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STUDIES ON SOIL–PLANT–ATMOSPHERE SYSTEM IN *HEVEA* : II. SEASONAL EFFECTS ON WATER RELATIONS AND YIELD

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Influence of soil moisture status during dry and wet periods on yield, yield components and water relations was studied in four *Hevea* clones (RRII 105, RRII 118, G1 1 and Tjir 1). Low dry rubber yield in all the clones was associated with high plugging index and low initial flow rate of latex in the dry season. However, decrease in plugging index and increase in initial flow rate of latex more than compensated for the drop in dry rubber content in the wet season. RRII 105 had higher rubber yield in both the seasons. Transpiration rate was also low in RRII 105 in both the seasons. High latex vessel turgor and low latex solute potential in this clone in the dry season reveal osmotic adjustment. Maintenance of high plant moisture status in RRII 105 was also associated with higher stomatal resistance and higher xylem sap speed. The transpiration coefficient of different clones varied between 0.11 to 0.24 in the summer month and between 0.90 to 1.13 in the wet month. The results indicate that low transpiration coefficients are associated with high yields and drought tolerance in RRII 105 and G1 1. Significant seasonal differences are not observed in the minimum stomatal resistance. In *Hevea*, low latex yield during the dry period need not be due to low plant moisture status alone. Drought induced biochemical changes leading to higher plugging may also be important, which need further studies.

Key words – Hevea, Drought tolerance, Yield, Yield components, Water relations, Plant moisture status, Plugging, Transpiration coefficient

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INTRODUCTION

Latex from the Para rubber tree, *Hevea brasiliensis* (Willd. ex Adr. de Juss). Muell. Arg. exudes when the bark is severed on tapping, resulting in rapid elastic expulsion of the fluid cytoplasm (latex) due to the high hydrostatic pressure in latex vessels (Buttery and Boatman, 1976). The flow of latex is rapid in the beginning and declines gradually until it finally ceases as the latex at the cut ends of laticifers coagulates. Though latex flow characteristics including water relations of laticifers have been studied under moisture stress situations (Buttery and Boatman, 1976; Sethuraj and George, 1976; Raghavendra *et al*, 1984), no systematic approach has been made to find out the relationship between flow characteristics with various components of soil-plant-atmosphere system. This paper describes some of the observations made on the relationship between the factors governing water relations in a soil-plant-atmosphere system and yield during dry and wet seasons in a few clones of *Hevea*.

EXPERIMENTAL DETAILS

Observations were made on clones RRII 105 and RRII 118 (drought tolerant and drought susceptible, respectively, in terms of yield) at the Central Experiment Station (CES), Chethackal (9°22'N, 76°50'E) of the Rubber Research Institute of India and on clones Gl 1 (drought tolerant) and Tjir 1 (drought susceptible) at Malankara estate, Thodupuzha (9°55'N, 76°40'E). Clones RRII 105 and RRII 118 were selected considering the seasonal variation in monthly yield. Clones Gl 1 and Tjir 1 were selected for their contrasting drought tolerant characteristics in terms of yield based on earlier reports (Sethuraj and George, 1976). The trees at CES were 10 years old and those at Malankara were 22 years old. Observations were made during the moisture stress (dry) period (01–04–1987 and 03–04–1987 at Malankara and 21–04–1987 and 23–04–1987 at CES) and wet period (21–12–1987 and 22–12–1987 at Malankara and 13–01–1988 and 14–01–1988 at CES). The soils were of oxisol type. All the clones were under ½ S d/2 system of tapping. Five uniform trees of representative girth were selected for sampling from each clone.

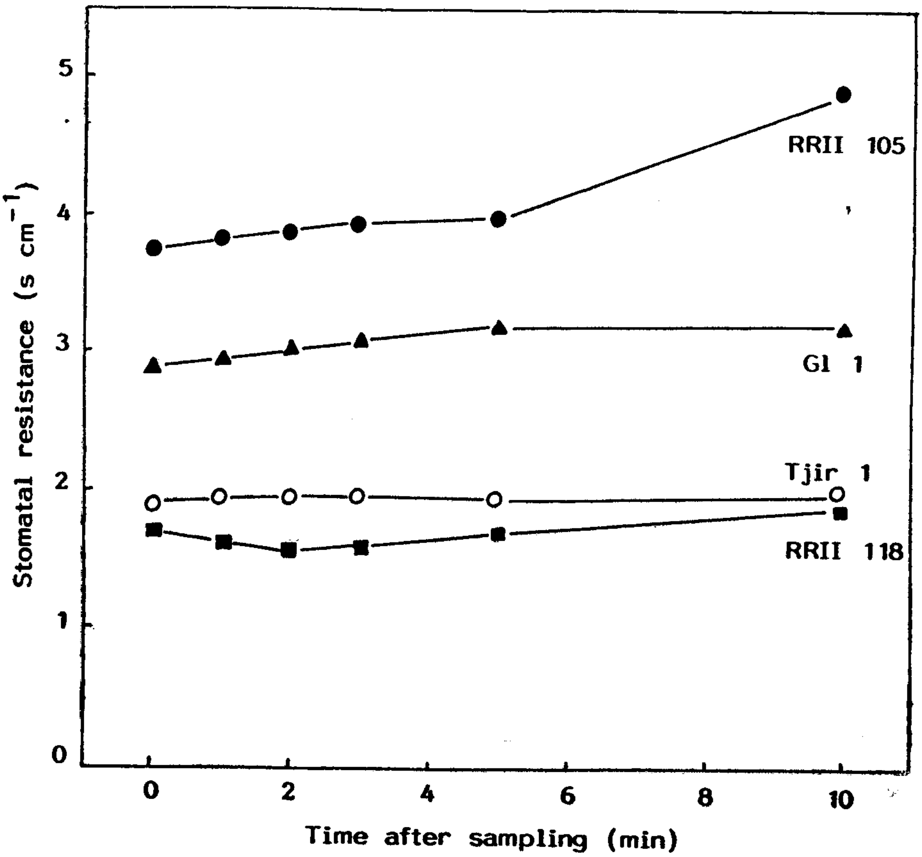

Fig. 1. Changes in stomatal resistance in excised leaves of *Hevea* clones with time.

Observations on diurnal changes in components of soil-plant-atmosphere system were monitored in all the clones (Gururaja Rao *et al*, 1988). Detached sun leaves from the periphery of the canopy were sampled for psychrometer and porometer recordings. The stomatal resistances were found not to differ much upto five min after excision (Fig. 1). Leaf water potentials (Ψleaf) and latex solute potentials (Latex π) were measured using C–52 sample chamber psychrometer (Wescor Inc., Logan, Utah, USA) connected to HR 33T Dew Point Microvoltmeter. Stomatal resistance (r_s) and transpiration(Tn) rates were measured using LI – 1600 Steady State Porometer (Licor Instruments, USA). Xylem sap speeds (xss) were monitored using Model HP–1 Sap Flow Meter (Hayashi Denkoh, Japan). The sensor and heat probes were installed above the tapping cut (already tapped portion) to a depth of 3.5 cm into the wood. Latex vessel turgor (P_{lv}) was estimated using disposable mini-manometers comprising No. 48 polythene surgical tubing sealed at one end and fitted with 21 gauge hypodermic syringe needle at the other (Raghavendra *et al*, 1984). The total length of the manometer was 20 cm. The length of the air space trapped was measured and the turgor pressure was estimated using a calibration curve prepared against known pressures. Turgor pressure was estimated 5 cm below the tapping cut.

