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RESEARCH ARTICLE

Characterization of Anatomical and Physiological Adaptations in *Cassytha filiformis* L.—An Advanced Obligate Hemiparasite on *Morinda tinctoria* Roxb.

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ABSTRACT: A study was conducted to understand the host-parasite relationship in terms of anatomical and physiological adaptations in *Morinda tinctoria* Roxb. and *Cassytha filiformis* L. Anatomically the haustorium of *Cassytha* is found to have two parts, the upper haustorium and the endophyte. The former is the portion of a haustorium that lies external to the host organ, whereas the endophyte is the portion of a haustorium that penetrates host tissues. It was also observed that the host organ triggers the dedifferentiation of cortical parenchyma to develop dense cytoplasm, conspicuous nuclei and numerous starch grains and these cells are found to serve as the initials of upper haustorium. The level of Chl *b* was lower than Chl *a* and xanthophylls in *Cassytha* when compared to *Morinda.* The photosynthetic activity was measured in intact leaves/stems of both the host and parasitic plant using Chl *a* fluorescence induction kinetics, which revealed that the photosynthetic efficiency was very low in the infected sample as well as in the parasite stem. Over all, the reduction in the photosynthetic efficiency was correlated to the poorly developed PS II complex.

KEY WORDS: Anatomy, *Cassytha filliformis*, Chlorophyll, endophyte, fluorescence kinetics, hemiparasite, haustorium, photosystem II.

INTRODUCTION

A wide variety of plants and animals are parasites in their mode existence. There are about 18 to 22 angiosperm families representing 230 genera and 3100 species of parasitic plants. The slender stem of some parasitic plants is devoid of well-developed leaves and roots. Instead they develop haustoria, which penetrate into the host tissue by a combination of both mechanical pressures and enzymatic digestion (Peirce, 1894; Reid et al., 1995; Hong et al., 2011) and act as absorptive structures. The structure and mode of operation of the haustorium can contribute to an understanding of parasitic relationships amongst angiosperms i.e. parasitic plant and its host plant (Kuijt, 1977). The physiological concepts of the association between parasitic angiosperms and their hosts were explained by Tsivion (1978). *Cassytha filiformis* L. (Common name: Love-vine) is a leafless and rootless angiospermic parasite belonging to the family Lauraceae. The parasite infects host stem, petiole, leaf lamina and itself. It is filiform twining, advanced obligate hemiparasite that infests a wide variety of hosts. It is common on *Morinda tinctoria* Roxb. including young trees, bushes and develops haustorial process in stem, leaves etc. The advanced obligate hemiparasites can acquire host carbon from phloem by making connection with haustorium and thus leads to the loss of photosynthetic function for at least to some degree or during some stage of the life cycle (Nickrent, 2002). Recently, Luo et al. (2012) studied hemiparasitic mechanism of *Thesium chinense* and concluded that it acquires water and nutrition from its host by haustorium and can mostly be independent as for C supply through photosynthesis.

Cassytha filiformis is an advanced obligate hemiparasite. Although many reports are available on parasitism between *Cuscuta* and its host *Clerodendron*, haustorial development and parasitic mode of nutrition between *Cassytha* on *Morinda* is scanty. Hence the parasitic relationship between *Cuscuta* and its host (Lee and Lee, 1989) was taken as model to study the parasitic mode of interaction between *Cassytha* and its host plant *Morinda*.

The haustorium development and mode of nutrition have been studied for many parasitic angiosperms on variety of hosts. However, very little information is available regarding the precise mode of action of haustorial process and the manner in which the metabolites are absorbed from the host tissue. The relationship between *Cassytha filiformis* L. and its host *Morinda tinctoria* Roxb. has been studied by analyzing the structure and development of the haustorium, photosynthetic adaptation in terms of pigment compo-

sition, absorption spectra and photosynthetic activity using Chl *a* fluorescence induction kinetics.

MATERIAL AND METHODS

Haustoria of *Cassytha filiformis* L. growing on the host plant *Morinda tinctoria* Roxb. were collected from Achankulam (Latitude – 9°31'N and Longitude – 77°37'60E; altitude – 146 m asl), Virudunagar District of Tamil Nadu, India. The host viz., *Morinda tinctoria* Roxb., locally known as '*Manjanathi*' in Tamil, belonging to the family Rubiaceae is a small tree with normal foliage. In the traditional system of medicine, leaves and roots of *M. tinctoria* are used as astringent, deobstrent, emmengogue and to relieve pain in the gout (Nadkarni and Nadkarni, 1955). In the rural area, it is exploited for use as firewood.

