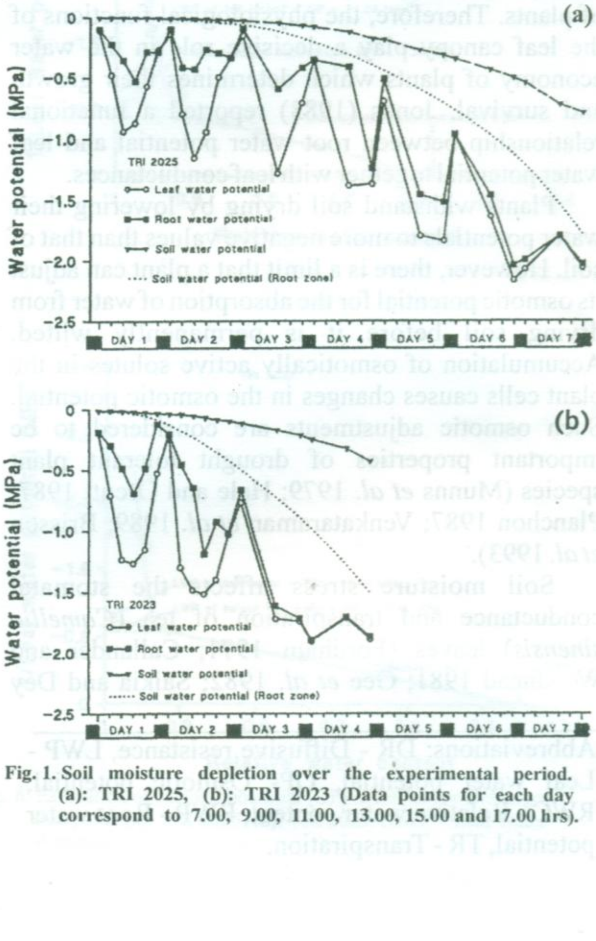

Fig. 1. Soil moisture depletion over the experimental period. (a): TRI 2025, (b): TRI 2023 (Data points for each day correspond to 7.00, 9.00, 11.00, 13.00, 15.00 and 17.00 hrs).

similar for both clones studied, but the period of completing a drying cycle was shorter for TRI 2023 (4 days) than for TRI 2025 (7 days).

Effect of soil moisture stress on diurnal variations

The comparison of diurnal changes of relative water content, leaf water potential and diffusive resistance of moisture stressed and well watered plants are summarized in Tables 1-3. Moisture stress reduced relative water content and leaf water potential and increased diffusive resistance of both clones. The diurnal pattern of these variables of water stressed plants was similar to that of well watered plants. The effect of soil moisture stress on above parameters of TRI 2025 plants was comparatively less than that on TRI 2023. However, very high values of diffusive resistance were recorded by the leaves of drought susceptible TRI 2023 on the third day evening as they were reaching turgor loss point, i.e. they were permanently wilted by the fourth day morning.

Table 1. Effect of soil moisture on relative water content on 3rd day

Time	TRI 2025		TRI 2023	
(Hrs)	Wet	Dry	Wet	Dry
07.00	0.971	0.959	0.974	0.945
13.00	0.945	0.930	0.934	0.776
17.00	0.975	0.940	0.969	0.812
Mean	0.964	0.943	0.959	0.845

$LSD_{p=0.001}$ (For means) = 0.0517
CV = 4.2%

Table 2. Effect of soil moisture on leaf water potential (MPa) 3rd day

Time	TRI 2025		TRI 2023	
(Hrs)	Wet	Dry	Wet	Dry
07.00	-0.137	-0.153	-0.280	-0.767
13.00	-0.580	-1.286	-1.033	-1.720
17.00	-0.120	-0.713	-0.166	-1.740
Mean	-0.279	-0.718	-0.493	-1.409

$LSD_{p=0.001}$ (For means) = 0.198
CV = 19.0%

Table 3. Effect of soil moisture on diffusive resistance (s cm^{-1}) - 3rd day

Time	TRI 2025		TRI 2023	
(Hrs)	Wet	Dry	Wet	Dry
07.00	80.0	92.8	28.5	78.6
13.00	4.8	6.9	2.6	25.4
17.00	31.5	19.7	8.1	59.4
Mean	38.8	39.8	13.1	54.5

$LSD_{p=0.01}$ (For means) = 22.35
CV = 16.1%

Changes in leaf water potential and relative water content of water stressed plants