Yield (g, tree^{-1} tap^{-1}) and yield components like initial flow rate (F, ml cm^{-1} min^{-1}), rubber content (C_r, per cent, w/v) and plugging index (p) were recorded on the days of observation. Plugging index was determined according to Milford *et al*, (1969) using the equation:

$$p = \frac{\text{Mean flow rate during the first 5 min x 100}}{\text{Total latex yield (ml)}}$$

Soil moisture levels were determined gravimetrically and the values were converted to potential units using the moisture release curves.

Vapour pressure deficits (vpd) were calculated from the measurements on wet bulb and dry bulb temperatures made in the open area adjacent to the experimental site and represent that of bulk air. Irradiance (Ir) was monitored using LI–1800 Spectro radiometer (Licor Instruments, USA) in the open.

Daily transpiration (mm d^{-1}) rates were obtained by integrating the hourly observations for the day time and by taking the mean value of pre-dawn and dusk transpiration rates as the mean of night transpiration. The sap flow rates for 12 h (day time) were worked out by taking the cumulative values of hourly readings. The relative ratios of transpiration to potential evapotranspiration (ET_o) were also worked out. Potential evapotranspiration rates were estimated according to the Penman method (Frere and Popov, 1979).

RESULTS

SOIL WATER POTENTIALS

Soil water potentials (Ψsoil) at 0–30 cm depth were –0.203 MPa and –0.30 MPa at CES and Malankara, respectively, during the dry season. Soil water potentials were below the wilting point at 30–90 cm depth (< -1.5 MPa) at both the locations. The higher water potentials in the surface layer were found to be due to the light showers received prior to the observations.

ATMOSPHERIC FACTORS

Diurnal changes in ambient temperature, vpd and Ir on different days of observation are presented in Figs. 2–9. The evapotranspiration values were around 5.4 mm d^{-1} in the dry season and 4.0 mm d^{-1} in the wet season on the days of observation.

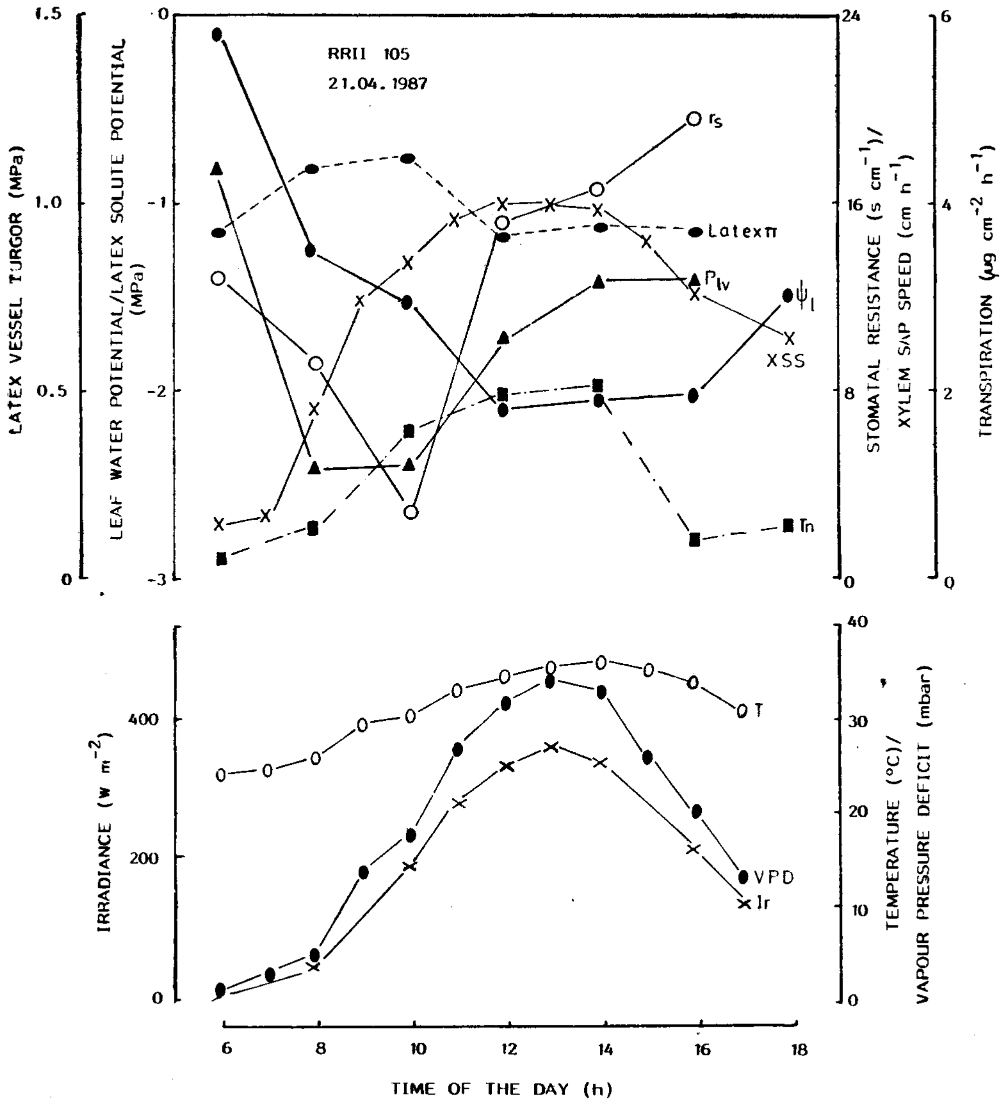

Fig. 2. Diurnal changes in components of plant water relations (leaf water potential, Ψ_l; latex vessel turgor, P_{lv}; latex solute potential, Latex π ; stomatal resistance, r_s; transpiration, Tn and xylem sap speed, xss) and atmospheric factors (ambient temperature, T; vapour pressure deficit, vpd and irradiance, Ir) in clone RRII 105 observed during the dry season of 1987. Soil water potentials (-MPa) were 0.203 at 0-30 cm depth and < 1.5 at 30–60 cm and 60–90 cm depths.