For this study, all experiments were carried out with fresh specimens. Stems of *Cassytha* parasitizing *Morinda tinctoria* Roxb. were employed for studying characterization of anatomical and their physiological adaptations. Structure and development of the haustorium was studied using light microscope with sections stained in saffranin and fast green (Johansen, 1940). Free hand sections of *Cassytha* and *Morinda* were used for all the anatomical studies. Welburn and Lichtenthaler (1984) formulae were used for estimating the content of Chl *a,* Chl *b* and total chlorophyll. Fractionation of carotenes and xanthophylls from chlorophylls was done using solvent extraction method (Davies, 1965). All absorption spectra were recorded at room temperature (25°C) using a Hitachi U-2000 UV–visible spectrophotometer. *In vivo* Chl *a* fluorescence transients were followed in intact *Cassytha* stem, normal *Morinda* leaves and infected leaves after excitation with broad band blue light (420–620 nm, Corning, CS4-96) at a photon flux density of 100 W m^{-2}. The photomultiplier (Hamamtzu R376) placed at 90° to the excitation beams was protected by an interference filter (λ max 690 nm, half band width 12 nm, Schott, Germany). The signal from the photomultiplier was directly displayed either on a SERVO recorder (Hitachi Model 056) or stored in a digital storage oscilloscope (Iwatsu SRI 100, Japan). The signal was triggered with the help of an electric shutter with an opening time of 100 milliseconds. For *Cassytha,* the stems were cut in longitudinally and arrange in an acrylic holder and placed diagonally in a 4 ml glass cuvette to face the photomultiplier at 45° angle. The stem/leaves were incubated in dark for 10 minutes prior to illumination. The variable (F_v) to maximal (F_m) chlorophyll fluorescence ratios (F_v/F_m) was determined from the transients.

All the data were analysed statistically using STATISTICA 6.0. ANOVA was used to compare the variations in pigment contents and chlorophyll fluorescence ratios amongst *Cassytha* stems, unaffected *Morinda* leaves and parasitized *Morinda* leaves. The level of significance (*p*) in all the cases was held at 0.05.

RESULTS

Development of haustorium

In the present investigation, it was found that growth of *Cassytha* was very rapid as it forms a thick mat on host *Morinda* within 30–40 days after infection. After attachment with the host, *Cassytha* obtained its food material *via* establishment of haustoria and eventually destroy the host plant viz., *Morinda* (Fig. 1). During the initial stage, the contact between the host and parasite through haustorium was very slack and easily separable which later became tight as endophyte developed. In order to cognize the morphogenesis of haustorial development, differentiating the internal cell arrangements of the parasite stem without haustoria is first important (Fig. 2). *Cassytha* stem is made up of single layered epidermis, five or seven layers of cortex, and pith at the centre consisting of parenchymatous cells. After the *Cassytha* stem had made contact with the host leaf/stem, first, the cortical cells in the middle layers under goes a rapid internal changes like dense cytoplasm which further dedifferentiate to form the upper haustorium (Fig. 2). These fast dividing cells advance inside the host *Morinda* by breaking with mechanical pressure and pervade with its cell contents into the host. At this stage, the haustorial cells were more elongated than before its contact with the *Morinda* stem. These elongated cells protuberate further inside the host and modified into finger like structure called digitate cell (DC). Digitate cells further penetrate into the host by the cell mechanical pressure differentiated into hypha like structure with several branches called lower endophyte (Fig. 2D).

Composition of photosynthetic pigments and spectral analysis

Pigments analysis revealed that reduction in chlorophyll *a*, *b* and total chlorophyll pigment of the host due to infection of *Cassytha filiformis* (Table 1). Among the photosynthetic pigments, *Cassytha* showed ca. 80% reduction in Chl *a* and *b* as compared to *Morinda* and 68% reduction in total chlorophyll was observed in *Cassytha.* The Chl *a/b* ratio in the parasite was however insignificantly higher (3.28) than its host (3.17). Carotene and xanthophyll reduced to 57% and 71% respectively in *Cassytha* as compared to *Morinda.* Moreover, the photosynthetic pigments declined rapidly in the stems of *Cassytha* when compared to *Morinda* (Table 1).

