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Vapour pressure deficit affects diurnal girth fluctuation of rubber trees (*Hevea brasiliensis*)

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Abstract

Diurnal variation in stem girth as affected by three different ranges (0.43, 1.78 and 2.11 kPa) of air vapour pressure deficit (VPD) under minimum soil water stress was studied in mature rubber trees (*Hevea brasiliensis*) in Northeast Thailand. Diurnal cycle of shrinkage and swelling of stem girth was observed in all ranges of VPD. Stem girth as expressed by maximum daily trunk shrinkage (MDS) decreased during the day in association with high sap flow and high VPD, and then stem girth increased during the night when VPD and sap flow were low. Stem girth fluctuation was inversely related to VPD and sap flow, especially at higher ranges of VPD. A positive and significant correlation of MDS on VPD ($r = 0.42$, $p \leq 0.01$) and negative correlation of MDS on sap flow ($r = -0.41$, $p \leq 0.01$) were observed, whereas positive correlations of trunk growth rate (TGR) on VPD ($r = 0.19$) and of TGR on sap flow ($r = 0.18$) were not significant. This indicates that MDS was sensitive to air moisture conditions. Measurement of MDS could be easily automated and MDS signal intensity could be used as a tool for predicting plant water status and utilizing crop modeling.

Keywords: Atmospheric demand; dendrometer; sap flow density; trunk shrinkage; trunk expansion.

Abbreviations: MDS-maximum daily trunk shrinkage; REW-relative extractable soil water; TGR-trunk growth rate; TTD-thermal dissipation method; VPD-vapour pressure deficit; θ -soil water content.

Introduction

Rubber tree (*Hevea brasiliensis*) is indigenous to the tropical rain forests of the Amazon Basin. This region is characterized by high temperatures (30-35°C) with annual rainfall of 1,500-2,000 mm (Watson, 1989). However, when rubber trees are grown in areas with more seasonal variation of climatic conditions away from the Amazon forest such as long dry season, lower rainfall, these variations affect annual increments in stem diameter. Variations in rainfall, temperature and humidity also influence latex yield (Jacob et al., 1988; Rao et al., 1990). Change in stem diameter is associated with diurnal fluctuation of the water balance in stems (Kozłowski, 1967; Simonneau et al., 1993). This is mainly due to the imbalance between hydration and dehydration caused by transpiration (Perä-mäki et al., 2001; Perä-mäki et al., 2005), leaf water potential (Ueda and Shibata, 2001) and soil water availability (Sevanto et al., 2005). Diurnal variation in trunk diameter has been used to indicate plant water status as it can be measured automatically in the field, in contrast with measurement of leaf water potential which cannot be easily automated (Goldhamer and Fereres, 2001). Circumference has been used in place of diameter as it has large values and its measurement is more accurate than diameter. Maximum daily trunk shrinkage (MDS) and trunk growth rate (TGR) and are

two parameters derived from trunk circumference that have been commonly used as water stress indicators. MDS and TGR patterns are closely related to sap flow rate and transpiration in Norway spruce (Zweifel and Häslér, 2001; Zweifel et al., 2001). Stem tissues serve as a water reservoir during the early part of transpiration, and daily deviations in stem diameter (caused by shrinkage and swelling) reflect the dynamics of water balance and water potential in these tissues (Offenthaler et al., 2001; Zweifel et al., 2006). Most studies conducted previously have assessed the sensitivity of MDS and TGR to differences in soil water availability and found that evaporative demand had a large influence on MDS (Fereres and Goldhamer, 2003; Ortuño et al., 2004; Moreno et al., 2006). Diurnal changes in MDS and TGR reflect differences in water status of the stem during the course of the day (Wronski et al., 1985; Brough et al., 1986). In general, MDS was higher for a given evaporative demand during dry periods of the year compared with wet periods in olive trees (Intrigliolo and Castel, 2006) and tomato (Gallardo et al., 2006). However, review of the literature did not indicate any information available regarding the relationship between stem girth fluctuation and daily variation in climatic conditions when soil water is near field capacity. Thus, assessment of the relationship of climatic

variation and stem girth fluctuation could provide valuable insight into how atmospheric demand can influence overall tree performance. The objectives of this study (1) to determine the effect of vapour pressure deficit on important parameters determining plant water status (MDS and TGR) under minimum water stress conditions in the field, (2) to investigate how does the mature rubber trees response to the wide variation in VPD occurring during the course of the day and under conditions with adequate water (3) to evaluate the usefulness stem girth as an indicator of water status for mature rubber tree plantation growing in the field. The results of this study may also contribute to a better understanding of trunk shrinkage and growth in relation to changing environmental conditions.