The daily averages of relative water content and leaf water potential of water stressed TRI 2025 and TRI 2023 are shown in Fig. 2. Soil drying has resulted in the reduction of leaf relative water content and leaf water potential. All water stressed TRI 2023 plants used for measurements were permanently wilted (*i.e.* Plants remained wilted by the morning) by the fourth day of the experiment and recording was stopped on the seventh day by which time all water stressed TRI 2025 plants were also permanently wilted. The effect of soil moisture stress on relative water content and leaf water potential of TRI 2025 was significant about 3 days after withholding watering; however, corresponding data for TRI 2023 showed a significant effect by the second day. The rate of reduction in leaf water potential and relative water content appeared to be lower for TRI 2025 relative to TRI 2023 (Fig. 2).

Relationship between diffusive resistance, leaf water potential and relative water content of moisture stressed plants

In order to study the effect of soil moisture on leaf water relations, the daily averages of measurements from both moisture stressed and well watered plants were pooled together. The effects of lowered relative water content brought about by soil moisture stress on leaf diffusive resistance and transpiration of tea leaves are shown in Fig. 3. Daily averages (9.00 - 15.00 hrs) of diffusive resistance and were found to be unaffected by relative water content above 0.93-0.94. Moreover, diffusive resistance of TRI 2025 for a given relative water content was comparatively

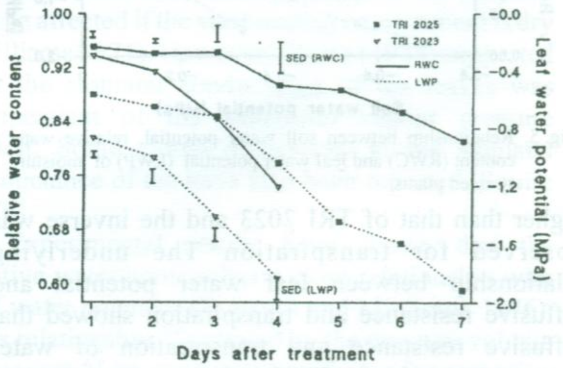

Fig. 2. Daily averages of relative water content (RWC) and leaf water potential (LWP) of moisture stressed plants.

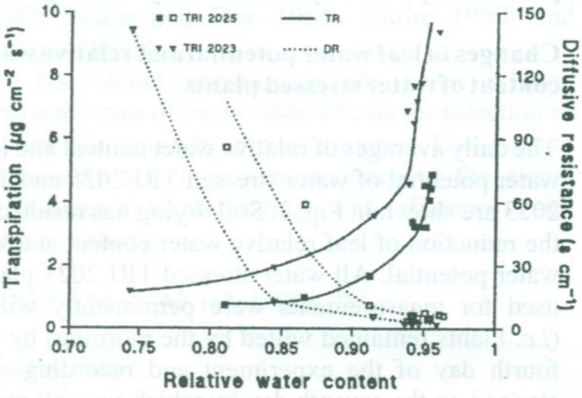

Fig. 3. Relationship between relative water content, transpiration (TR) and diffusive resistance (DR) (Data from both well watered and moisture stressed plants).

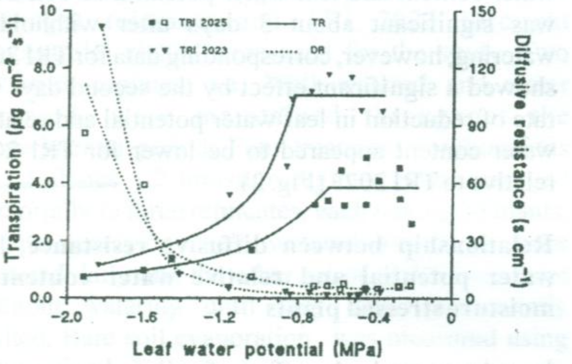

Fig. 4. Relationship between leaf water potential, transpiration (TR) and diffusive resistance (DR) (Data from both well watered and moisture stressed plants)

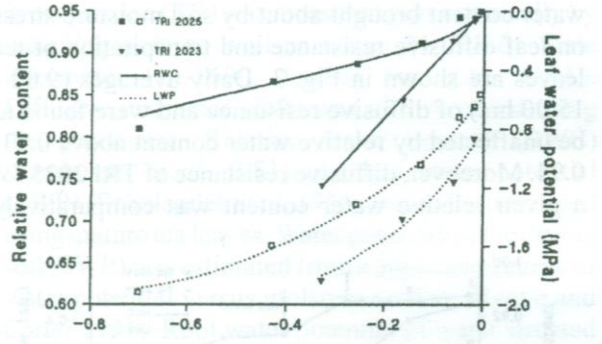

Fig. 5. Relationship between soil water potential, relative water content (RWC) and leaf water potential (LWP) of moisture stressed plants.

