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Water relations of clonal tea (*Camellia sinensis* L.) with reference to drought resistance: i. Diurnal variations

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ABSTRACT

The diurnal variations of water relations of the tea plant were studied using potted young tea plants with particular reference to drought tolerance. Glasshouse experiments showed that the diurnal changes of plant water relations of tea are largely governed by the environmental factors such as solar radiation and saturation vapour pressure deficit. Accordingly, diffusive resistance and relative water content of both drought tolerant and susceptible clones were low during the mid day. Drought tolerant tea clones possess higher stomatal diffusive resistance, lower transpiration rates and higher leaf turgidity over the day time. Moreover, they conserve moisture by reducing transpiration rate at the latter part of the day earlier than that of drought susceptible clones.

Key words: drought, tea, transpiration, water potential

INTRODUCTION

In Sri Lanka, tea is grown as a rain-fed plantation crop. All tea growing areas receive sufficient total rainfall to satisfy evaporative demand but rainfall distribution is not uniform throughout the year to maintain a continuous growth. Mature tea bushes with well developed, deep root systems can withstand drought to a greater extent than shallow rooted young tea. Under prolonged dry weather conditions, growth of tea is adversely affected by plant water deficits created by lack of soil moisture and associated high saturation vapour pressure deficit of the air (Wijeratne and Ekanayake, 1990). Squire (1979), Sandanam *et al.*, (1981), Callander and Woodhead (1981) have reported that stomatal responses of tea were also greatly influenced by the vapour pressure deficit and solar radiation. Irrigation is often not possible during severe droughts due to the lack of locally available water resources. Hence, the use of drought tolerant tea clones with high water use efficiencies is of utmost importance in drought prone regions. To fully benefit from such alternatives, it is necessary to understand the diurnal variations of water relations of the tea clones. Therefore, the following study was undertaken to investigate how a drought tolerant and susceptible clone differ in the changes of water relation characteristics during the course of the day.

Abbreviations: RWP - Root Water Potential; LWP-Leaf Water Potential; PAR - Phytosynthetically Active Radiation; SVDP - Saturation Vapour Pressure Deficit; TR - Transpiration Rate; RWP - Relative Water Content

MATERIALS AND METHODS

A glasshouse experiment was conducted at the Tea Research Institute, Low Country Station, Ratnapura, Sri Lanka (6° 40' N, 80° 25' E, 60 m amsl).

Treatments and the experimental design

A group of seven month old vegetatively propagated (VP) plants of TRI 2025 (drought tolerant) and TRI 2023 (drought susceptible) was used. They were transferred to 4 liter plastic pots filled with soil (Ultisol with a soil pH of 5.0). Two months after replanting two moisture regimes viz. well watered (Field capacity) and water stressed (no watering after commencement of the experiment) were imposed.

All potted tea plants were thoroughly watered and then allowed to drain for about 24 hrs prior to imposing the above moisture regimes. The treatments were arranged factorially in three replicates (blocks) each having 80 plants composed of 4 plots (rows) and were given four randomly allocated treatment combinations (i.e. two clones and two soil moisture regimes). Plants receiving the well watered treatment were watered daily in the morning and the other set of plants (water stressed) were allowed to dry out without watering until they were permanently wilted. Three plants per treatment combination were randomly selected from each of three different replicates and weighed for estimating the average transpiration over the day. One healthy mature leaf per plant was tagged for measuring leaf diffusive resistance and transpiration rates using Steady State Porometer (Li-1600, Li-Cor inc. Ltd., USA). Leaves were selected to be at similar age on the basis of their appearance and position on the main stem. To estimate the bare soil evaporation, 6 pots containing the same soil, but with plants removed by cutting below the soil surface, were placed in the 3 separate replicates. Half of these pots were well watered and the balance allowed to dry out along with the water stress treatment.

Measurements

All tagged plants and pots without plants were weighed 6 times daily at two hourly intervals, between 7.00 hrs till 17.00 hrs, using an electronic balance (Mettler 5PN,±0.1g). Immediately after weighing the diffusive resistance and transpiration rates of tagged leaves (three leaves/treatment combination) were measured on the abaxial surface using the Steady State Porometer (Li-1600, Li-Cor inc. Ltd., USA).