Results

Weather data and soil moisture

Total rainfall during the experiment was 955 mm (Fig. 2a). The rainfall pattern in this area is uni-modal and rainfall during the study was more than half the annual rainfall for this area (1,200 mm). Rainfall was distributed fairly evenly in the first half of the study period, resulting in low drought stress. Mean daily VPD and sap flow were 0.73 kPa and 2.49 L dm⁻² h⁻¹, respectively. Variations in sap flow during the study period were generally stable. However, large sap flow reductions were observed on 7 August (1.55 L dm⁻² h⁻¹) and 4 October (0.56 L dm⁻² h⁻¹) during periods of low rainfall (20 mm) and low VPD. VPD fluctuated throughout the study period. Mean VPD was lower during months with more rainfall events, August (0.25 kPa) and October (0.30 kPa) with amount rainfall 378 mm and 338 mm respectively, and higher during the month with a longer rainless period, September (1.11 kPa) with amount rainfall 238 mm. Based on these VPD fluctuations, we defined the three levels of VPD as low VPD (0.43 kPa), intermediate VPD (1.78 kPa) and high VPD (2.11 kPa), respectively. Variation in soil moisture (θ) was higher in the topsoil than in the subsoil (Fig. 2b). The highest soil moisture content was observed in October at the time of the highest rainfall, on day 287. Although soil moisture in the topsoil (19 cm³/100 cm³ of soil) fluctuated considerably (range of 13.78-28.05 cm³/100 cm³ of soil), it was consistently higher than that of the subsoil on all days (range of 9.78-18.97 cm³/100 cm³ of soil). The values of θ measured by both the capacitance probe and the neutron probe showed marked change in the topsoil, with a continuous decrease starting in mid-September (Fig. 2b). Soil water content measured by both capacitance and neutron probes indicated that water content in the subsoil remained constant around 10-14 cm³/100 cm³ of soil, except a short period in October when it rose to 16.70 cm³/100 cm³ of soil. However, soil moisture in the subsoil, although low, remained above the permanent wilting point (10 cm³/100 cm³ of soil) even during dry periods in September and October.

Diurnal pattern of maximum daily trunk shrinkage (MDS) and trunk growth rate (TGR)

Diurnal variation in MDS is shown in Fig. 3a. Marked decreases in MDS (days 218, 225, 228, 258, 276, 281) coincided with marked decreases in VPD and lesser decreases in sap flow on the same days. These decreases all followed major rainfall events (compare Fig. 2a and 3a). The highest MDS (1,045 μ m) was observed at the end of August, following a period of rainless days, while the lowest MDS values were found during early August (-83 μ m), a period of

frequent rainfall events, and mid October (-57 μ m), after a period with the highest high rainfall event of over 200 mm. Progressive increase in stem circumference was observed in rubber trees throughout the study period (Fig. 3b). Trunk expansion reached its maximum value of 2,581 μ m at the end of the study. Although there was high variation in VPD and sap flow, the rate of daily trunk expansion was largely constant from the onset to the end of the study, except on day 219, when both VPD and sap flow decreased (0.42 kPa and 1.55 L dm⁻² h⁻¹, respectively).

Diurnal patterns of stem girth fluctuation, sap flow value and VPD

Fig. 4 shows diurnal patterns of VPD, sap flow and stem girth fluctuation. Similar patterns were observed for all ranges of VPD, but the variations in VPD, sap flow and stem girth fluctuation were different in magnitude. At the low range of VPD (average 0.43 kPa), the highest sap flow at 10:30 was 1.53 L dm⁻² h⁻¹, and stem girth fluctuation varied between 0 and 364 μ m (Fig. 4a). Negative values of stem girth variation indicating stem girth contraction were not observed. At the intermediate range of VPD (average 1.78 kPa), sap flow was highest at 12:30, reaching 2.49 L dm⁻² h⁻¹, nearly double that of the low range. At the same time, stem girth fluctuation registered a negative value (-114 μ m), indicating that stem girth contracted at that time (Fig. 4b). At the high range of VPD (average 2.11 kPa), sap flow was highest (2.72 L dm⁻² h⁻¹) around 13:30, slightly higher than the peak at intermediate range (Fig. 4c). The pattern of stem girth variation at the high range of VPD was similar to that at the intermediate range of VPD, but the lowest negative value was considerably lower than that at intermediate range, indicating even greater contraction of stem girth at the highest range of VPD.

