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ECOPHYSIOLOGY OF A HOST-PARASITE RELATIONSHIP IN TEAK

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Ecophysiology of a host-parasite relationship in teak

(Draft Report of the Research Project No: KFRI/271/97 March-1997 to September-2001)

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Abstract of Project Proposal

1. Project No. **KFRI 271/97**
2. Title of the project : **Ecophysiology of a host-parasite relationship in teak**
3. Objectives
    - a) To understand the water relations, transpiration and gas exchange characteristics of the hemiparasite *Dendrophthoe falcata* in relation to its host, the teak tree.
    - b) To examine the interaction of the water relations of the hemiparasite with the nitrogen and mineral nutrition of teak.
    - c) To study the ecophysiological factors that promotes the growth of the parasite on teak.

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Authors

Symbols and abbreviations

ψ	Water potential
10RC/ABS	Photon flux absorbed per 10 Reaction centres
ABS/CSm	Energy absorption per membrane cross section
ABS/CSo	Energy absorbed per excited cross section
ABS/RC	Average absorption per active reaction centre
Area	Area between fluorescence curve and F_m
D	Vapour pressure deficit
DIo/CSm	Dissipated photon flux per membrane cross section
DIo/CSo	Dissipated photon flux per excited cross section
DIo/RC	Ratio of total dissipation to the amount of active reaction centres
dV/dto	Initial slope of the relative variable fluorescence
dVG/dto	Slope of the relative variable fluorescence
ETo/CSm	Energy flux corresponding to electrons transported per membrane cross section
ETo/CSo	Energy flux corresponding to electrons transported per excited cross section
ETo/RC	Energy flux corresponding to electrons transported per reaction centre
Fm	Maximal fluorescence intensity
Fo	Fluorescence intensity at 50 µs
Fo/Fm	Ratio of the extrema
Fv/Fo	Ratio of the difference to initial fluorescence
g_s	Stomatal conductance
Kn	Non-photochemical rate constant
Kp	Photochemical rate constant
MPa	Megapascals
N	$S_m.M_0.(I/V_j)$ turnover number Q_A

PHI(Do)	Yields
PHI(Eo)	ET_0/ABS
PHI(Po)	Fv/Fm
PHIo/(1-PHIo)	Vitality Index
PI(abs)	Performance Index based on equal absorption
PI(csm)	Performance index based on cross section of membrane area
PI(cso)	Performance index based on cross section of leaf area
P_n	Net Photosynthesis
PSIo	ET_0/TR_0
PSIo/(1-PSIo)	Vitality Index
r.h.	Relative humidity
RC/CSm	Reaction centers per membrane cross section
RC/CSo	Density of active reaction centers per cross section
RWC	Relative water content
SFI(abs)	A phenomenological parameter
Sm	Normalized area =Area/(F_M-F_0)- multiple turn-over in the closure of reaction centres
Sm/T(fmax)	Rate of multiple turn-over in the closure of reaction centres
Sum K	Sum of K_n and K_p
Tf(max)	Time to reach maximal fluorescence
TRo/CSm	Trapping flux per membrane cross section
TRo/CSo	Trapping flux per excited cross section
TRo/RC	Trapping flux per reaction centre
Vi	Relative variable fluorescence at point I
Vj	Relative variable fluorescence at point J
VPD	Vapour Pressure Deficit
WUE	Water use efficiency

ABSTRACT

This document reports the ecophysiological aspects of a host-parasite relationship in teak infested with *Dendrophthoe falcata*. Diurnal measurements of water potential revealed that the parasite always maintained lower water potential than its host. Stomatal conductance (g_s) measurements indicated that teak is having stomata on the abaxial side only whereas *Dendrophthoe* possesses stomata on both sides of its leaf. The g_s values during pre-monsoon were almost similar in both host and the parasite with values less than 600 mmol m^{-2} s^{-1}. The low values of g_s indicated that both host and the parasite have good stomatal control during the stress period. Net photosynthesis ($\boldsymbol{P_n}$) was higher in teak than in *Dendrophthoe*. Teak showed a maximum photosynthetic rate of 13 μmol m^{-2} s^{-1} against 9 μmol m^{-2} s^{-1} in *Dendrophthoe* during pre-monsoon. The post monsoon values of net photosynthesis for teak were much higher than that for *Dendrophthoe,* where P_n decreased to less than 4 μmol m^{-2} s^{-1}. The light availability to the parasite and host showed that the parasite received only 30% of the light as received by the host during post monsoon. The integrated PAR (photosynthetically active radiation) received by the upper canopy increased up to 7000 mol m^{-2} h^{-1}, while the lower canopy of the mistletoe received a maximum of 2500 mol m^{-2} h^{-1}. Leaf temperature measurements indicated that both host and the parasite maintained 2 to 3^{o}C higher temperature than atmospheric temperature. Sap flow measurements in an infected twig showed that the parasite had lower values of flux during morning and evening, which exceeded that of teak in the noon hours. Leaf number and leaf area developments of selected twigs showed that teak had minimum leaf number and area in January and February. Profuse leaf fall was noticed in teak during this period. In *Dendrophthoe* there was decrease in leaf area and number from November to January. Profuse flowering in teak occurred in July followed by fruit setting that ended in March. Sporadic flowering was also noticed in both cases. Nutrient analysis conducted using mature leaves collected from different plants of both host and the parasite from different locations indicated higher rates of Potassium in *Dendrophthoe* compared to teak.

Ecophysiological studies on the teak and the parasite *Dendrophthoe* reveal the high ecological and physiological adaptations of the parasite to survive on the host tree

1. Introduction

Infestation of teak plantation by mistletoes is common all over India. The hemiparasite, *Dendrophthoe falcate* var. *pubescens*, like any other hemiparasite, is believed to draw water and minerals from the host tree, at the same time, capable of photosynthesizing in its own leaves. The infested trees show enormous growth retardation, and at a later stage even complete death. It is really perplexing to note that a small parasitic plant can damage a large tree such as teak seriously. Is the amount of food that is withdrawn by the parasite from the host plant substantial to kill the host plant? To find an answer to this question, we have studied the ecophysiological relations between the host and the parasite with the following objectives:

a. To understand the water relations, transpiration and gas exchange characteristics of the hemiparasite *Dendrophthoe falcata* in relation to its host, the teak tree.
b. To examine the interaction of the water relations of the hemiparasite with the nitrogen and mineral nutrition of teak.
c. To study the ecophysiological factors that promote the growth of the parasite on teak.

For the past few years, Kerala Forest Research Institute has been actively involved in the study of parasite control in teak (see Ghosh et al. 1984; Balasundaran and Ali 1989). The above studies have been directed to control the infestation of the parasite in teak plantations. Except for some limited success on individual trees, methods aimed at controlling the mistletoe on teak on a plantation scale have not succeeded. This is probably because of the lack of understanding of the phenomenon of parasitism, particularly, the host-parasite relationship. Although much work has been done to understand the ecophysiological relationship between the host and parasite in several temperate trees, there is hardly any such detailed study from the tropics.

In this study, an attempt has been made to undertake the host-parasite relationship between teak (*Tectona grandis*) and its most common parasite, *Dendrophthoe falcata*, from an ecophysiological angle. The difficulty in accessing the parasite on such a tall tree has certainly limited the number of samples we could measure during the study, however, sophisticated instrumentation has helped us to make meaningful ecophysiological measurements on the limited samples available.

2. Materials and Methods

2.1 Site details

Detailed measurements on the physiological parameters on teak infected with *Dendrophthoe falcata* were carried out for three years at two locations *viz.* Peechi and Kayampoovam. The site details of the two locations are presented in Table 1.

Table 1. Site details of the two locations where observations and experimental measurements were made during the study.

S.No	**Particulars**	**Site-I (Peechi)**	**Site –II (Kayampoovam)**
1	Forest Division	Thrissur	Palakkad
2	Forest Range	Pattikkad	Machad
3	Section	Peechi	Kayampoovam
4	Latitude	10^{o} 32`N	10^{o} 42`
5	Longitude	76^{o} 20`E	76^{o} 24`
6	Altitude	100 msl	120 msl
7	Annual rainfall	2500 mm	1500 mm
8	Year of planting	1984	1969
9	Average dbh of teak trees	20 cm	22.75 cm
10	No of stems/ha	Multi-tier	700
11	Planting distance	4 x 2 m	2 x 4 m
12	Average tree height	10 m	12 m
13	Period of study	1997-1999	2000-2001

In the first site, located at Peechi, the teak trees were heavily infested with *Dendrophthoe falcata* in the multitier experimental plot of KFRI Peechi campus. A steel scaffold tower of 12 m height was erected near a heavily infested tree to access the crown of both the host and the parasite for the physiological measurements (Fig. 1). In the second site, the plot was a pure teak plantation and is maintained by the Kerala Forest Department. Most of the teak trees were infested with *Dendrophthoe falcata*. A scaffold tower was erected here also to access the host and the parasite. Besides, this plot had several small teak trees with the mistletoe infestation that could be reached from the ground for various measurements.