higher than that of TRI 2023 and the inverse was observed for transpiration The underlying relationship between leaf water potential and diffusive resistance and transpiration showed that diffusive resistance and transpiration of water stressed TRI 2023 and TRI 2025 were affected at leaf water potentials below -0.75-0.85 MPa (Fig. 4) Further, it shows that the leaf water potential affecting transpiration and diffusive resistance of TRI 2025 is comparatively higher than that of TRI 2023. The relative water content and leaf water potentials of water stressed plants affected by soil water potentials are shown in Fig. 5. For a given soil water potential, TRI 2025 plants had a higher leaf water potential than those of TRI 2023. The same is true for the recorded relative water content at different levels of soil water potential.

Pressure volume curves for the two clones are given in Fig. 6. These figures show that the osmotic potentials (OP) of TRI 2025 and TRI 2023 leaves, at full turgor, were - 1.06 and -0.99 Mpa, while those at zero turgor (incipient plasmolysis) were -1.33 Mpa and -1.17 Mpa, respectively. Relative water content at zero turgor has been estimated as 0.90 for TRI 2025 leaves and 0.92 for TRI 2023 leaves. Further, the proportion of appoplastic water content of the leaves were 0.58 and 0.45 for TRI 2025 and TRI 2023. Linear relationship between leaf water potential (LWP) and relative water content (RWC) given below confirmed the significant difference

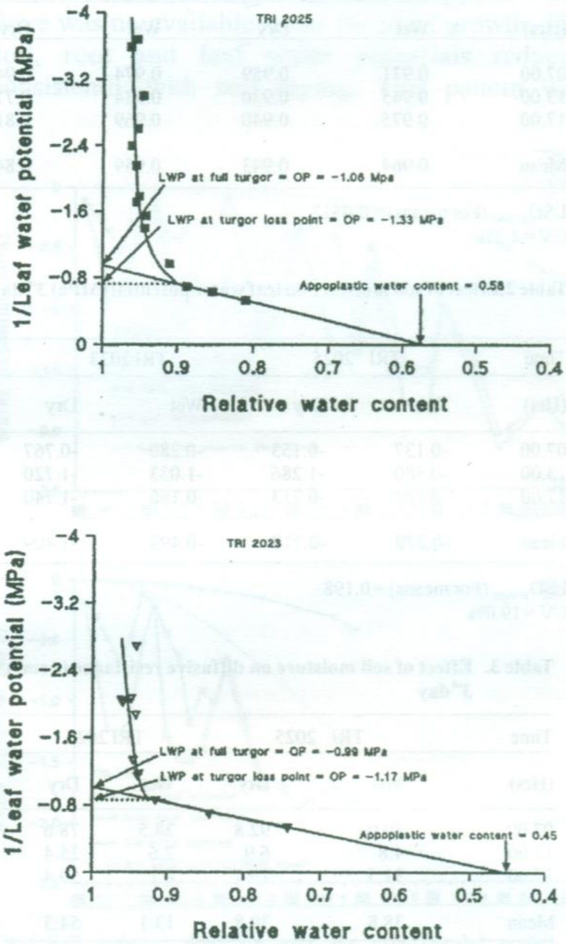

Fig. 6. Estimation of osmotic potential (OP) at full turgor and turgor loss point. (a): TRI 2025, (b): TRI 2023. (LWP = Leaf Water Potential).

between the two data sets ($p<0.001$) and hence that of the above estimated values.

$LWP = [23.4\,(\pm0.72) - 24.3\,(\pm0.78)\,RWC]^{1/2}$ --- 2025
$R^2 = 99\%$, $p<0.001$
$LWP = [14.3\,(\pm 1.04) - 14.7\,(\pm 1.13)\,RWC]^{½}$ --- 2023
$R^2 = 95\%$, $p<0.001$

This relationship also shows that soil drying lowers the leaf water potential of TRI 2025 at a higher rate per unit reduction of relative water content, than TRI 2023. Moreover, the relative water content for a given leaf water potential of TRI 2025 leaves was higher than that of TRI 2023 as described previously.