Relationship between stem girth variations, sap flow rate and VPD

Diurnal hysteretic relationships between change in stem girth and VPD and between stem girth and sap flow were observed at all three ranges of VPD (Fig. 5). However, the resulting hysteretic loops formed by the decline phase from morning to midday (downward side of the loop) and the recovery phase from midday to evening (upward side of the loop) at the high and intermediate ranges of VPD were larger, and the position of the two phases reversed in the high and intermediate ranges of VPD, compared to the low range of VPD. At the low range of VPD (0.43 kPa) (Fig. 5a and 5d), stem girth variation became more positive in the early morning while VPD was still very low. Then, as VPD increased in the morning, stem girth variation entered the decline phase, decreasing to nearly zero (no expansion) by midday (white data points from right to left). Thereafter, in the recovery phase in the afternoon, as VPD decreased from midday to night, stem girth variation became more positive again (black data points from left to right), indicating resumption of girth expansion. The final stem girth expansion value at the end of the recovery phase exceeded the corresponding value at the morning starting point. The relationship between stem girth and sap flow at the low range of VPD was similar to that of stem girth and VPD, but the loop was slightly larger. At the intermediate range of VPD (1.78 kPa) (Fig. 5b), stem girth variation increased positively in the early morning while VPD was still close to zero, but as VPD began to increase, stem girth variation entered the decline phase and became negative (indicating contraction) (white data points from right

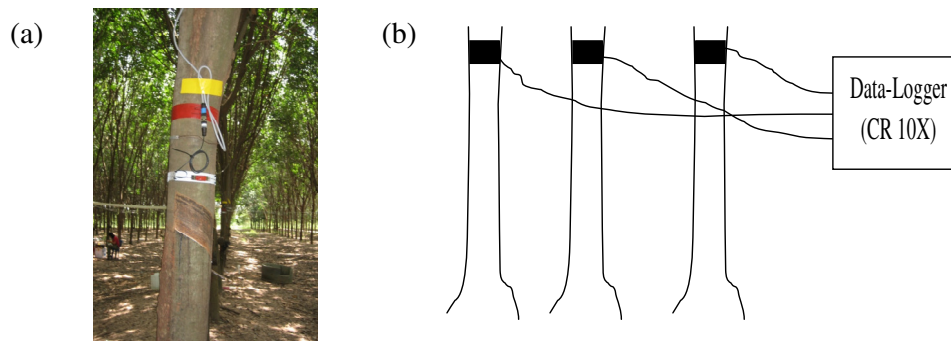


Fig 1. Photograph of (a) electronic dendrometer sensor for measuring micro-change of trunk girth variations and setting at a height of 180 cm above the ground level. Each dendrometer sensor attached to each of the three mature rubber trees. The three dendrometer sensors (b) were connected to a data logger (model CR 10X).

to left), reaching its lowest value at midday. Thereafter, in the afternoon recovery phase, stem girth variation again increased as VPD declined (black data points from left to right), finally becoming positive again with a maximum which was slightly higher than the initial point of the decline phase. The pattern of the loop was reversed from that of the low range of VPD, with the values in the afternoon recovery phase (black data points) less than the morning decline phase (white data points). Differences between the two phases were also larger than at the low range of VPD. In the same intermediate VPD range, stem girth variation increased to higher positive values during low sap flow in the early morning (Fig. 5e), but when sap flow was higher during midday, stem girth variation became negative. Thereafter, in the recovery phase, stem girth variation increased and returned to positive values (expansion) by night as sap flow declined. Again, the pattern of the loop was reversed from that of the low VPD range, with the decline phase higher than the recovery phase. Differences in stem girth values between the two phases were much higher at the same sap flow, and the final value at the end of the recovery phase was slightly higher than the initial point in the morning. At the high range of VPD (2.11 kPa) (Fig. 5c), a twist loop was observed when stem girth variation was plotted against VPD. Recovery phase values exceeded decline phase values in the early afternoon (right hand side of Fig. 5c, black data points above white data points), but recovery phase values became lower than decline phase values (black data points lower than white data points) as VPD fell below 1.0 kPa later in the recovery phase. In contrast, the loop of stem girth against sap flow was not twisted (Fig. 5f), with recovery phase values lower than decline phase values for all values of VPD. This pattern was similar to the intermediate range of VPD (Fig. 5e). Stem girth variation increased to greater positive values while sap flow was still very low in the early morning. Then, as sap flow increased until its highest points (about 2.79 kPa) at midday, stem girth variation decreased and became negative, indicating contraction. Thereafter, as sap flow declined again from midday to night, stem girth variation increased and finally became positive (indicating expansion).