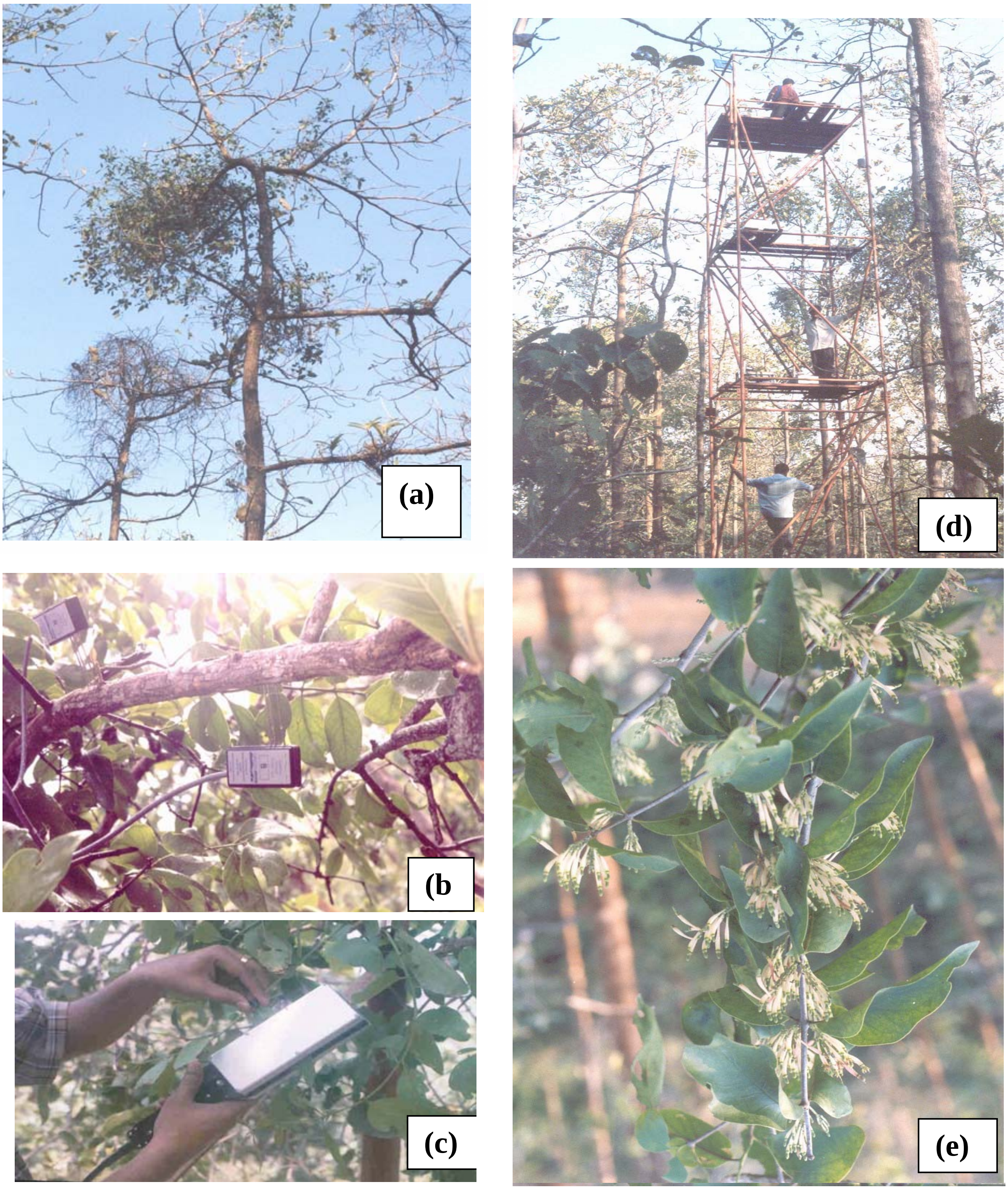


Fig. 1. (a) Teak tree infected with *Dendrophthoe*. The teak trees have only few leaves while *Dendrophthoe* is in full flush. (b) Sap flow sensor fixed to the branches of a *Dendrophthoe* (c) Leaf area measurement in *Dendrophthoe* using Leaf area meter. (d) A 12 m scaffold tower to reach the canopy of the teak tree. (e) One flowering twig of *Dendrophthoe*.

2.2 Weather parameters

The weather parameters of the locations, namely atmospheric temperature, relative humidity, wind velocity, solar radiation and rainfall were collected hourly using an automated weather station. Temperature was measured using a thermistor; relative humidity by an RH sensor; wind velocity, by cup counter anemometer with a switch closure mechanism and solar radiation by a Pyranometer. All the sensors were connected to a data logger (Minimet, Skye Instruments, UK). The data were logged for every 30 seconds and averaged hourly. The data were further transferred to a computer and analysed.

2.3 Water status

Water status of the leaves was checked by measurements of relative water content and water potential.

2.3.1 Relative water content (RWC)

Physiologically mature leaves were selected from both host and the parasite. Discs of 1 cm diameter were cut from fresh leaves and fresh weights were recorded. The discs were then floated on distilled water in closed petridishes under diffused light for 4-5 hours. When the leaf-discs attained constant weight, the turgid weight was determined using an electronic balance. The discs were then dried by keeping in a hot air oven at 85^{o}C for 48 hours and dry weight was determined. RWC is calculated as

$$\text{RWC (\%)} = \frac{(\text{FW-DW})}{(\text{TW-DW})} \times 100$$

where, FW= fresh weight, DW= dry weight, TW= turgid weight.

2.3.2 Pressure-volume curves

The pressure-volume curve analysis helps to determine the symplastic values of solute potential and the turgor pressure of living tissues of plants. This was done according to the recommendations of Turner (1988). A leafy twig was cut under water for preventing entry of air bubbles. Initial weight of the leafy twig was taken, the twig was then covered with a polythene bag and kept in dark for 3-4 hours, keeping the cut end in water and allowed to saturate till turgid weight was attained. Water potential (ψ) of the leafy twig was taken at this point along with weight measurements. The twig was then allowed to dry over a laboratory bench and intermittent measurements of water potential were recorded. Weighing and ψ measurements were repeated for both teak and *Dendrophthoe* leaves. For each measurement, corresponding RWC was also calculated. A plot of the reciprocal of ψ versus RWC will yield PV curve. The point at which the curve becomes linear was determined graphically with the help of stepwise linear regression. The point of intersection of Y-coordinate will give the reciprocal of water potential at zero turgor and the Y-coordinate of the line obtained by linear regression at RWC equals 1.0 will give the inverse of the tissue osmotic potential at full hydration. The point at which this line touches the X- coordinate gives the value of water content of tissue apoplasm.

2.3.3 Leaf water potentials (ψ)

The leaf water potentials of both the host and the parasite were measured at regular intervals on the parasite and the host from pre-dawn to dusk using a pressure chamber. The sample leaves selected for the measurements were enclosed in a polythene bag just before detaching them from the plant and all the precautions required for measuring water potential were taken according to Turner (1988).

A Scholander type pressure chamber (Soil Moisture Corporation, Ohio, USA) was used for finding the balancing pressure. The balancing pressure was practically taken as the water potential as described below (Milburn, 1979)

$$\Psi = \Psi_p + \Psi_s$$

where

Ψ = water potential

Ψ_p = the balancing pressure

Ψ_s = solute potential.

The solute potential of the xylem sap was assumed to be negligible.

2.4 Stomatal conductance (*g_s*)

Stomatal conductance of the host and parasite leaves was measured using a Steady State Porometer (Model Li-1600, Li-Cor, Nebraska, USA). An average of eight leaves were measured on an hourly basis starting from sunrise to sunset. In teak, stomata were present only on the abaxial side of the leaf, while in *Dendrophthoe falcata*, stomata were present on both sides. The g_s was measured at the abaxial side in teak and on both sides for the parasite, every hour, on selected days in every month representing pre- and postmonsoon seasons.

2.5 Net photosynthesis (*P_n*)

Leaf net photosynthesis was measured using a portable infrared gas analyser (Model LI-6200, Portable Photosynthesis System, Licor Inc., Nebraska, USA) using a one-liter leaf chamber. The leaf chamber is provided with sensors for measuring photosynthetically active radiation (PAR), relative humidity, leaf and chamber temperatures. Physiologically mature leaves were selected for each measurement. At least ten randomly chosen leaves from different sunlit branches were measured every hour from dawn to dusk. The P_n was calculated in the instrument's console using the software provided with it.

2.6 Chlorophyll *a* fluorescence

To study the structure, conformation and function of the photosynthetic apparatus of the host and parasite leaves, a JIP-test was applied based on the description of this method by Strasser *et al.* (1996). *Chlorophyll a* fluorescence was measured in the field using the direct fluorescence method employing a direct fluorescence meter (Handy PEA, Hansatech, UK). Sample leaves of the parasite and the host were selected from the same branch so that separate measurements could be made for the proximal and distal leaves of the host in comparison to the parasite. The sample leaves were dark-adapted using leaf clips for 30 minutes before taking the fluorescence measurements. The measurements were made on two trees in the second site. The actinic light generated by the instrument was given at 1500 μmol m^{-2} s^{-1} and applied for one second.

The fluorescence transient curves were transferred to a computer and the curves were analysed using the JIP-test analysis software, *Biolyzer*, developed by Dr. R.M. Rodriguez, University of Geneva, Switzerland. The various parameters were subjected to analysis of variance (ANOVA) and means were later subjected to a paired T-test assuming equal variance between the samples paired in the following way:

Parasite vs. teak distal leaves to the parasite attachement
Parasite vs. teak proximal leaves to the parasite attachement
Parasite vs. teak uninfected leaves
Distal vs. proximal leaves
Distal vs. uninfected leaves
Proximal vs. uninfected leaves.