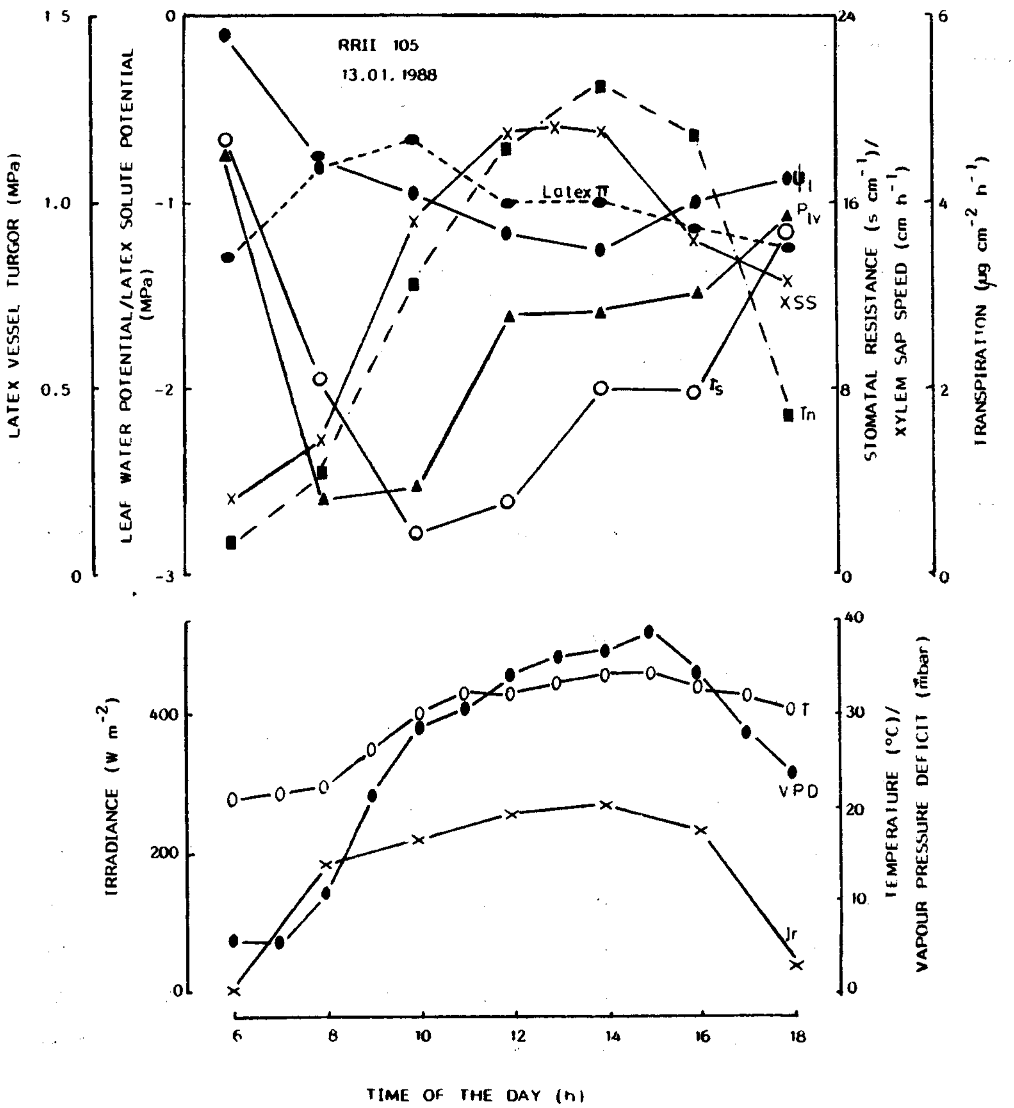

Fig. 3. Diurnal changes in components of plant water relations and atmospheric factors in clone RRII 105 observed during the wet season. Ψsoil = -0.05 MPa.

PLANT FACTORS

Yield and Yield Components

The dry rubber yields were very low during the dry period (61–82 per cent less) compared to wet season in all the clones (Tables 1 and 2). Increase in yield in the wet season was found to be associated with decrease in plugging index and enhanced initial flow rate. The changes in these two components more than compensated for the significant drop in dry rubber content in the wet season. The higher yield of clone RRII 105, in both wet and dry seasons, when compared to other clones, was associated with low p and high F. Though the absolute yield was higher for RRII 105 during the dry season, the per cent drop when compared to the wet season's yield was similar to that of clone RRII 118. Clonal difference between Gl 1 and Tjir 1 was not noticed in yield and yield components in the wet season. However, during the dry season Gl 1 had significantly higher yield which was associated with a higher F and a lower p. There was no difference in the C_r of the latices of these two clones during the dry season.

Table 1. Yield, yield components and components of water relations in RRII 105 and RRII 118 during dry and wet seasons at CES

Parameter	Dry Season		Wet Season		C. D $_{0.05}$		
	RRII 105	RRII 118	RRII 105	RRII 118	Seasons	Clones	S x C
Yield (g tree^{-1} tap^{-1})	46.26	18.62	119.50	50.70	9.41**	9.41**	13.31**
Initial flow rate (ml cm^{-1} min^{-1})	0.107	0.064	0.162	0.095	0.0065**	0.0065**	0.0092**
Rubber content (%, w/v)	44.20	45.60	35.90	39.90	1.334**	1.334**	1.886*
Plugging index	3.95	6.59	2.02	3.20	0.148**	0.148**	0.209**
Pre-tapping P_{lv} (MPa)	1.10	0.88	1.11	0.89	NS	0.068**	NS
Minimum P_{lv} (MPa)	0.30	0.17	0.288	0.224	NS	0.024**	0.034*
Latex solute potential (–MPa)	1.29	1.06	1.15	0.92	0.061**	0.061**	NS
Pre-dawn Ψleaf (–MPa)	0.15	0.26	0.123	0.18	0.047**	0.047*	NS
Mean Ψleaf (–MPa)	1.59	1.98	1.11	1.39	0.150**	0.150**	NS
After-noon Ψleaf (–MPa)	1.88	2.42	1.28	1.66	0.167**	0.167**	NS
Minimum r_s (s cm^{-1})	2.18	1.82	2.10	1.76	NS	0.319*	NS
Mean r_s (s cm^{-1})	14.62	6.82	10.42	5.86	0.663**	0.663**	0.988*
Transpiration (mm day^{-1})	0.597	1.08	3.491	4.468	0.0628**	0.0628**	0.0889**
Transpiration coefficient	0.111	0.242	0.898	1.039	0.0075**	0.0075**	0.010**
Xylem sap speed (cm/12 h)	135.97	72.34	158.26	106.84	3.54**	3.54**	5.01**
Pre-tapping P_{lv} (MPa) (March, 1987 & Wet season)	0.78	0.65	1.11	0.89	0.046**	0.046**	0.066**

** — Significant at 1% error;
* — Significant at 5% error;
NS — Non-significant

Table 2. Yield, yield components and components of water relations in Gl 1 and Tjir 1 during dry and wet seasons at Malankara