Relationships among MDS, TGR and VPD

The relationship of MDS on VPD was significant ($r = 0.42$; $p \leq 0.01$), whereas relationship of VPD on stem growth rate

was not significant ($r = 0.19$) (Fig. 6). These results indicate that trunk shrinkage responded quickly to variation in VPD, whereas variation in VPD had no real effect on stem growth. The relationship of MDS on sap flow was significant ($r = 0.41$; $p \leq 0.01$), whereas the regression of TGR on sap flow rate was not significant ($r = 0.18$) (Fig. 7). The fact that MDS respond similarly to both VPD and sap flow rate suggests that sap flow and VPD are closely related, so either could be used to predict MDS.

Discussion

The period from 1 August to 31 October, 2007, was selected for this study because rainfall during this period is generally high and distributed more evenly than earlier periods during the rainy season. The total rainfall of 955 mm during the study was rather high, and the maximum number of days without rainfall during the 90 day study period was 20 days. Limited soil water stress would be expected under these weather conditions (Fig. 2a and 2b). Air humidity was reported as VPD, which is the inverse of relative humidity, indicating the amount of moisture in the air needed to reach the saturation point. VPD was then divided into three ranges to evaluate the effects of different ranges of VPD on MDS and TGR under naturally occurring minimum water stress conditions. The purpose was to study the effects of VPD with minimum interference of soil water stress. Good association between mean daily VPD and MDS (Fig. 2b and 3a), between VPD and girth fluctuations at 30 min intervals (Fig. 4) were observed. The results showed that VPD did affect variation in MDS even under limited water stress. VPD was low at night and in early morning but high during midday. The diurnal variation in VPD was associated with the diurnal variation in sap flow. High VPD has resulted in stomatal closure, attributed to increased transpiration rate (Beyschlag et al., 1992; Bunce, 1996) or decreased leaf water potential (Turner et al., 1984). A good association between sap flow and VPD has also been reported in other crop species such as Eucalyptus (Yin et al., 2004), lemon (Alarcón et al., 2005) and papaya (Fabrício et al., 2009). However, VPD had very little effect on trunk growth rate (TGR) as indicated by the non-significant regression of TGR on VPD (Fig. 3b and Fig. 7). The effect of VPD on TGR was small because the loss of water during periods of high VPD is temporary and water can

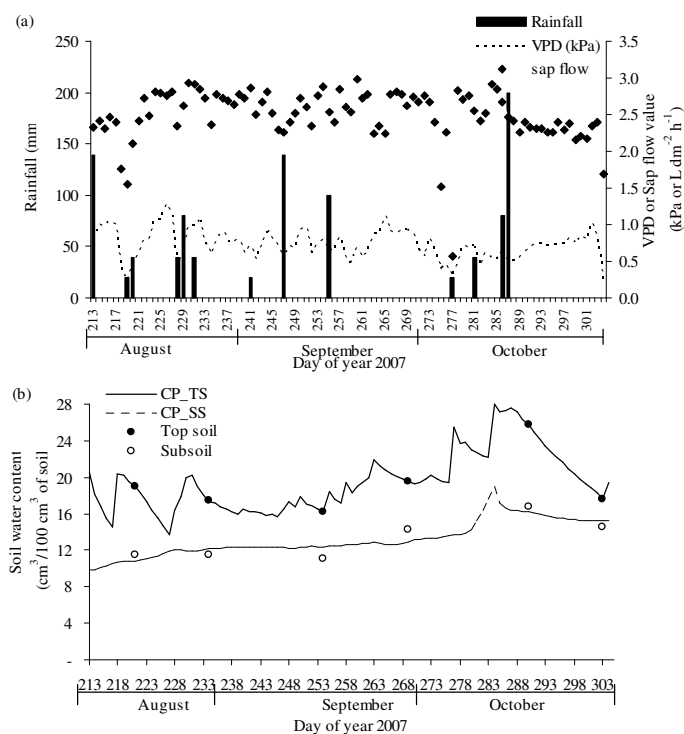


Fig 2. Daily values of meteorological variables: (a) rainfall (bars), mean air vapour pressure deficit (VPD; dotted line) and mean sap flow value (sap flow; closed diamond), (b) volumetric soil water content (θ) in the topsoil (closed circles) and subsoil (open circles) measured by a neutron probe, and volumetric soil water content recorded by a capacitance probe in the topsoil (continuous line, CT_TS) and subsoil (dotted line, CT_SS), 1 August - 31 October, 2007.