2.7 Transpiration

The water that flows through the branch of a tree where the parasite is attached was measured using Sapflow gauge (Greenspan Technology, Warwick, Australia). This is a direct method of measuring transpiration. By using a brief (e.g. 1 second) pulse of heat as a tracer, and determining its rate of ascent in the sapwood (xylem), we can infer sap flow velocity and ultimately the flux of water flowing through the plant. Sap flow instrument has two sets of heaters and sensor probes, each sensor probe with two sensors. Using an electric drill, two sets of holes were made on the host branch and the parasite stem, attached to the same branch. Implants of the heaters and sensor probes were made such that the upper and lower probes were 10 and 5 mm above and below the heater probe respectively. Before starting measurements, the actual probe spacing depth at which sensors lie in the sapwood, wound width, depth of the sapwood boundary, volume fractions of wood and water in the sapwood were found out. The logging interval, length of heat pulse to be used, specifications of probe sets, starting time and tree parameters were all determined by preliminary sets of measurements. The heartwood radius and cambium radius for each probe were measured for the particular branches in use. Heartwood radius is the distance from the centre of the tree to the inner sapwood boundary or heartwood interface. Cambium radius is the distance from the centre of the tree to the inner cambium or outer sapwood boundary. Area of the conducting pathway was calculated thus:

Conducting path area = (Total crossectional area of the wood) – (Area of the heartwood).

These parameters were fed to the logger with the help of a PC using the SAPCOM2 program. The power supply to the logger was given using a 12 V battery. The data collected from the data logger were further analysed using a program called SAPCAL.

2.8 Leaf area

A non-destructive method of leaf area measurement was followed on the twigs using a leaf area meter (Model LI-3000 A, Li-Cor Inc., Nebraska, USA). Three twigs were selected in each tree infested with the mistletoe and they were tagged for following up throughout the study period. Ten trees were thus followed for leaf area measurements at monthly intervals for a period of two years at Site I, and one year at Site II. In teak, an allometric relation between leaf area and its length-breadth dimension was worked out for the non-destructive sampling. This is because of the large dimensions of the teak leaves that made them difficult to pass through the scanner of the leaf area meter. For *Dendrophthoe*, leaf area meter was used non-invasively for the leaf area measurements.

2.9 Phenology

Phenological behaviour of teak and *Dendrophthoe* with respect to flushing, flowering and fruiting was observed at fortnightly intervals in the field for four years. Observations on 100 trees at various locations in Kerala were recorded.

2.10 Microclimate

2.10.1 Light requirements

The light availability to the host and the parasite was measured by fixing two light sensors, first a point sensor, above the canopy of the host (Quantum sensors, Model LI-190SA, Li-Cor Inc., Nebraska, USA) and the second, a line quantum sensor (Line Quantum Sensor, Li-Cor Inc., Nebraska, USA), within the teak canopy, just above the clumps of the parasite. The sensor fixed below the canopy was a line quantum sensor. Logging at 30 seconds interval and integrating them at hourly intervals for two weeks using a data logger made continuous recording of Photosynthetically Active Radiation

(PAR). For pre- and postmonsoon periods similar measurements were made. By using the software package PC208 (Campbell Scientific Inc., Logan, Utah, USA) the PAR data were integrated for each day and the stored data were later transferred to a computer for further analysis.

2.10.2 Leaf temperature

Leaf temperature of the host and the parasite was measured by fixing very fine wire thermocouple sensors (Model .001, Campbell Scientific, USA) at the lower side of the leaves and connecting them to a data logger (CR-10, Campbell Scientific, USA). Here also, continuous recording was made at every 30 seconds interval, and averaged hourly. The measurements continued for two weeks during different seasons.

2.11 Nutrient Analysis

The leaves were collected during different seasons of the year from the two sites. They were later dried and pooled separately for each site. Powdered leaf samples (0.3-0.5 g) were pre-digested with 5 ml of concentrated sulfuric acid and a pinch of Sodium salysilate overnight. The pre-digested samples were then digested for 3 hours at 350^0C in presence of hydrogen peroxide. The Nitrogen and Phosphorus contents in the digested samples were then determined by salysilate-hypochlorite and ascorbic acid reduced molybdophosphoric acid blue color method, respectively, using an autoanalyser.

The exchangeable bases K^+, Na^+, Ca^{2+} and Mg^{2+} in the acid digests were determined using Atomic Absorption Spectrometer with respective halo-cathode lamps.

3. Results

3.1 Relative Water Content (RWC)

The relative water content of leaves of teak and *Dendrophthoe* was measured in summer months. Leaf discs from mature leaves were used for the measurements. An average RWC of 81.7 % was observed for teak while 76.5 % for *Dendrophthoe*. It can be seen that the

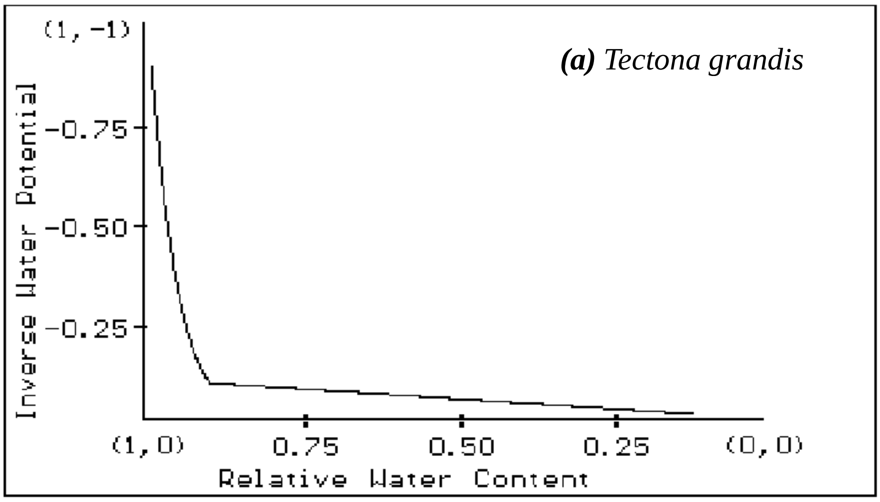
RWC of *Dendrophthoe* is lower than teak by 5%. This indicates higher demand for water in the leaves of Dendrophthoe. The water saturation deficit for teak has been found to be 18.2% and that for *Dendrophthoe* is 23.5% during summer months.

3.2 Pressure Volume Curve

A plot of $1/\psi$ vs. RWC was used to derive the osmotic potential at full turgor ($\psi_{\pi 0}$) and osmotic potential at zero turgor ($\psi_{\pi z}$) (Fig. 2). The apoplasmic water content (A) was found on percent basis. The curves obtained by plotting $1/\psi$ vs. RWC gave a relatively straight line portion for lower RWC values and a logarithmic portion reaching full turgor at RWC = 100%. The straight line portion of the curve corresponded to non-turgid state, where ψ is supposed to be equal to osmotic potential (ψ_{π}). To extract information from PV curves, linear regression was performed on the experimental points situated along the straight line portion (non turgid region) and extrapolated this straight line to the turgid region until RWC= 100%. Extrapolated values are supposed to represent ψ_{π} in the turgid region and to give the turgor potential by taking the difference in the actual curve. The intersection of the straight line with x-coordinate at $-\psi_{\pi}^{-0} = 0$ yield the value of apoplasmic fraction, which is usually supposed to stay finite and constant (Cutler et al. 1979). Following PV-curve analysis in *Dendrophthoe falcata*, values of volume average osmotic potential at full turgor ($\psi_{\pi 0}$) and osmotic potential at zero turgor ($\psi_{\pi z}$) are shown in Table 2 and Fig.2 a and b.

Table 2. Water relations parameters of the teak and the parasite leaves after analysis of the PV-curve.

No.	Water relations parameter	*Dendrophthoe*	Teak
	Tissue osmotic potential at full turgor	-13.3	-9.0
2	Water potential at turgor loss point	-13.4	-9.2
3	Apoplasmic water content	1.3%	10.5 %



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Tissue Osmotic Potential at Full Hydration = - 9.062358
Tissue Osmotic Potential at Zero Turgor     =  -9.185269
Relative Water Content of Tissue Apoplasm  =   -0.104991
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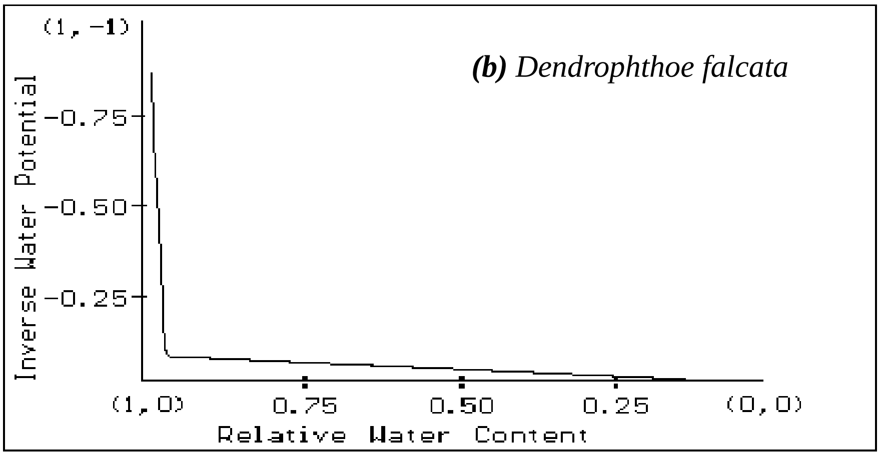

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Tissue Osmotic Potential at Full Hydration = - 13.241436
Tissue Osmotic Potential at Zero Turgor     =  -13.932611
Relative Water Content of Tissue Apoplasm  =   0.013009
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Fig.2. (a) PV curve depicting turgid and non turgid regions for *Tectona grandis* and (b) *Dendrophthoe falcata*

Solute potential at both full saturation **($\psi_{\pi 0}$)** and at zero turgor **($\psi_{\pi z}$)** were significantly lower in *Dendrophthoe*. The apoplasmic water content was 1.3 % in *Dendrophthoe* while in teak it was 10.5 % which was significantly higher than that of *Dendrophthoe.* Larger values of **($\psi_{\pi 0}$)** imply better maintenance of cell turgor at given water potential. Evergreen species may develop a higher leaf turgor at lower leaf water potentials than deciduous species. This was related to a lower solute potential at full turgor in evergreen species than deciduous species. Compared to teak, *Dendrophthoe* behaved just like an evergreen species.