Parameter	Dry Season		Wet Season		C. D. $_{0.05}$		
	Gl 1	Tjir 1	Gl 1	Tjir 1	Seasons	Clones	S x C
Yield (g tree $^{-1}$ tap $^{-1}$)	35.92	17.56	96.50	99.20	5.53**	5.53**	7.82**
Initial flow rate (ml cm^{-1} min $^{-1}$)	0.089	0.062	0.091	0.093	NS	NS	NS
Rubber content (%, w/v)	43.60	41.90	39.30	36.90	2.384*	NS	NS
Plugging index	5.49	8.08	1.89	1.81	1.09**	1.09**	1.546**
Pre-tapping P_{lv} (MPa)	0.95	0.89	1.02	1.08	0.0664**	NS	NS
Minimum P_{lv} (MPa)	0.194	0.196	0.246	0.274	0.019**	NS	NS
Latex solute potential (-MPa)	1.02	1.01	0.92	0.91	0.093*	NS	NS
Pre-dawn Ψleaf (–MPa)	0.23	0.25	0.14	0.15	0.028**	NS	NS
Mean Ψleaf (MPa)	1.90	1.94	1.32	1.27	0.161**	NS	NS
After-noon Ψleaf (–MPa)	2.32	2.64	1.66	1.58	0.212**	NS	0.299*
Minimum r_s (scm^{-1})	1.42	1.66	1.08	1.50	NS	0.314*	NS
Mean r_s (scm^{-1})	9.36	9.42	7.92	8.70	0.983*	NS	NS
Transpiration (mm day^{-1})	0.832	1.331	4.516	4.549	0.0976**	0.0976**	0.138**
Transpiration coefficient	0.151	0.224	1.039	1.130	0.0237**	0.0237**	0.034**
Xylem sap speed (cm/12 h)	89.70	97.76	108.76	109.58	2.675**	2.675**	3.78**

** — Significant at 1% error; * — Significant at 5% error; NS — Non-significant

Physiological Parameters

Leaf water potential (ψleaf): All the clones showed higher ψleaf during the wet season. The ψleaf of all the four clones was maximum shortly before sunrise, after which it became more negative and reached a minimum value at or after midday and showed some recovery at dusk. Of all the clones, RRII 105 showed high ψleaf in both dry and wet seasons.

Stomatal resistance (r_s): Stomatal resistance measured in the abaxial surface was minimum at 10.00 h followed by an increase afterwards. In all the clones, r_s was less during the wet season. RRII 105 was found to have higher r_s compared to all the other clones in both the seasons. No appreciable change in r_s was noticed in dry and wet seasons at the time of maximum stomatal opening.

Transpiration (Tn): Inhibition of transpiration was high in the dry season. Tn was maximum at or after midday during both the seasons. Transpiration rate was found to be less in RRII 105 in both the seasons.

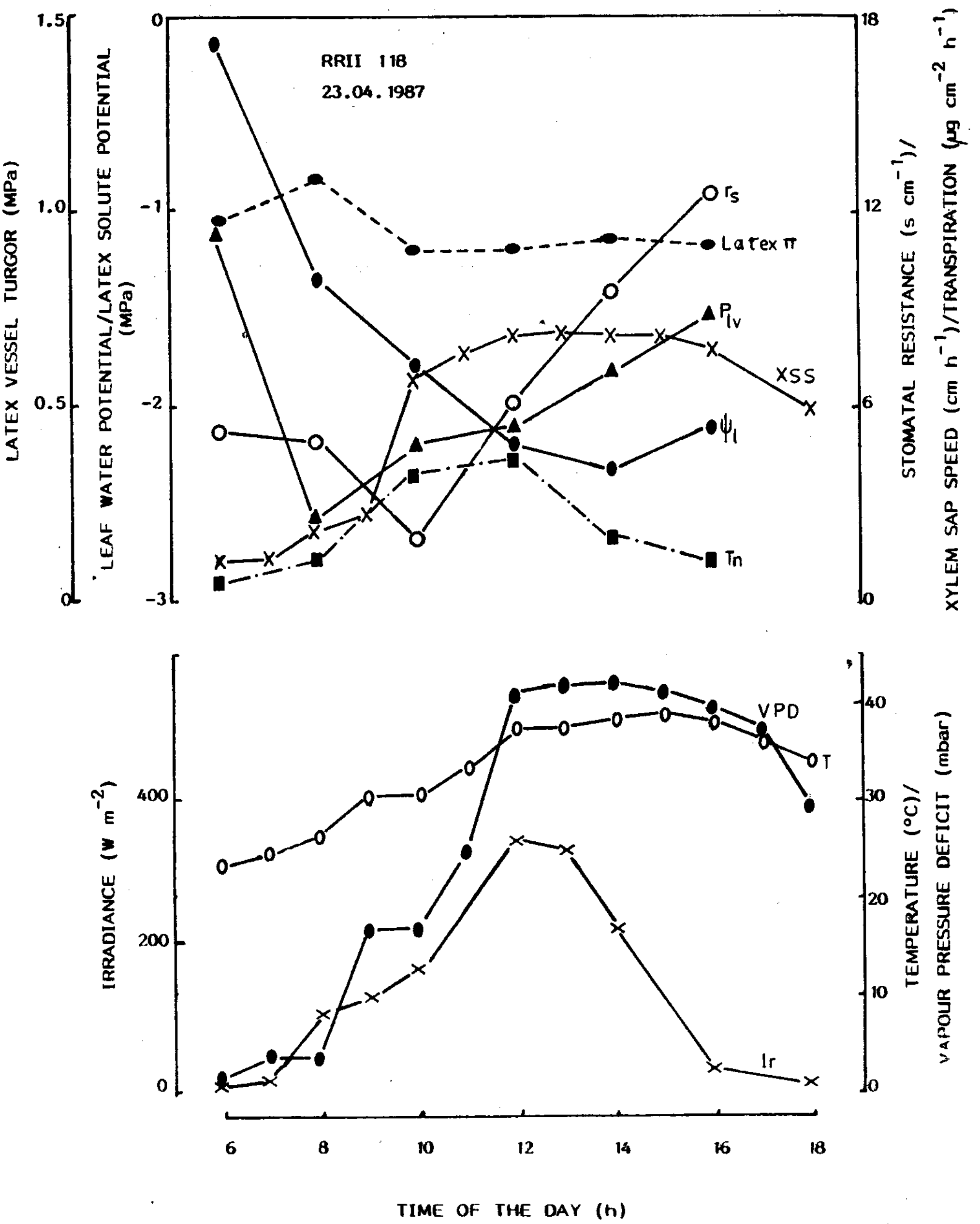

Fig. 4. Diurnal changes in components of plant water relations and atmospheric factors in clone RRII 118 observed during the dry season. (Ψ_{soil} is as in Fig. 1)