be replenished soon after transpiration is reduced. However, Major and Johnsen (2001) found a negative effect of VPD on stem growth. High VPD reduced cell enlargement and growth because of its indirect effect on cell turgor pressure. Under drought conditions, water cannot be replenished as indicated by low predawn leaf water potential, and so full recovery of water loss is not possible (Pallardy and Rhoads, 1997; Thomas and Eamus, 1999). Higher stem growth increments observed in mid to late afternoon and early evening are likely associated with increases in the osmotic potential of phloem and cambium cells, and consequent diurnal patterns of photosynthate accumulation (Hsiao, 1973). Similar results were obtained in peach (Simonneau et al., 1993), conifer (Waring and Running, 1978; Waring et al., 1979), Scot pine (Sevanto et al., 2002) and Norway spruce (Offenthaler et al., 2001). On the other hand, Herzog et al. (1995) reported that stem growth and sap flow were lower in the afternoon than in the morning in Norway spruce. These contrasting results may be due to the differences in diurnal transpiration patterns depending on climatic region. VPD affected trunk shrinkage as high VPD removed water from the trunks at a faster rate than the ability of roots to replenish the lost water. Trunks act as a temporary reservoir of water in the plants, and shrinkage of trunks occurs when transpiration is higher than water uptake. Therefore, higher levels of VPD caused higher trunk shrinkage than did lower levels of VPD. Diurnal changes in girth fluctuations as a function of diurnal fluctuations of VPD and sap flow created hysteresis loops (Fig. 5), which show clearly the mechanism of how VPD and sap flow affected MDS (Fig. 4). The loops were small in the low VPD range and larger in the intermediate and high VPD ranges. Meinzer

et al. (1997) did not find hysteresis loops at low VPD but did find them at high VPD. Under hot and humid tropical conditions, the VPD values were observed in the range of 1-2 kPa (Fig. 6). Under temperate climatic conditions, the VPD values as high as 2-3 kPa for apple (Swaef et al., 2009) and 5 kPa or more for plum (Intrigliolo and Castel, 2006) have been observed. The difference in the ranges of VPD in different studies can largely be attributed to differences in climatic conditions. Different plant species may show different responses of trunk girth circumference growth at different ranges of VPD such as yellow poplar trees (McLaughlin et al., 2003). In a latex crop such as rubber tree, trunk circumference can be expected to be more sensitive to evaporative demand than other tree crops because its bark contains much water. As the relationship of MDS on VPD was significant (Fig. 6), VPD may be used to predict trunk shrinkage in rubber trees. In other crop species, it has been used successfully to predict trunk shrinkage of olive trees (Moreno et al., 2006) and almond trees (Egea et al., 2009). VPD could thus be used to predict trunk shrinkage and water transpiration in mature rubber tree under minimum drought conditions.

Materials and methods

Study area

The study was carried out in a rubber plantation planted with clone RRIM 600 in Satuk District, Buriram Province, Northeast Thailand (N15° 16' 23.6" E103° 04' 51.3") during the latter part of the 2007 rainy season. Trees of 11 years ages

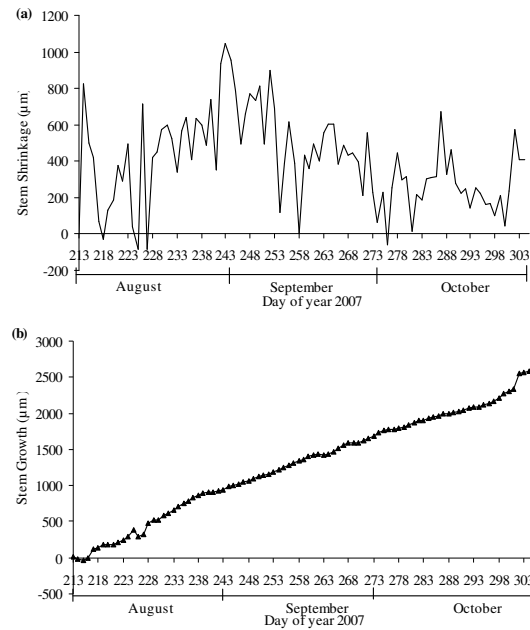


Fig 3. Diurnal course of (a) maximum daily trunk shrinkage (MDS) and (b) trunk circumference growth (expansion shown as positive values; contraction as negative values) in mature rubber trees measured at 180 cm above the ground level, 1 August - 31 October, 2007. Each data point represents the mean daily change in MDS and growth of three mature rubber trees under non-limiting soil moisture.