Relative water content and water potential of tea leaves were measured 6 times on the first 2 days for studying the diurnal variation and subsequently only 3 times daily (7.00, 13.00 and 17.00 hrs.) to minimize destructive leaf sampling. Three mature leaves were removed from 3 different plants/treatment combination/replicate (not used for weighing) for the determinations of relative water content as described by Sandanam *et al.* (1981).

Leaf water potential was measured on a similar set of mature leaves sampled from the same plants used for relative water content assessment (the adjacent leaf to that removed for relative water content determination). Leaf water potential measurements were carried out inside the glasshouse, using a Plant Water Status Console- Model-3005,Soil Moisture Equipments, USA (Scholander *et al.* 1965).

In addition to the above assessments, permanently wilted plants i.e., those not rehydrated overnight, were removed daily in the morning and soil within their root zone was sampled for soil moisture estimation. At the end of the experiment, fresh and dry weight of leaves, stems and roots, (oven dried at 90°C for 24 hrs) and leaf area (using Delta-T Area Measurement System, Delta-T Devices Ltd.) of the tagged plants and fresh and dry weight of soil in the tagged pots with and without plants were recorded. Dry weight of soil was also determined at the end of the experiment. The soil moisture content in drying pots at any given time was also estimated.

Daily Minimum and Maximum temperatures (Minimum and Maximum Thermometer) and Dry and Wet Bulb temperatures (Assman Hygrometer) were also recorded inside the glasshouse. Saturation vapour pressure deficit (SVPD, kPa) was estimated from dry and wet bulb temperatures.

Water potentials of the drying soil, during the experimental period, were estimated from a calibration curve of water potential *versus* moisture content for the soil used for the experiment (Reeve and Carter 1991). Moisture tension increases with soil drying. There is a linear relationship between the relative soil moisture content (moisture content/saturated moisture content) and the moisture tension on the log scale. Accordingly, soil water potential of the drying soil at a given time can be estimated.

Root water potentials (RWP) of water stressed (droughted) plants were estimated using data on leaf water potential (LWP) and diffusive resistance of well watered control (C) and droughted (D) plants as described by Jones (1983) in the following relationship:

$$RWP(D)=LWP(D)-[LWP(C)\,g_s(D)]/g_s(C)$$

where g_s = 1/diffusive resistance.

RESULTS

Environmental conditions inside the glasshouse *viz.*, air temperature (minimum and maximum), saturation vapour pressure deficit (SVPD), and solar radiation averaged over the experimental period are shown in Fig.1. On average, solar radiation (measured as Photosynthetic Active Radiation - PAR) was comparatively low early in the morning and later in the afternoon. The saturation vapour pressure deficit and temperature followed a similar trend. The highest temperature and SVPD were observed around midday along with the maximum intensity of solar radiation (Fig.1).

Diurnal variations of leaf water relations

The patterns of variation of plant and soil water potentials *viz.* for leaf, root and the soil are shown in Fig.2. On day 1, the pre-dawn water potentials of plants were near zero, and they decreased towards midday developing the largest gradient of water potentials between soil and the plant. In the afternoon plants regained their water potentials to the original values. The root and leaf water potentials of the drought susceptible TRI 2023 were less as compared to drought tolerant TRI 2025.