3.3 Leaf water potential (ψ)

Diurnal changes in leaf water potentials were measured on the parasite and the host during pre- and post-monsoon period from November 1997 to March 2000. The measurements done on both the host and the parasite revealed that the parasite always maintained lower water potential compared to the host tree. Predawn water potential showed a maximum of – 0.05 MPa in teak and – 0.34 MPa in the parasite. The lowest water potentials recorded in teak was – 1.07 MPa and –1.8 MPa in parasite at Peechi. At Kayampoovam, slightly lower water potentials were observed for both host and the parasite. The midday water potential of *Dendrophthoe* decreased down to –2.2 MPa and of teak to –1.8 MPa. It can be seen that in both places decrease in water potential before noon was faster, but in *Dendrophthoe* the recovery was slow in the afternoon (Fig.3).

Fig.3 and 4 show that the water potential always had lower values during the premonsoon on both the host and the parasite at both sites examined. More interestingly, the parasite always maintained a lower value of water potential compared to the host. It may be noted from Fig.3 and 4 that this difference can be as high as ≈1.0 M Pa. This difference in water potential will certainly help the parasite to create a large gradient suitable for absorption of water from the host tree, which maintains higher water potential. It may be pointed out here that it is this gradient in water potential which helps the upward movement of water in a tree.

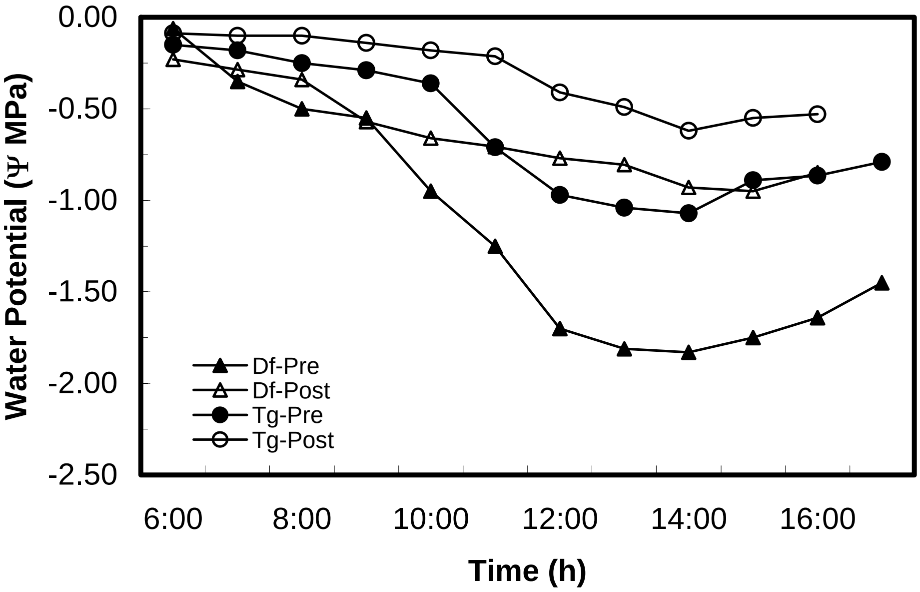


Fig:3. Water potential measurements in teak and *Dendrophthoe* during pre- and postmonsoon at Site I (Df- *Dendrophthoe*; Tg- *Tectona*; Pre- Premonsoon; Post- Post monsoon)

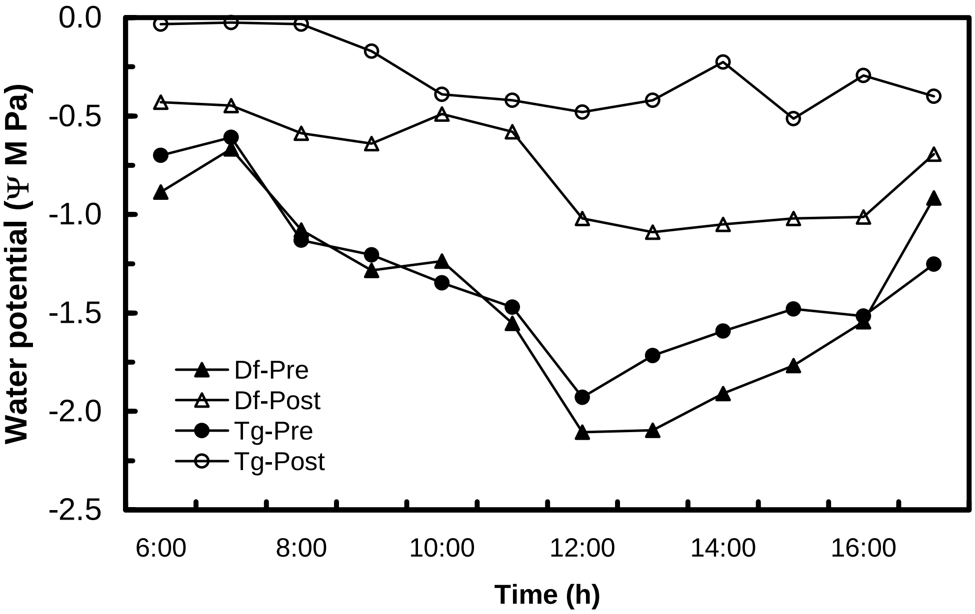


Fig:4. Water potential measurements for *Tectona* and *Dendrophthoe* at Site II for pre- and postmonsoon seasons

3.4 Stomatal conductance(g_s)

Gas exchange measurements made on both parasite and the host seasonally for the above-mentioned period. Measurements could not be taken during the rainy season owing to wet canopy and the high atmospheric humidity. Stomatal conductance of the host and the parasite leaves was measured using a porometer. The stomatal conductance measurements indicated that teak is having stomata on the abaxial side only, whereas parasite is having stomata on both sides. The conductance values recorded during both periods showed that the parasite has lower conductance values compared to the host during post-monsoon and the opposite during pre-monsoon period (Fig. 5). This could be an effect of the difference in light availability to the parasite during the two periods. Maximum values of conductance ranged from 500 to 600 mmol m^{-2} s^{-1} both in the host and the parasite (Fig. 5). A midday closure of the stomata was very apparent in teak, but not in the parasite.

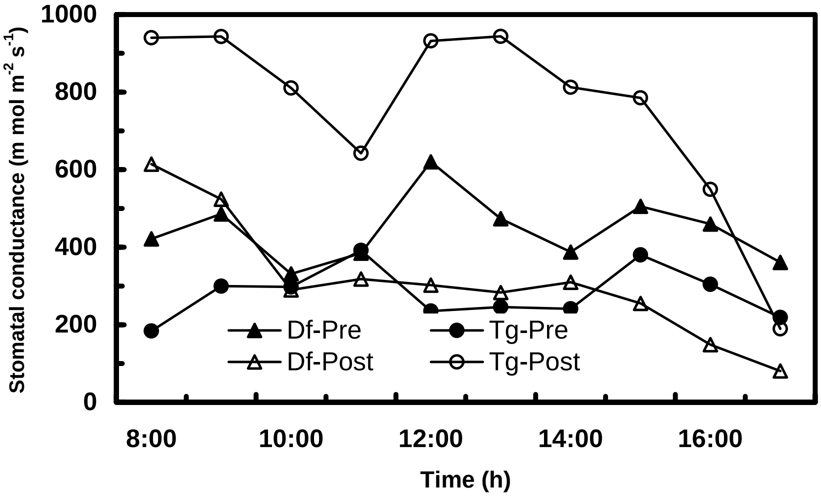


Fig:5. Diurnal variations in stomatal conductance in teak and *Dendrophthoe* during pre- and postmonsoon seasons at Peechi

3.5 Net photosynthesis (P_n)

Net photosynthesis was higher in teak compared to the parasite during both periods (Fig. 6). A maximum net photosynthesis of 12 μmol m^{-2} s^{-1} was observed in teak whereas the parasite showed values less than 6 μmol m^{-2} s^{-1} (Fig. 6). It is interesting to note that the parasite showed higher photosynthetic rates during the premonsoon period compared to the post monsoon period. This is because the leaves of the parasite are well exposed to sunlight during the premonsoon period when the host leaves are already shed or in the process of shedding. This indicates that the parasite has the capacity to perform photosynthesis at higher rates if light is not limiting. The leaf area measurements indicated that parasite is in full flush even when teak is completely leafless.