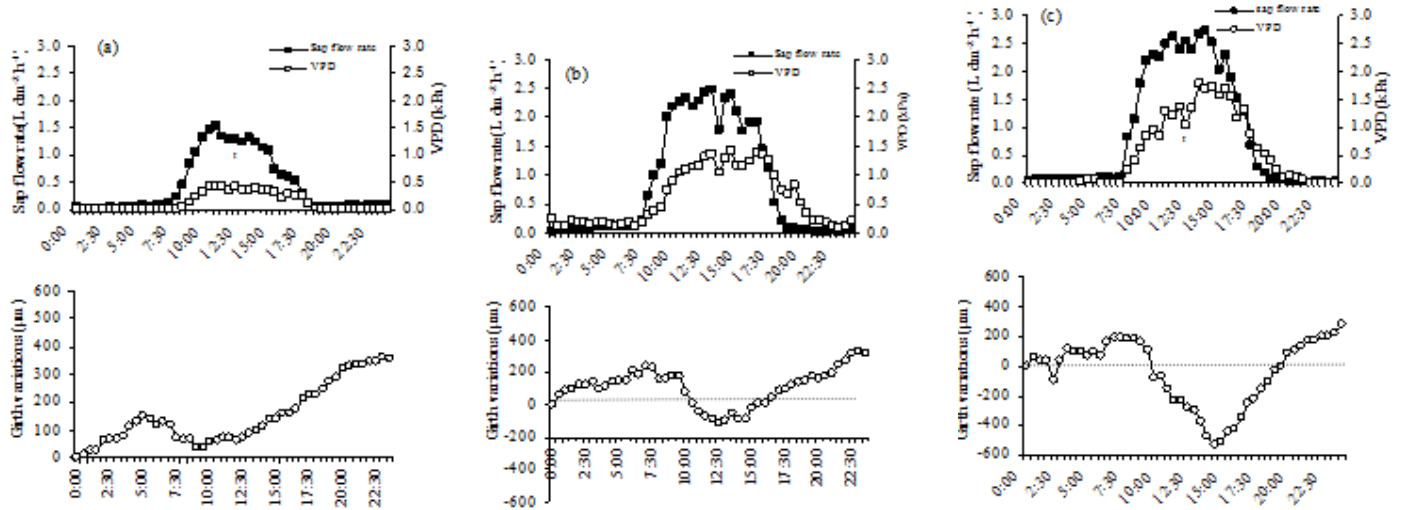


Fig 4. Diurnal patterns and mean values of stem girth fluctuations (○), air vapour pressure deficit (VPD) (□) and sap flow rate (■) of three mature rubber trees under non-limiting soil moisture. Values were recorded every half hour over the course of the day, 1 August - 31 October, 2007. Stem girth fluctuations represent the difference between girth at the time of measurement, and girth 30 min earlier. Each data point represents the mean of three rubber trees for corresponding value of girth fluctuation, VPD, or sap flow rate, shown in three ranges of VPD (a) low VPD (< 1 kPa, average 0.43 kPa), (b) medium VPD (1-2 kPa, average 1.78 kPa), and (c) high VPD (> 2 kPa, average 2.11 kPa).

which have the similar circumference were selected for this study. Measurements were made from 1 August to 31 October, 2007, under minimum water stress conditions.

Meteorological measurements

An automatic weather station with a data logger (Minimet automatic weather station, Skype Instrument Ltd, UK) was installed in an open field 50 m from the experimental site to

record relative humidity, air temperature and rainfall at 30 min intervals throughout the study from 1 August to 31 October, 2007. This period was selected for the study because water stress is low. Atmospheric vapour pressure deficit (VPD) was calculated from the above measurements using the formula of Allen et al. (1998). Three ranges of VPD, low range (< 1 kPa: average 0.43 kPa), medium range (1 kPa to < 2 kPa: average 1.78 kPa) and high range (> 2 kPa: 2.11 kPa),