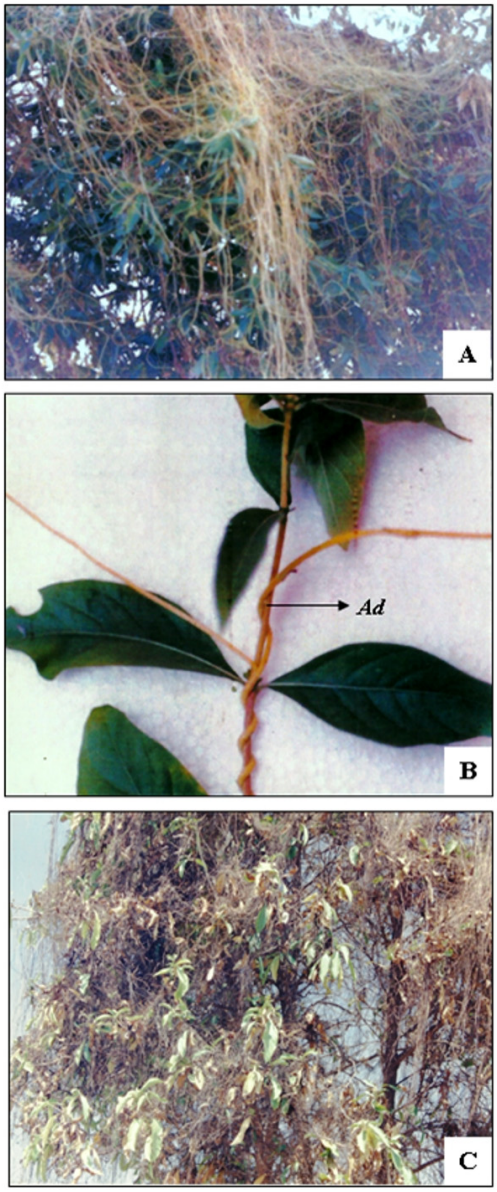

Fig. 1. *Morinda tinctoria* infected by *Cassytha filiformis*. A: Initial stage. B: Attachment orientation. C: Final stage of infection. *Ad* – Adhesive disc. Photos were taken from the same plant.

The red light absorption maxima of chlorophyll extract of both the plants was same at 667 nm without any change in the blue light absorption peak of 429 nm. When compared to *Cassytha*, the extracts of *Morinda* showed strong absorption in both red and blue wavebands (Fig. 3).

Chlorophyll *a* fluorescence kinetics

Chlorophyll *a* fluorescence kinetics for healthy parasitized (infected) *Morinda* leaves and parasite *Cassytha* showed a typical OIDPST curve in the fast transients (Fig. 4). For instance, O corresponds to the constant fluorescence, I refers to the rise in the level, I–D refers to the initial dip in the fluorescence and D–P corresponds to the increase in the electron transport from P_{680} to the plastoquinone Q_B molecule (in PS II electron transport). The constant fluorescence (F_0) level was almost the same in all the three samples. However, the difference was noticed in the level of variable fluorescence (F_V). F_V was found to be lowest in the infected *Morinda* leaf and *Cassytha* stem. Since the F_V and F_m is considered to reveal the performance of the PS II mediated photosynthetic efficiency, the ratios were calculated from the fast transients (Fig. 4). It was very obvious that the photosynthetic activity was high in the host *Morinda* leaves and medium in parasitized (infected) *Morinda* leaves and lowest ($F=9.84$, $P<0.05$) value in the parasite *Cassytha* (Fig. 5). In the slow fluorescence, the affected leaves and *Cassytha* stem showed pronounced steady state soon after the P state (Fig. 4).

DISCUSSION

The orientation of attachment of parasitic plants may be parallel to the axis of the host stem or coiled either obliquely or perpendicularly to the axis of the host stem. Initial attachment was facilitated by the parasite itself through a disc like glandular cells (Figs. 1 & 2). In each of these patterns, the haustoria are either in loose, close, or tight contact with the host, resulting in haustorial protuberances that are conical, flat, or not formed, respectively (Lee and Lee, 1989). In the present study, it was observed that *Cassytha filiformis* coiled around and perpendicular to the axis of the *Morinda tinctoria* stem. Haustorium forms a morphological and physiological bridge between the parasite and host. *Cassytha pubescens* develops a unicellular 'epithelium' consisting of trichomes upon initial contact with the hosts *Hibiscus rosa-sinensis* and *Pavonia praemorsa* (Heide-Jørgensen, 1991). The initials of haustorium and the meristematic cells were reported in *Cuscuta reflexa* (Thomson, 1925) and *Cuscuta campesteris* and elongated cells with rich protoplasm in *Cuscuta epilinum* (Koch, 1874). In contrast, the meristematic cells and the elongated cells corresponding to the meristem and the digitate cells, respectively in *Cassytha.* Kuijt (1977) divided the haustorium into two parts, the upper haustorium and the endophyte. The former is the portion of a haustorium that lies external to the host organ, whereas the endophyte is that portion of a haustorium that penetrate host tissues.