The diurnal variations of relative water content and leaf water potential of well watered plants are shown in Fig.3. Fig.4 shows the diurnal variation of transpiration and diffusive resistance of well watered plants. The diurnal fluctuations in relative water content and leaf water potential show a similar pattern with a higher relative water content being accompanied by higher leaf water potential and *vice versa*. The Relative water content and leaf water potential of TRI 2025 leaves were significantly higher than those of TRI 2023. In both clones lower leaf water potential and relative water

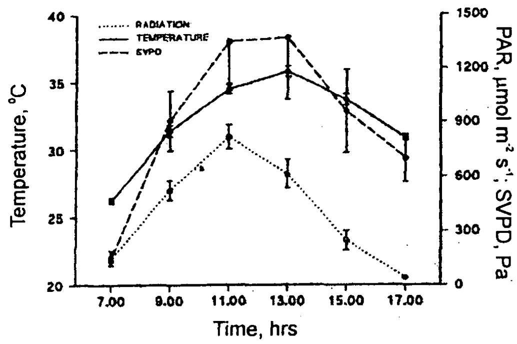

Fig. 1. Diurnal variation in temperature, SVPD and solar radiation in the glass house (means for the experimental period).

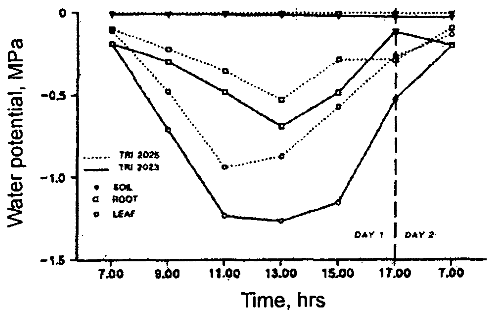

Fig. 2. Diurnal variations of soil, root and leaf water potentials of TRI 2025 and TRI 2023.

content values were recorded around midday, although recovery started earlier in TRI 2025 (13.00 hrs) than for TRI 2023 (15.00 hrs). The higher values of diffusive resistance combined with lower values of transpiration were observed at the beginning and at the end of day while higher transpiration and lower diffusive resistance were obtained during midday. TRI 2023 leaves had a significantly low diffusive resistance and high transpiration rate compared to TRI 2025 (Fig.4). The variation of diffusive resistance, after 7.00 hrs until about 15.00 hrs, was quite small in both clones compared to the diurnal variation of transpiration over the same period. However, diffusive resistance of TRI 2025 leaves appeared to increase with decreasing transpiration earlier than the other clone, *i.e.* after about 11.00 hrs for TRI 2025 as against 13.00 hrs for TRI 2023.

Relationship between stomatal opening and solar radiation, SVPD, relative water content and leaf water potential

Fig.5 shows the relationship between diffusive resistance and solar radiation (PAR). Although there was no clear relationship between stomatal diffusive resistance and light intensity, there was a tendency for the stomata to have very high stomatal resistance when the light intensity was less than 200 mol $m^{-2}s^{-1}$. A similar behaviour was observed between SVPD and diffusive resistance of well watered plants (Fig.6). SVPDs were also low in the morning when higher leaf diffusive resistances were recorded. Moreover, no clear

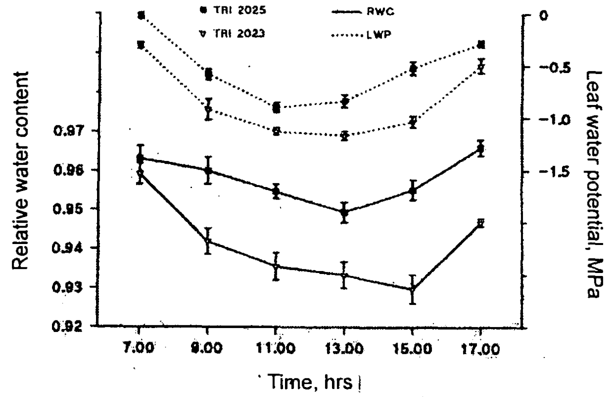

Fig. 3. Diurnal variation in relative water content (RWC) and leaf water potential (LWP) of well watered plants (mean values for day 1 and 2).