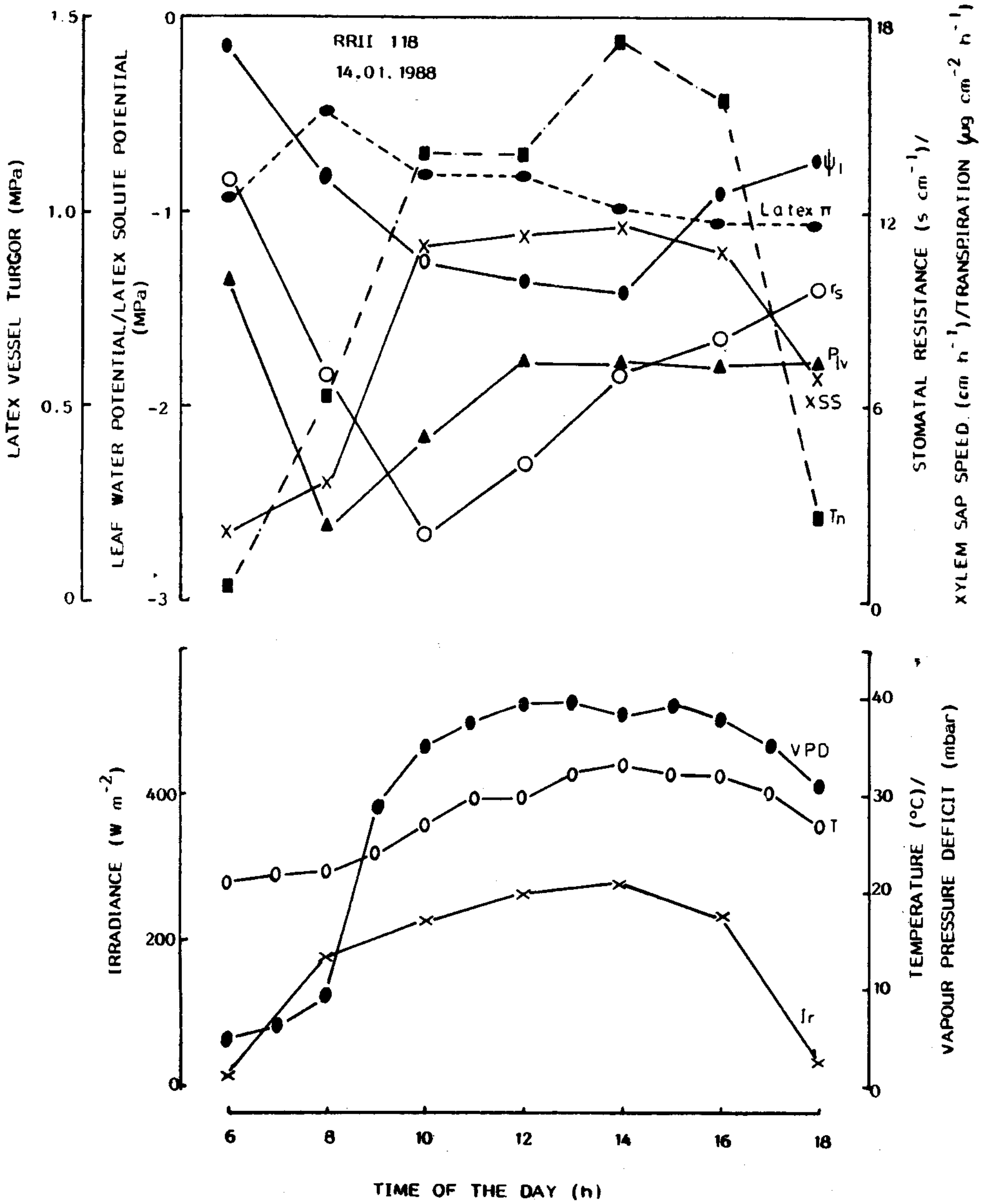

Fig. 5. Diurnal changes in components of plant water relations and atmospheric factors in clone RRII 118 observed during the wet season. Ψ_{soil} = –0.05 MPa

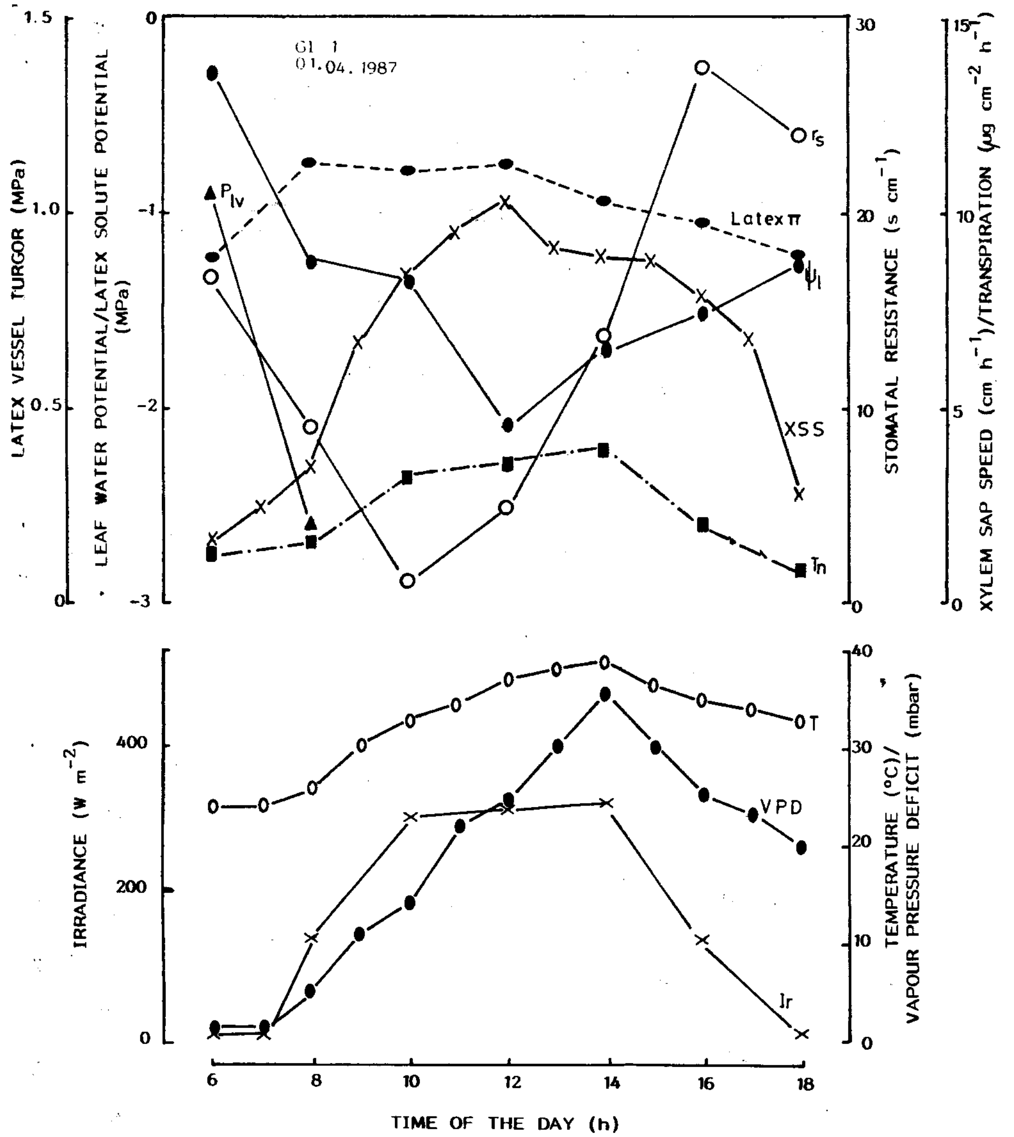

Fig. 6. Diurnal changes in components of plant water relations and atmospheric factors in clone Gl 1 observed during the dry season. Soil water potentials (–MPa) were 0.3 at 0–30 cm depth and < 1.5 at 30–60 and 60–90 cm depths.