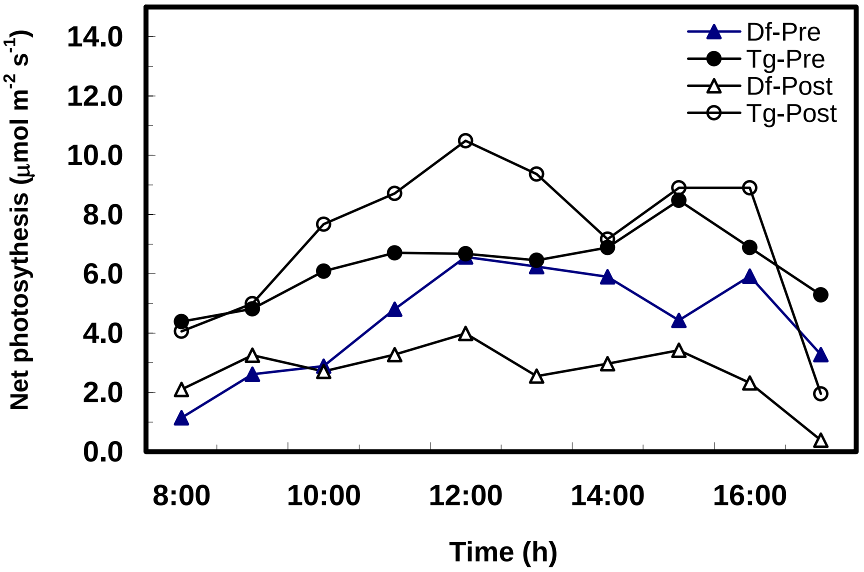


Fig:6. Diurnal variations in net photosynthesis in teak and *Dendrophthoe* during pre- and post monsoon seasons at Peechi

3.6 Chlorophyll fluorescence

Results of the *chlorophyll a* fluorescence transient curves analysis are presented in Table.3. A large number of parameters have been derived from the analysis of the transient curves from the parasite, proximal and distal leaves of the teak tree and leaves from uninfected branches of the teak tree. From Table.3, it can be noticed that out of 41 derived parameters, the parasite has more than 30 parameters common with the teak leaves. The Performance Index (PI), which gives an overall synthesized value, is not significantly different in the parasite and the host leaves. However, it is important to note that some of the specific parameters such as the electron transport capacity per cross-sectional area of leaf (Et_o/Cs_o) and the dissipated quantum flux per cross-sectional area (Di_o/Cs_o) are significantly different in the parasite and the host. This shows that the absorbed quantum is much more efficiently used in the parasite leaves compared to the host's leaves. It is also interesting to note that there was not much difference in the performance of the distal, proximal and uninfected leaves of the teak tree except that the electron transport capacity (Et_o/Cs_o) in the uninfected teak leaves were significantly higher than that of the proximal or distal leaves of the infected host.

Table 3. *Chlorophyll a* fluorescence parameters derived after analyzing the fluorescence transients from the distal and proximal leaves and leaves from uninfected branches of teak and leaves of the parasite, *Dendrophthoe falcata*. The leaves were dark adapted for 20 minutes before fluorescence measurements.

Parameter	Parasite	S.E	Teak-distal	S.E.	Teak-proximal	S.E.	Teak-uninfected	S.E.
Extracted and Technical Fluorescence Parameters								
Tf(max)	395.00^a	70.15	211.67^a	18.51	205.00^a	17.27	255.00^a	18.85
Area	44800.00^b	2566.57	28900.00^a	3820.91	31666.67^a	5097.62	49500.00^{ab}	9413.29
Fo	375.17	7.96	476.17^a	50.36	462.83^a	52.36	477.50^a	43.89
Fm	1957.67^a	65.68	1962.67^a	105.33	1911.83^a	53.68	1881.92^a	65.70
Fo/Fm	0.21	0.01	0.28^a	0.04	0.28^a	0.04	0.29^a	0.03
Fv/Fo	3.76^a	0.14	2.98^a	0.60	3.02^a	0.57	2.93^a	0.39
dV/dto	0.46^b	0.02	0.91^a	0.21	0.87^a	0.21	0.74^{ab}	0.15
dVG/dto	0.45^b	0.02	0.92^a	0.24	0.88^a	0.23	0.80^{ab}	0.18
Vj	0.37^b	0.01	0.61^a	0.10	0.58^a	0.11	0.48^{ab}	0.08
Vi	0.72	0.01	0.64^a	0.03	0.60^a	0.03	0.52^a	0.04
PHI(Po)	0.79	0.01	0.72^a	0.04	0.72^a	0.04	0.71^a	0.03
PSIo	0.63^b	0.01	0.39^a	0.10	0.42^a	0.11	0.52^{ab}	0.08
PHI(Eo)	0.50^b	0.01	0.30^a	0.09	0.32^a	0.10	0.40^{ab}	0.07
PHI(Do)	0.21	0.01	0.28^a	0.04	0.28^a	0.04	0.29^a	0.03
Sm	29.33^b	1.75	20.13^a	0.82	22.20^a	2.21	36.21^{ab}	6.63
N	36.56^b	1.85	28.70^a	2.20	30.03^a	1.50	60.52^{ab}	16.07
Sm/T(fmax)	0.09^a	0.01	0.10^{ab}	0.01	0.11^{ab}	0.00	0.14^b	0.02
Sum K	2.44^a	0.06	1.98^b	0.20	2.08^{ba}	0.26	2.05^b	0.15
Kn	0.52^a	0.02	0.52^b	0.03	0.53^b	0.02	0.54^b	0.02
Kp	1.93^a	0.05	1.46^b	0.23	1.55^{ab}	0.27	1.52^b	0.16
Specific Fluxes or Specific Activities								
ABS/RC	1.60	0.04	2.07^a	0.27	2.00^a	0.24	2.27^a	0.28
TRo/RC	1.26^a	0.03	1.43^b	0.09	1.40^{ab}	0.10	1.52^b	0.11
ETo/RC	0.79^b	0.02	0.51^a	0.12	0.53^a	0.12	0.78^{ab}	0.15
DIo/RC	0.34	0.02	0.65^a	0.18	0.60^a	0.15	0.75^a	0.20

Parameter	**Parasite**	**S.E**	**Teak-distal**	**S.E.**	**Teak-proximal**	**S.E.**	**Teak-uninfected**	**S.E.**
Phenomenological Fluxes or Phenomenological Activities								
RC/CSo	258.98^{a}	5.73	261.86^{a}	7.30	260.98^{a}	5.85	242.70^{a}	12.16
ABS/CSo	411.92	9.83	535.67^{a}	59.04	521.33^{a}	63.94	524.67^{a}	48.85
TRo/CSo	324.46^{a}	7.78	370.61^{b}	16.31	364.35^{ab}	26.59	356.39^{ab}	13.03
ETo/CSo	204.66^{b}	4.84	136.19^{a}	32.79	136.73^{a}	30.18	180.02^{ab}	27.17
DIo/CSo	87.46	3.50	165.05^{a}	43.03	156.98^{a}	38.21	168.28^{a}	38.90
RC/CSm	1236.12^{a}	52.39	1052.86^{a}	171.35	1046.44^{a}	147.39	980.99^{a}	129.87
ABS/CSm	1957.67^{a}	65.68	1962.67^{a}	105.33	1911.83^{a}	53.68	1881.92^{a}	65.70
TRo/CSm	1545.74^{a}	60.68	1426.99^{a}	159.32	1390.51^{a}	107.80	1357.23^{a}	100.34
ETo/CSm	978.26^{b}	43.71	635.64^{a}	205.20	635.14^{a}	199.43	778.17^{ab}	141.76
DIo/CSm	411.92	9.84	535.68^{a}	59.02	521.33^{a}	63.96	524.69^{a}	48.85
SFI(abs)	3.16^{a}	0.13	1.83^{b}	0.63	2.06^{ab}	0.75	2.24^{ab}	0.48
10RC/ABS	6.31^{a}	0.16	5.21^{b}	0.61	5.41^{ab}	0.66	5.06^{b}	0.52
PHIo/(1-PHIo)	3.76^{a}	0.14	2.98^{a}	0.60	3.02^{a}	0.57	2.93^{a}	0.39
PSIo/(1-PSIo)	1.74^{a}	0.08	0.92^{b}	0.35	1.13^{ab}	0.44	1.95^{a}	0.50
PI(abs)	42.25^{a}	3.71	23.87^{a}	11.83	31.42^{a}	14.48	39.69^{a}	11.85
PI(cso)	17168.84^{a}	1276.73	9925.64^{a}	4547.04	11900.62^{a}	5166.38	16373.25^{a}	4431.02
PI(csm)	83495.53^{a}	8164.83	52340.00^{a}	26657.60	62436.06^{a}	28703.62	81812.40^{a}	25934.67

Note: Values with the same letter as the superscripts in the adjacent rows are not significantly different ($P \leq 0.05$). Mean and S.E.(Standard Error) are presented for each parameter.

3.7 Transpiration

Transpiration measurements were made using sap flow gauges inserted in the twigs of host and parasite simultaneously. The complete weather data at hourly intervals were recorded for the site during this period (Fig. 9). Transpiration measurements for six days using sapflow sensor are given in Fig. 7. It shows that the parasite transpired less throughout the day as compared to teak. Since the quantity of water transpired depends on the leaf area, the above figure is only a comparative account of the diurnal variations in transpiration, helping us to compare the transpirational behaviour of the host and the parasite. Thus no quantitative figures can be derived from the above data. The chamber transpiration taken on the above days also indicates a higher rate during premonsoon in the parasite, particularly during noon hours (Fig. 8).