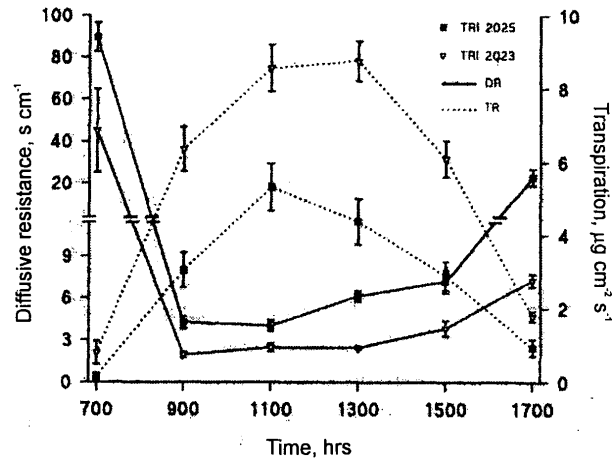

Fig. 4. Diurnal variation in diffusive resistance (DR) and transpiration (TR) of well watered plants.

relationship was found between diffusive resistance and PAR or SVPD above 200 mol $m^{-2}s^{-1}$ PAR and 0.4 kPa SVPD.

The results show that with higher PAR and SVPD, the diffusive resistance values were well below 12-15 s cm^{-1} in TRI 2025 leaves and 7-10 s cm^{-1} in TRI 2023 leaves. The relationships of diffusive resistance with relative water content and leaf water potential of well watered plants were also studied to evaluate their effects on stomatal opening. Both relationships were similar and hence only that between diffusive resistance and leaf water potential is shown in Fig.7. Higher values of leaf water potential (above -0.30 MPa) together with higher values of diffusive resistance were measured in the morning. The relative water content measured in the morning (7.00 hrs) was above 0.97 and the corresponding diffusive resistance was above 7-10 s cm^{-1} for TRI 2023 and 12-15 s cm^{-1} for TRI 2025. The lowest values of relative water content estimated during midday on well watered plants of both clones were about 0.91.

SVPD (kPa) and transpiration rate (TR, g $cm^{-2}s^{-1}$) of well watered plants was linearly related as demonstrated below. Data collected at 7.00 hrs and 17.00 hrs when light

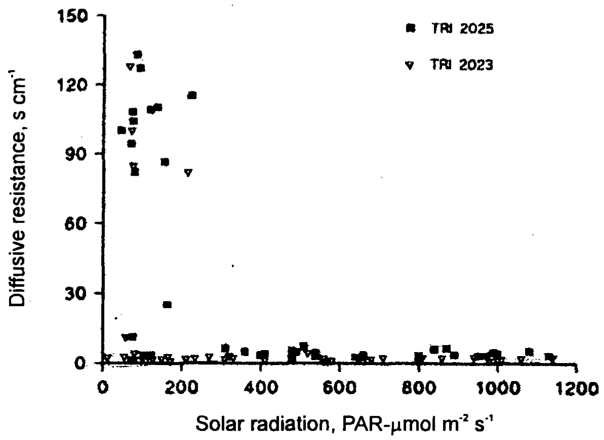

Fig. 5. Relationship betwen solar radiation and diffusive resistance of well watered plants.

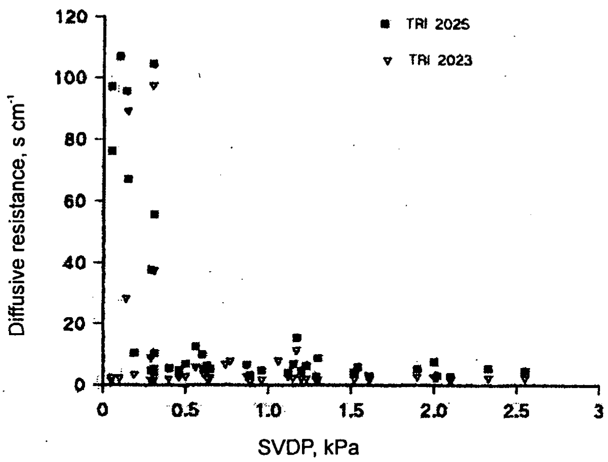

Fig. 6. Relationship between saturation vapour pressure deficit (SVPD) and diffusive resistance of well watered plants.