Xylem sap speed (xss): xss was found to be minimum at dawn and then it increased as the day progressed, attained a maximum value around noon and then declined reaching low values at dusk during both the wet and dry seasons. Among all the clones RRII 105 showed very high values of xss.

Latex vessel turgor (P_{lv}): Turgor pressure of laticifers of *Hevea* was in the range of 0.9 – 1.1 MPa. Tapping had resulted in a sudden drop in P_{lv} to the level of 0.2 – 0.3 MPa.

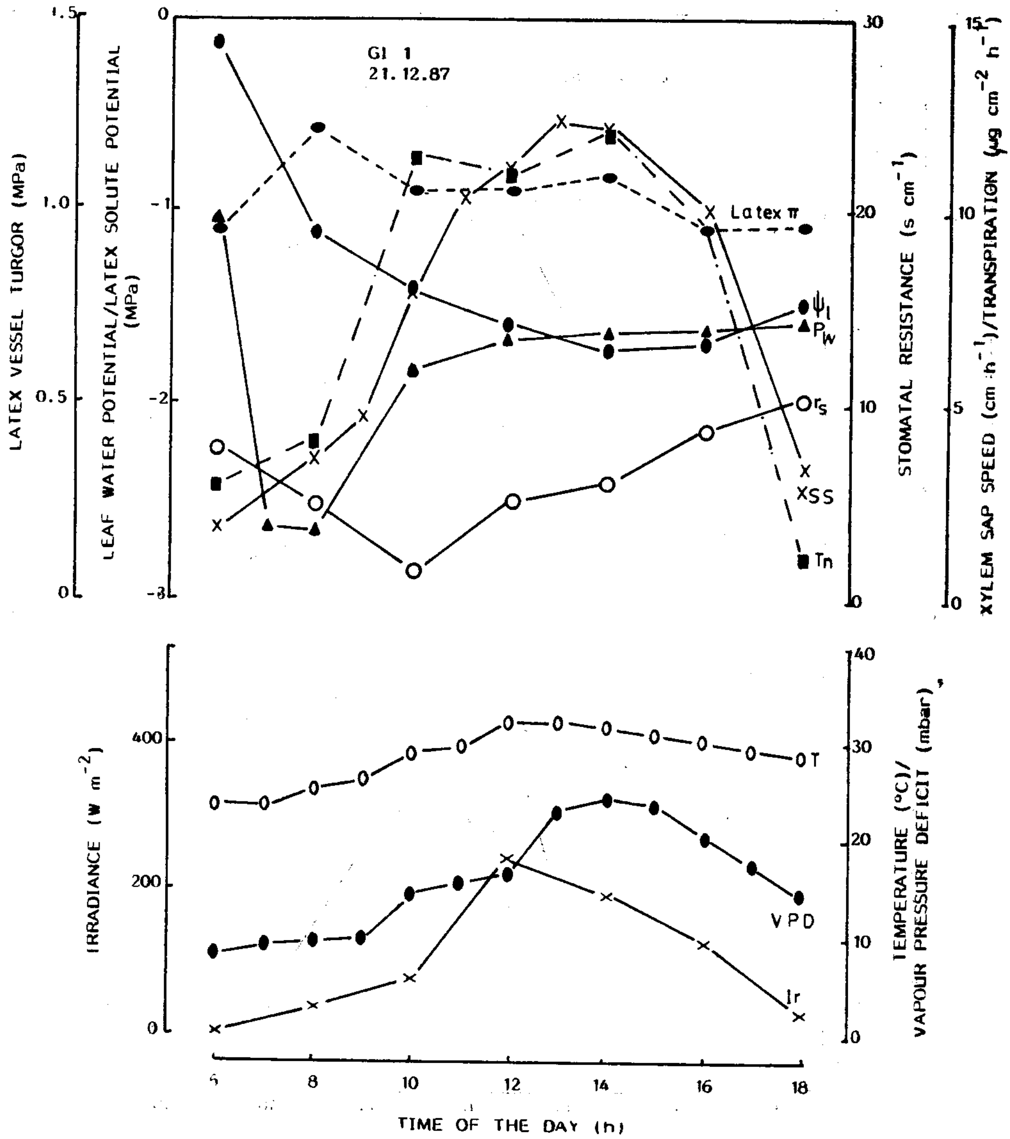

Fig. 7. Diurnal changes in components of plant water relations and atmospheric factors in clone Gl 1 observed during the wet season. $\Psi_{soil} = -0.05$ MPa.

Positive turgor was maintained throughout the day including the period of latex flow. Rebuilding of turgor was noticed with the cessation of latex flow.

Latex solute potential (Latex π): Solute potential of the latex prior to tapping was in the range of −1.0 to −1.3 MPa. Latex π increased after tapping and maintained almost a steady state during the flow period and decreased at the end of the flow period and later at dusk in both the seasons in all the clones.