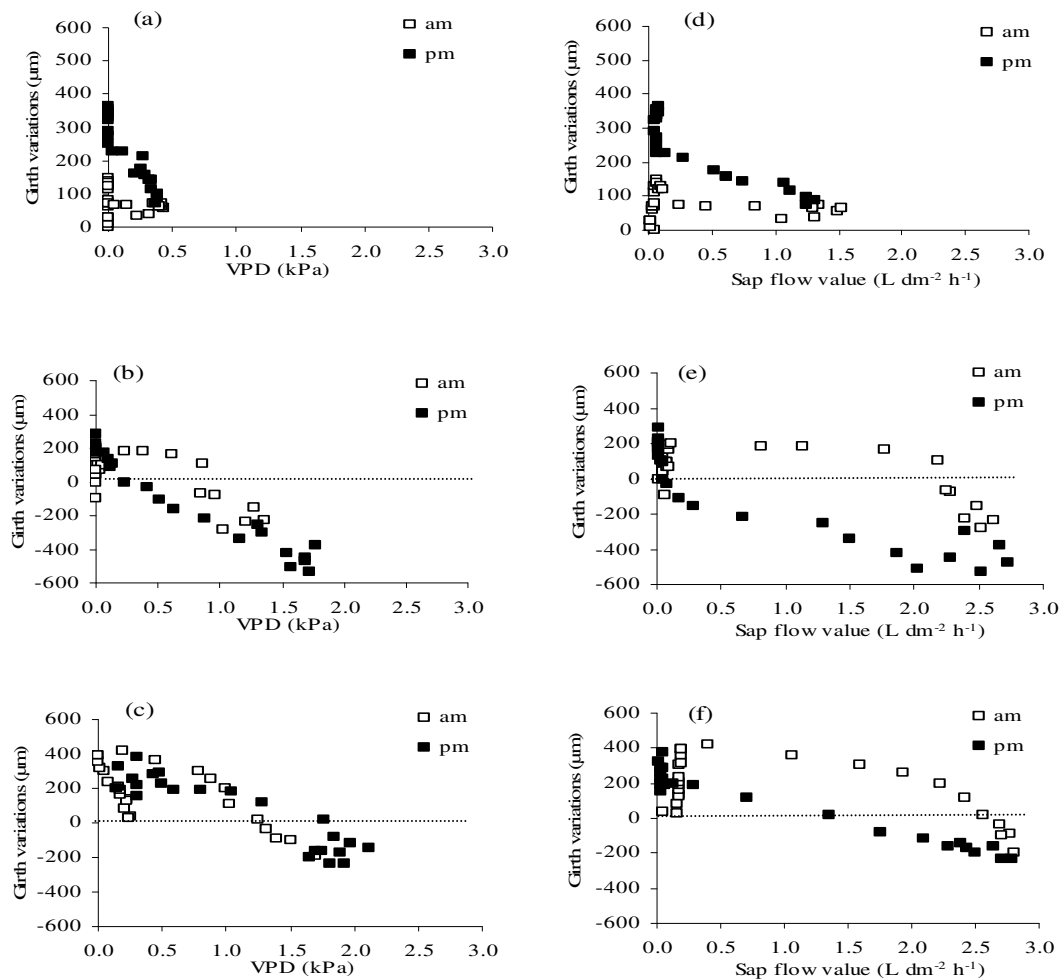


Fig 5. Diurnal course of changes in stem girth at different air vapour pressure deficit (VPD) and sap flow values for three mature rubber trees under non-limiting soil moisture. Each stem girth variation value is the difference between the girth at the time of measurement and the girth 30 min earlier, in the morning (am) or afternoon (pm) in three ranges of VPD. The upper panel presents data at the low VPD level (< 1 kPa, average 0.43 kPa) for VPD (a) and sap flow (d); the middle panel presents data at the medium VPD level (1-2 kPa, average 1.78 kPa) for VPD (b) and sap flow (e); and the lower panel presents data at the high VPD level (> 2 kPa, average 2.11 kPa) for VPD (c) and sap flow (f), during the period 1 August - 31 October, 2007.

were compared during the 90 days of observations. Days with VPD values outside of these ranges were not included in the analysis. Ranges were used as a proxy for atmospheric conditions. Each tree was considered to be a replication, for a total of three replications in a randomized complete block design.