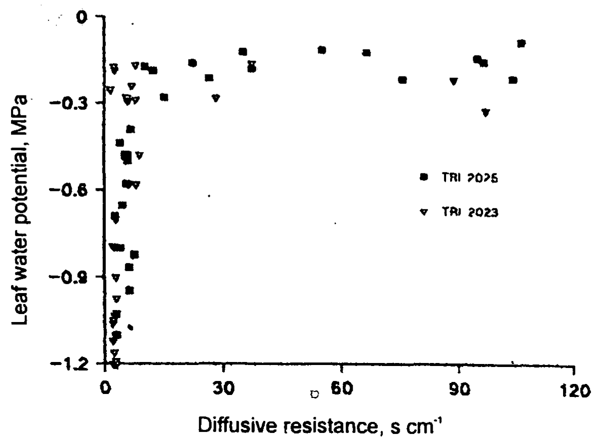

Fig. 7. Relationship between diffusive resistance and leaf water potential of well watered plants.

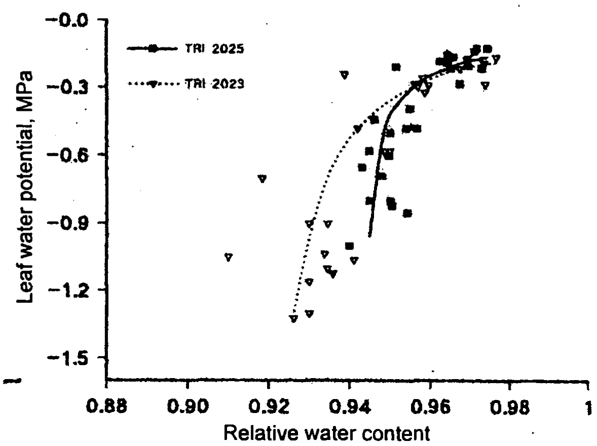

Fig. 8. Relationship between relative water content (RWC) and leaf water potential (LWP) of well watered plants.

levels limited stomatal opening, were excluded from the regression analysis.

TR = 0.38(±0.35) + 1.76(±0.29) SVPD ---- TRI 2025
R^2=59%, $p<0.001$
TR = 0.56(±0.60) + 3.60(±0.49) SVPD ---- TRI 2023
R^2=70%, $p<0.001$

The rate of increase in transpiration with increasing SVPD was significantly higher for TRI 2023 than for TRI 2025 ($p<0.05$). The relationship between SVPD and relative water content (RWC) of well watered plants can be summarized as:

RWC = 0.968(±0.002) - 0.009(±0.002) SVPD ---- TRI 2025
R^2=48%, $p<0.001$
RWC = 0.967(±0.004) - 0.019(±0.004) SVPD ---- TRI 2023
R^2=54%, $p<0.001$

Reductions in relative water content in response to increases in SVPD appeared to be comparatively higher for TRI 2023 than for TRI 2025, but the difference was not statistically significant. Given below is the negative linear relationship found between leaf water potential (LWP) and SVPD; clonal difference was significant ($p<0.05$).

LWP = -0.135(±0.049) - 0.256(±0.040) SVPD ---- TRI 2025
R^2=63%, $p<0.001$
LWP = -0.202(±0.071) - 0.422(±0.059) SVPD ---- TRI 2023
R^2=67%, $p<0.001$

As the slopes of regression lines were significantly different, the rate of decrease in leaf water potential of TRI 2023 leaves in response to increased evaporative demand of the air was higher than that of TRI 2025. Further analysis showed that the leaf water potential of both clones was linearly related to their transpiration rates as shown below in a common relationship.

LWP = -0.136(±0.050) - 0.112(±0.009) TR
R^2=80%, $p<0.001$

The relationship between leaf water potential and relative water content for both clones under well watered conditions is shown in Fig.8. It shows that at lower leaf water potentials, TRI 2025 plant can maintain higher leaf relative water contents than TRI 2023. Further, it shows that TRI 2023 leaves lose more water, thereby reducing their leaf water potential and relative water content to smaller values than the other clone. However, the rate of reduction of leaf water potential per unit reduction in relative water content was less in TRI 2023 leaves compared to TRI 2025 leaves.