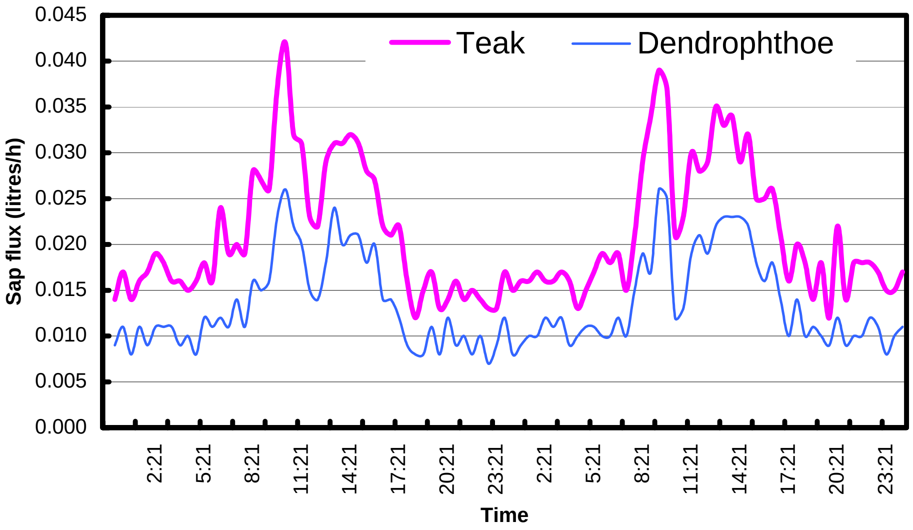


Fig. 8. Variations in the sapflow in the parasite and host branch of a teak tree infected with *Dendrophthoe* for two days (20 to 21 May 2001) at Site II.

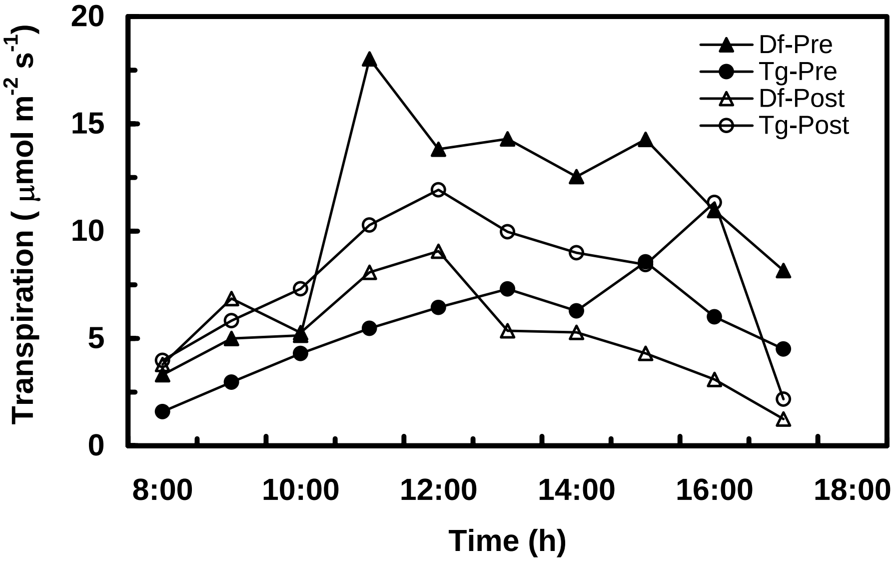
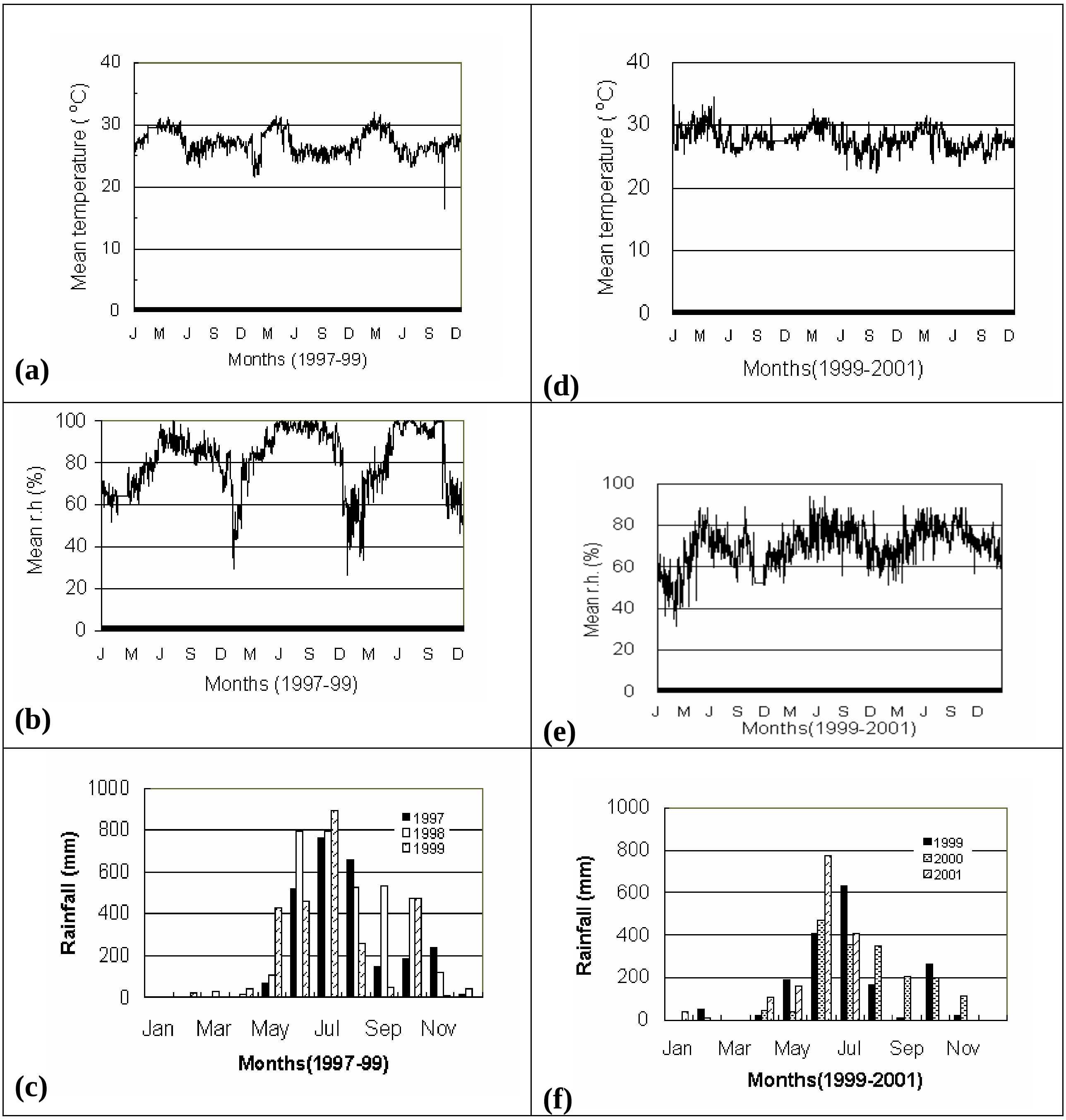


Fig: 8. Diurnal variations in chamber transpiration through leaves during pre- and postmonsoon seasons in teak and *Dendrophthoe* at Site II.

3.8 Weather data

Weather data collected during 1997 to 2001 from Site I and II are given (Fig:8 a,b,c,d,e,f). Daily mean temperature at both the sites was high during March, with low relative humidity. The rainfall was maximal during the months of June and July in both places.

Northeast monsoon also contributed a small share in both places. Site II recorded comparatively lesser rainfall than Site I.



Site I (Peechi) **Site II (Kayampoovam)**

Fig: 9. Daily variations in mean temperature (a), mean relative humidity (b) and rainfall (c) at Site I for the period 1997 to 1999 and the same (d), (e), (f) at Site II for the period 1999 to 2001 respectively.

3.9 Leaf area development

Monthly measurements of the leaf area development were recorded on selected twigs of the host and the parasite using a leaf area meter. Monthly observations were started from November 1997. An allometric relation between leaf area and its length-breadth dimension was worked out for teak leaves, and this was employed in the non-destructive sampling. Good correlation was found out between actual leaf areas by fitting breadth of teak leaves in the following equation.

$$\mathbf{Y = a+bx+cx^2}$$

where the following values were substituted: **a** = 0.7710, **b** =9.704, **c** =0.4801,
where **Y**= leaf area, **x** = leaf breadth. $R^2 = 0.97$.