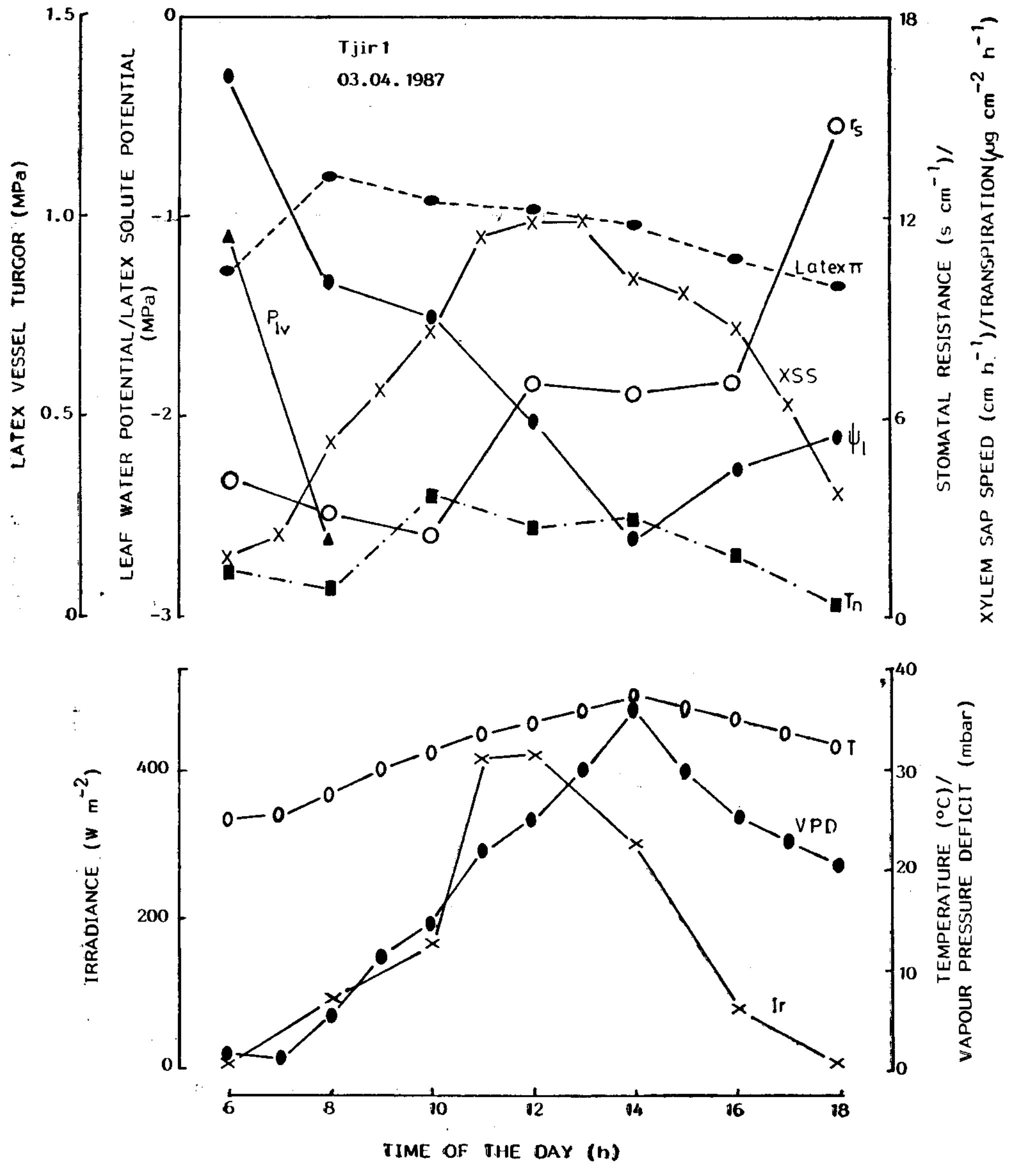

Fig. 8. Diurnal changes in components of plant water relations and atmospheric factors in clone Tjir 1 observed during the dry season (Ψ_{soil} as in Fig. 5.)

The pre-tapping turgor pressure in the latex vessels was significantly lower during the dry period. At CES the P_{lv} values recorded in the dry season were comparable to those in the wet season. However, in March the values were significantly lower. Observations on yield, yield components and P_{lv} in RRII 105 and RRII 118, made during March, 1987 are given in Table 3. Though the pre-tapping turgor pressures were similar

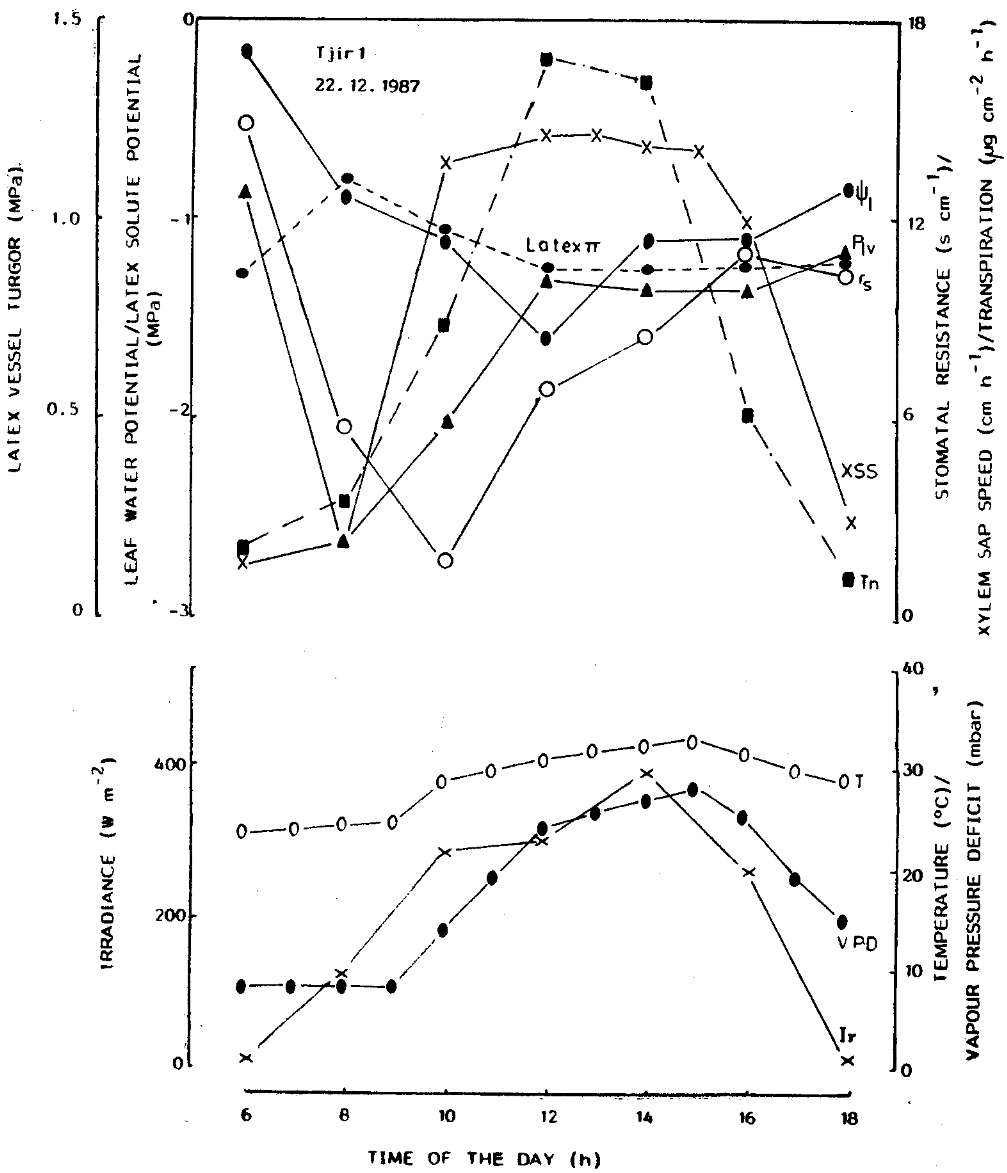

Fig. 9. Diurnal changes in components of plant water relations and atmospheric factors in clone Tjir 1 observed during the wet season. Ψ_{soil} = — 0.05 MPa.

in dry and wet seasons, the mean turgor during the latex flow period was lower in the dry season. The recovery of turgor was also slow in the dry season (Figs. 2 and 4). In both the dry and wet seasons, RRII 105 maintained better latex vessel turgor. Moreover, turgor build-up was also faster in this clone. The latex solute potentials were lower in the dry season in all the clones indicating osmotic adjustment. No difference was noticed between Gl 1 and Tjir 1 in their P_{lv} and Latex π in both the seasons.