Transpiration rates were inversely related to the corresponding diffusive resistance (DR) as shown below. As clonal difference was not significant, all values were pooled together to obtain the following relationship:

$$TR = 0.34(\pm 0.11) + 17.7(\pm 0.57)1/DR, \quad R^2=86\%, \; p<0.001.$$

DISCUSSION

Tea clones used in the present study *viz.* TRI 2025 and TRI 2023, are rated as drought tolerant and drought susceptible, respectively. The diurnal variation in the water relations of their leaves has been largely determined by SVPD of the air and radiation as discussed for tea by Squire (1979), Sandanam *et al.* (1981), Callander and Woodhead (1981) and Burgess (1992). TRI 2023, the drought susceptible clone was found to transpire at a higher rate and for a longer time during the day time, than the drought tolerant TRI 2025. The earlier reduction in transpiration coupled with increased diffusive resistance of TRI 2025 leaves would have contributed to its moisture conserving ability thus, at least in part, making it more drought tolerant as has been shown for many other plant species (Chaney 1981). Compared to TRI 2023, the higher relative water content and leaf water potential of TRI 2025 leaves were probably the result of its lower rate of water loss.

The relationships between transpiration and diffusive resistance were found to be similar for both clones and they were inversely related. Similar results have been previously reported for the same tea clones (Wijeratne 1986). There was no evidence of midday stomatal closure which is in agreement with the findings of Sandanam *et al.* (1981) and Gee *et al.* (1982)

The maximum vapour pressure deficit (2.5 kPa) experienced in the glasshouse during the period of experimentation was not large enough to affect the leaf diffusive resistance under well watered conditions. However, the rate of water loss from TRI 2023 leaves with increasing SVPD, was significantly higher than that of TRI 2025. As a consequence, the rate of reduction of leaf water potential in response to increasing SVPD was also greater on TRI 2023 leaves. Although not significant ($p>0.05$), a similar clonal difference was demonstrated in the relationship between relative water content and SVPD. This finding confirmed the influence of SVPD on stomatal control. Therefore, in an environment with high evaporative demand, drought resistant TRI 2025 plants can maintain a higher leaf turgidity than the drought susceptible TRI 2023. This characteristic of TRI 2025 plants may contribute to minimizing the adverse effect of dry environments on other biological functions such as photosynthesis which is considered to be another important characteristic of many drought resistant plant species (Hurd 1976; Planchon 1987). The daily variations in stomatal diffusive resistance and leaf water potential observed under well watered conditions were comparable to the results discussed by Sandanam *et al.* (1981) and Burgess (1992).

Higher transpiration rates in TRI 2023 are a result of its higher stomatal density compared to TRI 2025 (Wadasinghe and Wijeratne 1989). Similarly, higher stomatal densities and larger stomata have been found in drought susceptible peach (*Prunus persica*) leaves (Ryadnova and Lebedeva 1971). As found in this study on the tea clone TRI 2025, other researchers have shown that drought resistant plant species have a low rate of transpiration and high diffusive resistance, leaf water potential and relative water content (Hurd 1976; Sandanam *et al.* 1981; Handique and Manivel 1986; Kaufmann 1981; Planchon 1987).

According to the relationship between leaf water potential and relative water content, reduction in leaf water potential per unit reduction in relative water content was high in TRI 2025 leaves. This also appears to be a useful adjustment in drought tolerant plant species for increased soil water absorption (Jones *et al.* 1981; Planchon 1987; Karamanos and Papatheohari 1987).

It has been shown that some of the environmental factors and leaf water relations are not uniquely related. Such anomalies could have arisen from the measurements of leaf water relations under varying environmental conditions. For an example, a higher diffusive resistance could be obtained together with a high relative water content and a leaf water potential under well watered conditions, as a result of low irradiation. Moreover, due to the effect of soil moisture stress on stomatal opening, a higher diffusive resistance may be recorded at a low relative water content and a leaf water potential even in the presence of adequate irradiation.

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