In teak, the leaf area decreased December onwards and reaches minimum by February and again reached a maximum by July. But the parasite always maintained a uniform leaf area throughout the year as in an evergreen species (Fig. 7). No particular leafless stage was noticed for *Dendrophthoe.*

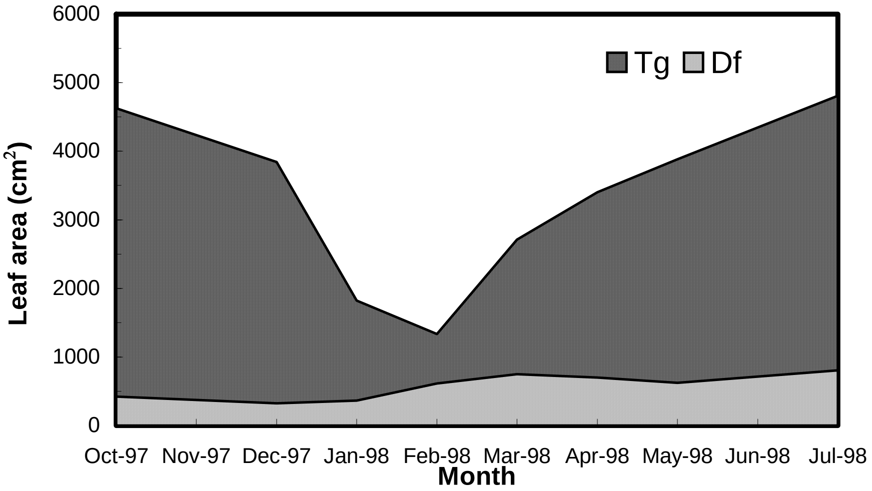


Fig. 10. Leaf area development of teak and *Dendrophthoe* twigs followed at monthly intervals at Site I.

3.10 Phenology

The phenology of the host and parasite was closely followed by making fortnightly observations in the field. Phenological observations on leaf fall, flushing, flowering and fruiting were made in teak and the parasite. Phenological differences existed between parasite and host (Table 4). Parasite flowered in February and the host in July.

Table 4. Fortnightly phenological observations in teak (T) and *Dendrophthoe* (D) made round the year at Peechi. The specific fortnight when each even occurs is depicted by a shaded square.

Event		**Jan**		**Feb**		**Mar**		**Apr**		**May**		**Jun**		**Jul**		**Aug**		**Sep**		**Oct**		**Nov**		**Dec**	
Leaf fall	T		🟩	🟩																					🟩	🟩	🟩
	D																										
					🟩	🟩																					
	D		🟩																								
Flowering	T			🟩	🟩									🟩	🟩												
	D	🟩	🟩	🟩	🟩																					🟩	🟩
Fruiting	T																					🟩	🟩	🟩	🟩		
	D			🟩	🟩	🟩																					

3.11 Microclimate

The microclimate parameters, especially light availability to parasite and host were measured. The measurements were carried out seasonally.

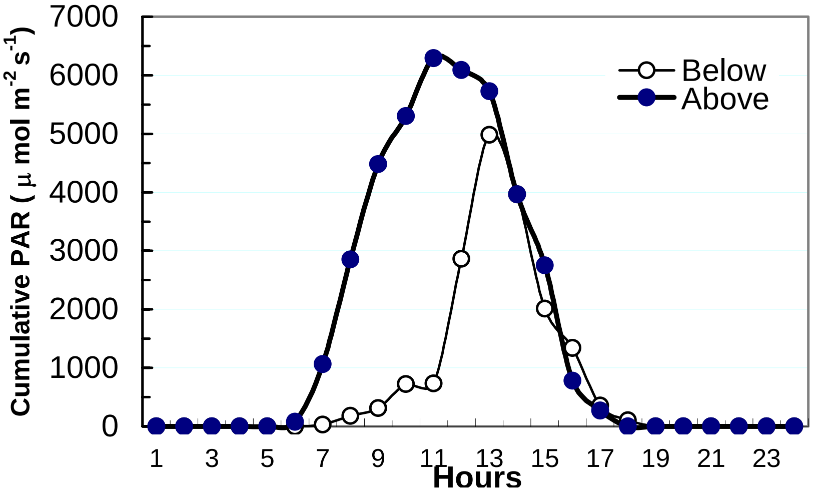


Fig.11. Hourly PAR received by the upper and lower canopy. The measurements are averages for 3 weeks during postmonsoon period.

The light availability was measured by fixing two light sensors one fixed above the canopy of the host and the parasite and the other below the canopy. Continuous recording at hourly intervals was made for several days. Light availability to the parasite and the host showed that the parasite received only 30 % of the light as received by the host (Fig. 11).

Parasite was seen to survive well in well-exposed situations and also when the host blocked 70% of the light. This gives an indication that the parasite is able to survive in both shade and exposed conditions.

Leaf temperature measurements indicated that both host and the parasite maintain 2 to 3 ^{o}C higher temperature than the atmospheric temperature (Fig. 12).

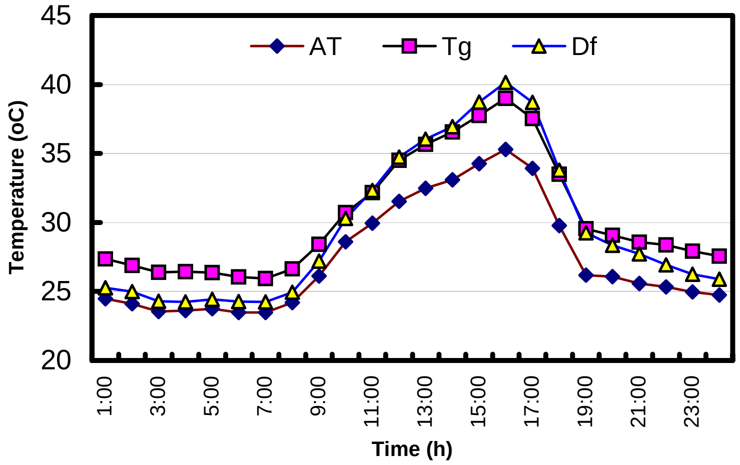


Fig. 12. Diurnal variations in atmospheric (AT) and leaf temperature in the host (Tg) and the parasite (Df).

3.12 Nutrient analysis

Leaf samples collected from both the sites during May 1999 and November 1999 when the host and parasite were in full flushes, were analyzed for nutrients such as Potassium, Magnesium, Calcium, Sodium, total Phosphorus and total Nitrogen. The Potassium and Sodium in the leaves of the parasite were found to be high as compared to the host.

Analysis done on the parasite during the leafless stage of the host also showed extremely high amount of Potassium (more than three times than the host) in the leaves of the *Dendrophthoe*. The Mg and Ca concentrations were similar in the host and the parasite. The Na concentrations were almost twice in the parasite compared to the host. Total P was very similar in the parasite and the host, however total N showed a slightly lower concentration in the parasite compared to the host. The results are presented in Fig. 13.

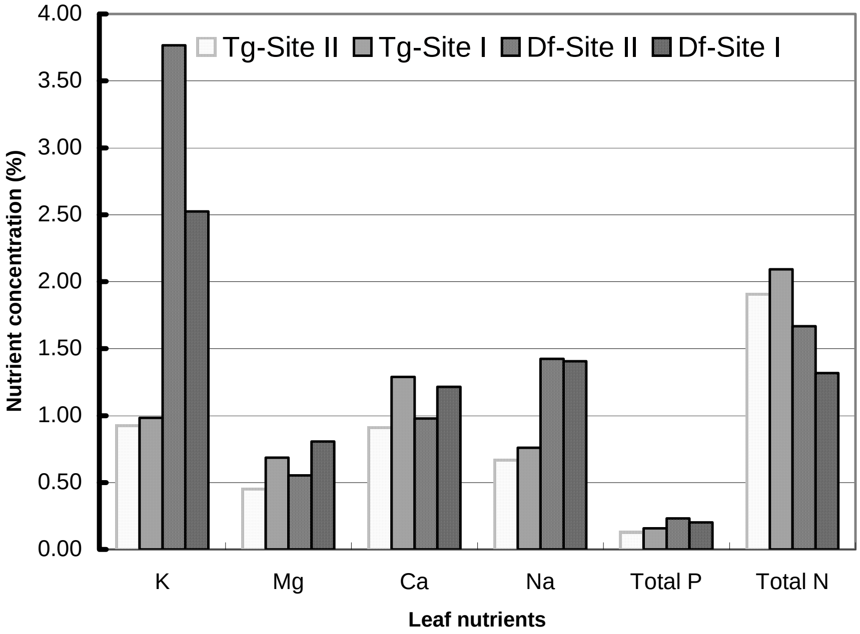


Fig. 13. Variations in nutrient levels in teak and *Dendrophthoe* leaves at Site I and II expressed as percentage of the total dry wt.

4. Discussion

Mistletoes are hemi parasites, they rely upon their hosts for water and minerals, and to some extent they photosynthesize and generate their own assimilate supply (Kuijt 1969) . This results in an unusual partitioning of water and carbon between the host and the parasite. Earlier studies in this respect have been reviewed by Glatzel (1983). Our investigations into the host- parasite relationship between teak and the hemiparasite *Dendrophthoe falcata* reveal several interesting ecophysiological relationships between the two plant species. These are discussed in the following paragraphs.