Table 3. Yield, yield components and pre-tapping latex vessel turgor in RRII 105 and RRII 118 during March, 1987

Parameter	RRII 105	RRII 118
Yield (g, tree $^{-1}$ tap^{-1})	36.30	9.60
Initial flow rate (ml, cm^{-1} min^{-1})	0.093	0.038
Rubber content (%, w/v)	44.72	46.67
Plugging index	4.44	7.86
Pre-tapping latex vessel turgor (MPa)	0.78	0.65

Leaf water potentials (ψ_{leaf}) were significantly lower during the dry season. Such variations were less in the pre-dawn ψ_{leaf} values when compared to the mean or afternoon leaf water potentials. Clone RRII 105 maintained better leaf water status during both dry and wet seasons when compared to all the other clones (Tables 1 and 2).

Minimum stomatal resistance was observed at 10.00 h (Figs. 2–9). Seasonal differences were non-significant. The minimum stomatal resistance was slightly higher in RRII 105 and Tjir 1 (significant at 5 per cent error). Significant differences were noticed in the mean r_s values between seasons in both the locations. Afternoon stomatal resistance was also higher in RRII 105 when compared to the other clones in both the seasons (Figs. 2–3). The maximum resistance was noticed in RRII 105 and the minimum in RRII 118. The differences were non-significant between Gl 1 and Tjir 1, in both the seasons.

The computed daily transpiration rates were higher during the wet season. The rates of Tn were lower in RRII 105 in both the seasons. Tjir 1 showed higher transpiration rates when compared to Gl 1.

The mean transpiration coefficient was 0.18 in the dry season and 1.06 in the wet season. Clonal differences were highly significant. The clone RRII 105 had much lower values in both the dry and wet seasons followed by Gl 1. RRII 118 and Tjir 1 had higher transpiration coefficient values.

The cumulative xylem sap speeds were markedly higher during the wet season. Of all the clones, RRII 105 had the highest values (136–158 cm/12 h) in both the seasons. RRII 118 had the lowest sap speed in the dry season. Though there was no clonal difference in the wet season between Gl 1 and Tjir 1, the latter had significantly higher sap speed in the dry season.

DISCUSSION

In a survey conducted during the drought period in March 1987, it was noticed that the soil water potential was below the wilting point upto 60 cm depth, in both the locations of the study. Even in the 60–90 cm layer, water availability was very poor. Severe soil water deficit was experienced due to the unusual rainfall pattern with very low precipitation during October and November, 1986 and almost total absence of rain in December, 1986 to March, 1987 (Vijayakumar *et al*, 1988). Latex vessel turgor at CES (Tables 1 and 3) during March and April, 1987 indicated that the scanty rains received a couple of weeks before the observations, were partially effective. Pre-tapping latex vessel turgor pressure observed during April, 1987 at CES was even comparable to that of wet season (Table 1). However, afternoon leaf water potential and other related physiological parameters (Table 1; Figs. 2 and 4) indicate that the trees were experiencing severe drought in April also. Though the P_{lv} of laticifers were significantly lower during the dry season, the differences were not marked. Probably the pre-tapping P_{lv} of laticifers would have been very low in the previous month.

In *Hevea brasiliensis* low rubber yield during summer is due to soil moisture stress as well as due to wintering and subsequent refoliation (Chua, 1970). Separate quantification of these two would be possible only with irrigation experiments. Low summer yield was associated with high plugging index which is in agreement with earlier findings (Sethuraj and George, 1976). Though the pre-tapping turgor pressure was not very low in April 1987 at CES, the initial flow rate was very low. Significantly higher C_r and subsequent higher viscosity of latex might have resulted in low F (Buttery and Boatman, 1976). However, the direct effect of pre-tapping P_{lv} on F is evident from Table 3. Increase in bursting index and lowered lutoid stability in summer months, leading to an increase in plugging index, were already reported (Premakumari *et al,* 1980). Lower latex yield in dry periods is the result of lower flow rate and reduced duration of flow. The stress induced biochemical changes leading to decreased lutoid stability need further investigations. The present yield data indicate that RRII 105 is relatively drought tolerant (Table 3), whereas the clone RRII 118 is very susceptible. The drought tolerance of Gl 1 and susceptibility of Tjir 1, reported in the present study, are in conformity with earlier reports (Raghavendra *et al,* 1984). Clonal variation in yield between RRII 105 and RRII 118 in summer months was associated with variation in latex vessel turgor, F, p and C_r. However, such yield difference in Gl 1 and Tjir 1 was mainly due to variation in p which occurred during summer. The drought susceptibility of the clone RRII 118 in terms of yield indicates that in *Hevea* tolerance to drought in terms of growth and yield are probably two separate phenomena.

The absence of differences in pre-tapping latex vessel turgor between dry and wet seasons (Table 1) can be ascribed to osmotic adjustment in the latex. In RRII 105, higher turgor in both the seasons is associated with lower latexπ. Such osmotic adjustments were already reported (Raghavendra *et al,* 1984). Absence of such differences in the osmotic potentials of the latices of Gl 1 and Tjir 1 indicates that osmotic adjustment need not always be essential to cause variation in drought tolerance.

Maintenance of higher plant water status in clone RRII 105 is associated with higher stomatal resistance and higher xylem sap speeds. A low reduction of Ψleaf in drought tolerant clones of *Hevea* subjected to water stress in pot experiments has been reported (Da Conceicao, 1985). However, in Gl 1 and Tjir 1, though the mean and afternoon leaf water potentials were the same, significant differences were observed in stomatal resistance during the morning hours in the dry season. Transpiration rates were higher for clone Tjir 1 in both the seasons. This may be because of more heat absorption due to the low cuticle thickness in Tjir 1 (Gururaja Rao *et al,* 1988). The present data suggest that maintenance of higher Ψleaf alone cannot completely explain the drought tolerance in terms of yield. Clonal variation in biochemical parameters as well as changes leading to variation in plugging, caused by drought, are also important.

Absence of seasonal variation in minimum stomatal resistance *ie.* the peak hours of photosynthesis (unpublished), low evaporative demand and almost negligible difference between clones in this parameter in the morning hours of dry season, need further investigation. Such adaptations are important for better water use efficiency (WUE) under drought conditions.

The higher sap flow rates in RRII 105

inspite of low $\Delta\psi$ values indicate lower root resistance which may be due to either higher root density or better root permeability to water. Maintenance of higher r_s in spite of better water status in this clone might indicate genetic variation in stomatal response to leaf water potentials.

The transpiration coefficient reported in this study can be used as a tool to quantify soil moisture availability, as in tree crops such quantifications are often difficult using soil moisture data alone. The present study shows that lower transpiration coefficient is one of the parameters associated with high yield and drought tolerance in RRII 105 and Gl 1 (Tables 1 and 2).

In conclusion it can be stated that drought effect on latex yield are caused not only by the direct effect of plant moisture status but also by the drought induced biochemical changes leading to increased latex vessel plugging and decreased latex solute potentials. Maintenance of better plant water status including osmotic adjustment in the laticifers and low plugging indices are the observed characters of drought tolerant clones of *Hevea*.

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