DISCUSSION

Effect of soil moisture stress on leaf water relations

The soil drying pattern and variations in leaf, root and soil water potentials over the drying cycle are similar to those described by Slatyer (1967) and Jackson (1989). Soil water potentials at the end of the experiment, estimated from pot weights, were higher than those recorded for the root zone at permanent wilting. This is due to an over estimation of soil water potential for the whole soil volume in the pots which had not been fully exploited by the developing root systems of young plants. The root systems were largely confined to the top 2/3 of soil in the pots. The soil moisture content at the bottom of the pots of water stressed plants was thus comparatively higher than that at the top. The unevenness in moisture content was clearly evident during soil sampling from wilted plants and therefore, the average moisture content estimated from weighing pots was relatively high even when the plants showed signs of wilting. However, the pattern of soil drying was consistent over time and graphical interpolation of soil water potential in the root zone could be made from the assumption that pre-dawn water potentials of the whole system (plant and soil) are in equilibrium when there is no critical soil moisture deficit (Fig. 1). However, once all available water is depleted and the permanent wilting point has been reached, plant water potentials may not reset to the corresponding soil water potentials. The pre-dawn leaf water potential appears to be a useful measure of plant water status and also provides information on the highest values of leaf water potential over a drying cycle (Fitter and Hay 1983; Jones 1990; Jones 1992; Brisson *et al.* 1993).

The diffusive resistance and transpiration of both clones were affected significantly by soil moisture stress. When compared with drought susceptible TRI2023, the drought tolerant TRI 2025 maintained a higher leaf water potential and relative water content even at lower soil water potentials. Therefore, the adverse effect of soil moisture stress on drought tolerant clones would be incurred later during a dry spell. This relationship could therefore be used as a key for screening plants for drought resistance (Planchon 1987; Kaufmann 1981).

The soil moisture content, within the root zone, estimated at the permanent wilting point of TRI 2025 and TRI 2023 plants, were 5.08% and 5.89%. Therefore, TRI 2025 plants have been able to absorb soil moisture at a lower water potential than the other clone. The soil water potential measured for TRI 2023 plants at permanent wilting point (-1.47 ± 0.19 Mpa) is close to previous experimental results. In general, soil water potential at permanent wilting point is reported to be about -1.5 Mpa (Fitter and Hay 1983; Jackson 1989). Although the soil water potential at permanent wilting pint of TRI 2025 plants could be lower than that of the other (owing to the results discussed above), the measured value (-2.78±0.16MPa) was comparatively lower than the generally reported values for many plants. Water potential assessments in the present study also showed that the lower limit of soil moisture for plant growth (permanent wilting point) is not completely determined by the soil, but also depends on plant properties.

At the turgor loss point the osmotic potential equals the water potential (Fitter and Hay 1983) which was estimated to be about -1.33 MPa and -1.17 Mpa for TRI 2025 and TRI 2023 plants, respectively. The osmotic potentials at full turgor were estimated to be about -1.06 Mpa and -0.99 MPa for the same clones, respectively. These levels are comparable with those reported for tea by Othieno (1978). Leaf water potential and relative water content at turgor loss, estimated from pressure volume curves, were supported by data on leaf diffusive resistance. The stomatal closure of the two clones were indicated by diffusive resistance values above 12-15 s/cm for TRI 2025 and 7-10 s/cm for TRI 2023. The relationship betweeen leaf water potential and diffusive resistance (Fig. 4) shows that the daily average leaf water potentials corresponding to the above diffusive resistance values were about -1.3 Mpa for TRI 2025 and -1.2 Mpa for TRI 2023. The leaf water potentials estimated for turgor loss points were comparable to these values adding weight to the estimations of turgor loss points from the pressure volume curve.

The drought tolerant clone had a higher leaf water potential under well watered conditions and, was also able to withstand soil dring by lowering its plant water·potential to a more negative value than the drought susceptible clone. This achievement is a result of osmotic adjustment. Although both clones were able to reduce their osmotic potential in response to soil drying, the range was wider and more negative for TRI 2025 than for TRI 2023. Because of the ability to reduce the plant water potentials to more negative values, TRI 2025 plants can absorb water from drier soils compared to TRI 2023. The finding also agrees with the soil moisture records at permanent wilting point as discussed above. In addition, the high apoplastic water content of TRI 2025 leaves could also be considered as another characteristic of drought tolerant plant species as discussed by Ryadnova and Lebedeva (1971) who found a greater free water content and the water retaining capacity of drought resistant peach leaves.

The results of the present study demonstrate that the drought tolerant tea clone tides over dry periods by conservation of water through efficient stomatal control and effective osmotic adjustment, which enable it to absorb soil water at low water potential.

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