One of the important ecophysiological problems to be dealt within the host-parasite relationships is the dependence of the parasite on host for the nutrition. It is certain that in a xylem parasite, the parasite will be absorbing water and nutrients from the xylem sap of the host. Then the question is how good is the photosynthetic capacity of the parasite. It is reasonable to assume that if the parasite is photosynthetically efficient, then its virulence on the host plant is increased because the plant body can develop more leaves and thereby more water and minerals are also absorbed by the parasite. Our studies have shown that the parasite has photosynthesis (P_n) at nearly half the rate as that of the host plant. However, this was mainly because of light limitations, since the parasite grows in the shade of the canopy of the host. But during the leafless stage of the host, in the dry period, the parasite leaves are fully exposed to the sun and they are able to photosynthesize at a much higher rate, although not at the same rate as that of the host. Karunaichamy *et al*. (1993) recorded maximum P_n rates of 5.57 and 6.97 in *Azadirachta indica* and its parasite *Dendrophthoe falcata* respectively. Davidson *et al*. (1989) recorded higher g_s and transpiration in *Amyema* on *Casuarina*, however the P_n rates of the parasite were similar. Johnson and Choinski (1993) have shown that the parasite was photosynthetically less active than host plant; and the infection reduced the carbon assimilation rates in the host compared to uninfected trees in *Tapinanthus-Diplorhynchus* parasite-host relationship. Marshall *et al*. (1994 a) made a detailed analysis on the C gain by 11 mistletoe species (belonging to 3 genera) in Australia. They found that the difference in P_n between the host and parasite was not statistically significant. Moreover, the heterotrophic carbon gain from the host accounted for approx. 15% of the total C gained by the parasite. Marshall *et al*. (1994 b) have shown that the xylem - tapping mistletoes have low instantaneous water use efficiency (WUE). This is interpreted as a facility for assimilating N dissolved at low concentration in the xylem sap. However, during this process C dissolved in the xylem sap also gets assimilated heterotrophically. This finally results in almost similar net carbon gain in the host and the parasite.

Richter *et al.* (1995) have found that the photosynthetic characteristics (carboxylation efficiency , photosynthetic capacity) of the parasite were only little affected by the host species being parasitised.

Several aspects of the photosynthetic efficiency have been investigated in the present study by analyzing the transient fluorescence curves generated by the *chlorophyll a* fluorescence of the host and the parasite. From looking at the large number of parameters, it can be concluded that the photosynthetic abilities of the parasite and the host are not so different when we look at the Performance Index *(PI),* which is an overall synthesized parameter. However, when the parameter for electron transport capacity for unit crossectional area of leaf (Et_o/Cs_o) is taken into consideration, the parasite shows a much higher capacity compared to the distal and proximal leaves of the host teak tree. At the same time, there is no significant difference between the parasite leaves and leaves of an uninfected teak tree in the electron transport capacity. Similarly, the dissipated quantum flux (DI_o/Cs_o), which is the quantum absorbed by the leaves and dissipated as unused energy, is much lower in the parasite compared to the host. Close examination of some such parameters show that the parasite leaves have a much more efficient photosynthetic apparatus compared to the host tree leaves. This is indicative of the evolutionary adaptive nature of the parasite to survive on the host tree. Chlorophyll fluorescence measurements on several host-parasite pairs in Brazil have shown that photosynthetic efficiency was similar in both host and parasite (Lüttge *et al.* 1998). However, in the investigations made by the latter authors, the various parameters have not been analyzed as in our study.

The water relations of the host-parasite entity are also interesting. It has been observed by a number of previous investigators that the parasite always maintains water potential lower than that of the host. This is a contrivance for creating a gradient in water potential between the host and the parasite so that water movement occurs from the host to the parasite during transpiration. It should be realized that the point of attachment between the host and the parasite is a region of resistance because this is the region where the vasculature of two different species unite. This means that sufficient water potential gradient should be generated for the flow of water from the xylem of the host to the parasite. In the teak-*Dendrophthoe* relationship we have observed a gradient as high as 1.0 Mpa. The parasite that has amphistomatous leaves will be certainly having a higher stomatal conductance per unit leaf area, probably helping to lower the water potential during the daytime. Davidson *et al*. (1989) recorded higher g_s and transpiration in *Amyema* growing on *Casuarina* trees. Their experiments have shown that the difference in water potential gradient between the host and the parasite was due to the resistance at the haustorial junction and not due to differences in tissue water relations.

In our investigation on the solute potential of the host and parasite leaves, we found much lower solute potential in the parasite compared to the host. It is this property, which helps to maintain low leaf water potential in the parasite compared to the host. This can also give much more drought tolerance to the parasite compared to the host. The lower solute potentials are probably due to the presence of high K and Na concentration in the leaves of the parasite.

Few studies are available in the literature on the transpiration in host-parasite relationships. The measurement of sap flow using the heat pulse technique simultaneously in the host and the parasite is also not available in the literature. We have followed the transpiration in the host and the parasite simultaneously using the sapflow gauge. The quantity of water transpired certainly depends on the leaf area of the host or parasite. However, we could show that the pattern of water flux through the stem of the parasite and the host were the same. The microclimate parameters affected both the plants in a similar way. In the sample examined, it can be seen that the host transpired slightly more than the parasite at all times. In the chamber transpiration measurements also it was seen that host transpired more than the parasite during the postmonsoon period. However, the most interesting aspect is the high transpiration rates shown by the parasite during the premonsoon. This could be due to the presence of leaves that are about to senesce on the host tree. Since teak is a deciduous species, without leaves during two months of the year (January to February in the study area), the high water consumption by the parasite can be certainly very damaging to the tree. This is the time when the stomatal conductance increases in the parasite and the water potential decreases. At this time there is a good possibility that the parasite is deriving most of its water from the wood tissue because the flux of water from the soil is minimal at this period. This can cause permanent cavitations in the wood xylem, resulting in drying of the branches and finally the death of the tree. It may be pointed out here that the chance for a deciduous tree to be affected more severely is higher compared to an evergreen tree. This can be noted in the many mango (*Mangifera indica*) trees growing in the nearby locations, carrying heavily infected branches, but still surviving for several years. Evidence for the loss of hydraulic conductivity of the distal branches compared to the proximal wood has been presented in the host-parasite relationship of *Acacia acuminata-Amyema preissii* (Tennakoon and Pate 1996). Evidence for higher transpiration rate in the mistletoe was shown in *Arceuthobium* infecting juniper trees in Tajikistan (Molotpkovski and Konnov 1995). The high transpiration and the low rate of photosynthesis give the parasite low water use efficiency as shown in several host-parasite relationships (Hollinger 1983).

The nutrient concentrations in the host and the parasite have also been analysed in the present work. Na and K were found at much higher concentration in the parasite compared to the host. The changes in other nutrients were comparatively lesser except for total N, which showed a lower concentration in the parasite compared to the host. Glatzel (1983) found that the mistletoe *Loranthus europaeus* accumulated more nutrients in its leaves than its host, *Quercus petraea*. He attributed this accumulation to a higher rate of transpiration in the mistletoe than its host and to the absence of phloem connections between the parasite and the host. Some mineral elements, especially potassium, normally cycle back down the phloem, which does not happen here because of the absence of phloem connections. The same conditions could be applicable in the teak-*Dendrophthoe* relationship. Ehleringer *et al*.(1986) found higher concentration of N in the mistletoe leaves of *Phoradendron* compared to its host *Juniperus*. Most of this N was in the form of arginine. Panvini and Eickmeier (1993) who measured Cu and Zn showed that the mistletoe had nutrient concentrations 0.97 - 2.88 times greater than the host in *Phoradendron* and its several known hosts.

5. Conclusions

Based on the above studies, the following conclusions are drawn:

1. The parasite always maintains lower leaf water potentials compared to the host tree, helping in maintaining a water potential gradient between the host and the parasite, so that water is easily transported from the host to the parasite.
2. The stomatal conductance in the host and the parasite are nearly equal.
3. Transpiration per unit leaf area is more in the parasite leaves although sapflow measurements show the teak twig transpiring more than the parasite.
4. The net photosynthesis in the parasite leaves is lesser when compared to the host leaves.
5. The photosynthetic performance is more or less similar in the parasite and the host; however, electron transport ability and quantum energy use efficiency are better in the parasite leaves.
6. The K and Na content in the parasite leaves were much more than that of the host leaves. Since these are phloem mobile minerals, their high concentration indicates the absence of any phloem connections between the host and the parasite.
7. Since teak is a deciduous tree, there are two physiological states in the life cycle of the parasite; first, the parasite is able photosynthesize at lower rates when the teak is in full flushes. Second, the parasite leaves photosynthesize at full capacity when the teak is leafless. At the same time, the parasite is never leafless. The parasite is able to survive even when the teak leaves intercept 70% of the total solar radiation. This shows the high adaptation of the parasite to survive in both conditions of light.
8. All the ecological and physiological studies lead us to the conclusion that the parasite is highly adapted to surviving in stressed conditions, thereby giving it a high survival value.

6. Practical Utility

The reason for the death of the teak tree branches and finally the whole tree could be due to the uptake of water from the wood tissue near the attachment of the parasite to the host, creating permanent cavitations in the xylem. If this is so, controlling the parasite using tree injections will not be effective during the deciduous period of the tree. However, this is the time when the parasite is under maximum stress, especially for water. Application of herbicides directly on the parasite clumps could be effective during this period. If tree injections are used during the other period, that is, when the teak tree is in full flushes, there is the possibility of the host leaves absorbing the herbicides in larger quantities than the parasite, and getting killed.

Ecophysiological studies reveal that the parasite, *Dendrophthoe falcata* on teak trees has developed several ecological and physiological adaptations to help them survive on the teak trees even in adverse conditions. This makes the complete eradication of the parasite from the host trees rather difficult. Hence only management practices aimed at preventing the spread of the parasite in teak plantations can succeed. The results of the present study will be useful in planning the management strategies.

7. References

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