Soil water content measurements

Volumetric soil water content (θ) was measured with a neutron probe (3322, Troxler, North Carolina, USA). The probe was calibrated separately for topsoil (0-40 cm) and subsoil (40-180 cm) layers. Soil moisture content was measured two times a month during the study at 20 cm intervals of depth in the soil profile, starting from 10 cm below the soil surface down to 180 cm. Average field capacity was calculated as 19.8% of soil volume and permanent wilting points were calculated as 7% for topsoil and 10% for subsoil, respectively. A capacitive probe (Enviro flow sensors were connected to a data logger (model CR10X, Campbell Scientific, Leicester, UK) and data were recorded automatically every 30 min. Calibration was done by the method of Isarangkool Na Ayutthaya et al. (2010).

Data analyses

The experimental design was a randomized complete block design with three replications under three different VPD levels (low, intermediate and high). Analysis of variance was performed for individual datasets, which were collected at 30 min intervals. Data at 30 min intervals were grouped into three series based on VPD ranges (low, intermediate and high) were used to evaluate the diurnal variation in circumference of rubber trunk and the growth rate of the trunk. These mean values were plotted against times in 30 min intervals for each VPD range. MDS means were also plotted against VPD and sap flow for each VPD range. The significance of variation in MDS as a function of VPD and sap flow was assessed by regression analysis of the individual data points from three trees using SPSS Version 11.5 (SPSS Inc., Chicago, Illinois, USA).

Conclusion

Under minimum water stress conditions, stem girth fluctuation was greater at high ranges of VPD than at low ranges of VPD. Although soil water never fell below the permanent wilting point, during peak transpiration periods of

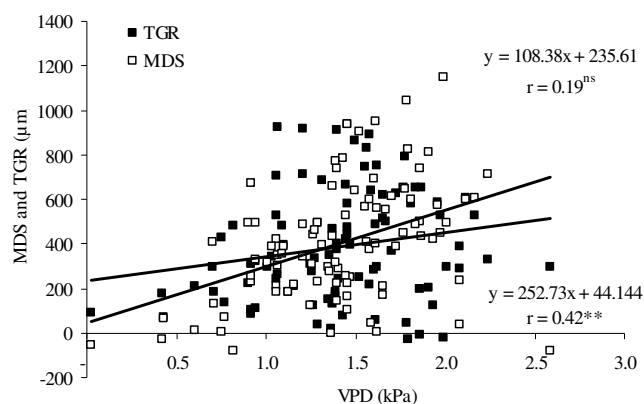


Fig 6. The relationship of maximum daily trunk shrinkage (MDS) and trunk growth rate (TGR) on air vapour pressure deficit (VPD) for three mature rubber trees under non-limiting soil moisture, 1 August - 31 October, 2007. Each data point represents a measurement taken on three trees (** significant at $p \leq 0.01$; ns = not significant).

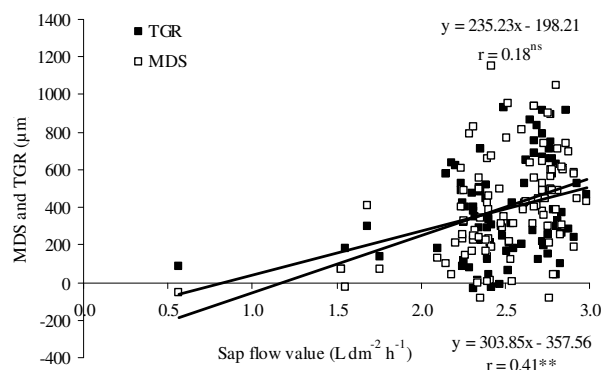


Fig 7. The relationship of maximum daily trunk shrinkage (MDS) and trunk growth rate (TGR) on sap flow of three mature rubber trees under non-limiting soil moisture, 1 August - 31 October, 2007. Each data point represents a measurement taken on three trees. (** significant at $p \leq 0.01$; ns = not significant).

the day, transpiration could exceed tree water uptake at the high ranges of VPD, and thereby created diurnal variation in MDS. However, as the temporary deficit in water uptake during the period of high VPD during the day could be compensated during by increased water uptake under low VPD at night, overall VPD did not affect TGR. Automatic recording of girth change by a dendrometer proved to be adequately sensitive to detect daily growth as well as trunk dehydration and hydration at 30 min intervals in response to diurnal VPD change. Conversely, VPD could be used to predict trunk shrinkage and water transpiration in mature rubber tree under minimum drought conditions. Finally, taken in their entirety, these results highlight the importance of considering atmospheric conditions when attempting to use MDS as an indicator of tree water status for mature rubber trees.

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