In the parasitic interaction between *Cassytha* and its host *Morinda,* elongated "searching hyphae" of the parasite penetrates the cortex and make contact with the host phloem and obtain nutrients. It is interesting to

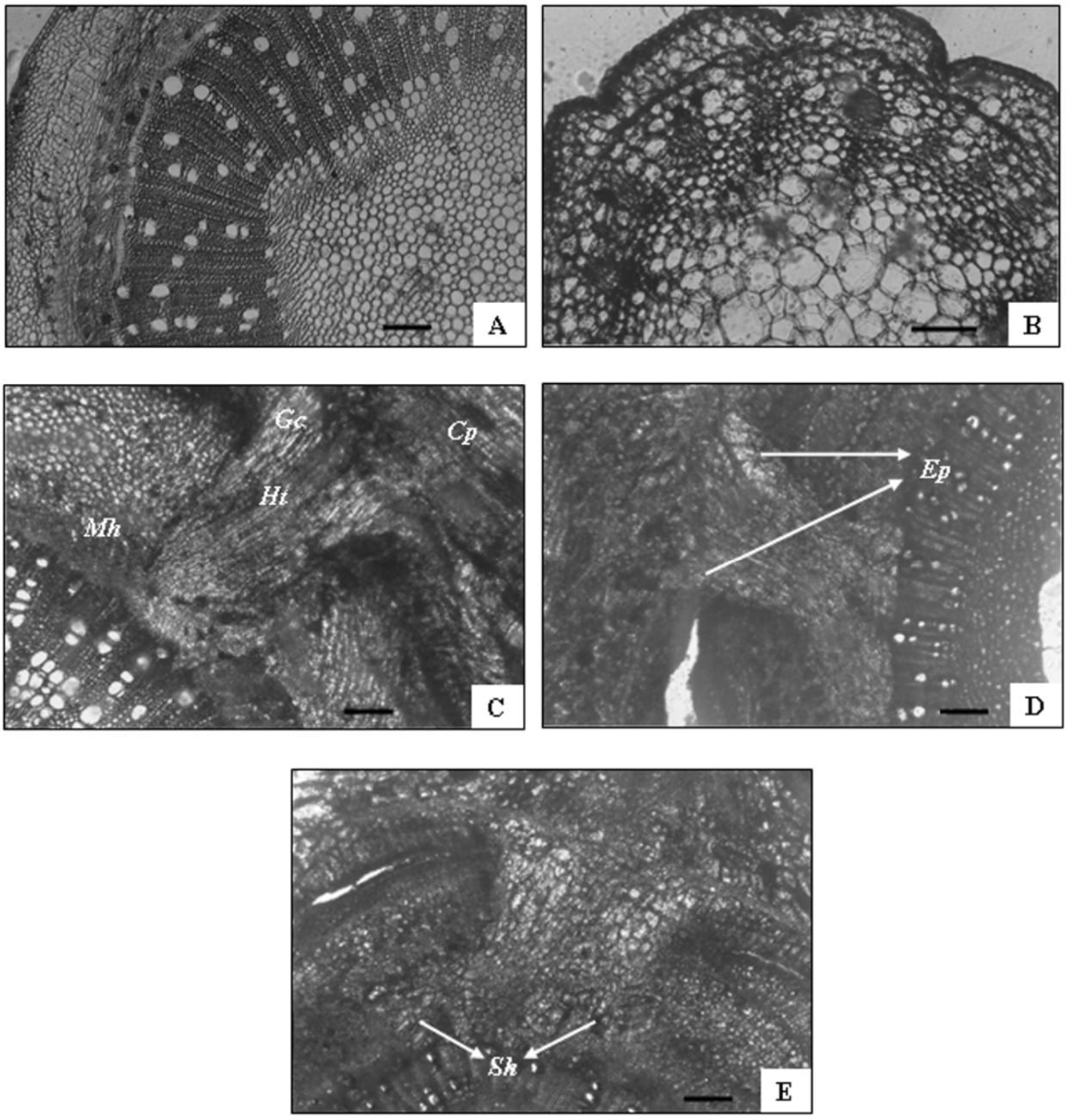

Fig. 2. Development of *Cassytha filliformis* haustorium inside host stems *Morinda tinctoria*. A & B: Transverse section of *Morinda* (Bar=50µm) and *Cassytha* (Bar=100µm) stems respectively. C–E: Different stage of haustorium development, Bar = 50µm. *Mh* – *Morinda* host; *Cp* – *Cassytha* parasite; *Gc* – Glandular cells; *Ht* – haustorim; *Ep* – endophytic primordium. *Dc* – Digitate cells; *Vb* – Vascular bundle; *Sh* – Search hyphae.

note that the host organ triggers the dedifferentiation of cortical cells in the middle layers of the parasite stem and causes vacuolated cortical parenchyma to develop dense cytoplasm, conspicuous nuclei and numerous starch grains and these cells were found to serve as the initials of upper haustorium. Evidently, Li and Yao (1992) found that accumulation of starch grains in the fully developed haustorial cell in *Cassytha filiformis* parasitizing on *Salix purpurea*. Normally a functional mature upper haustorium develops an endophyte primordium only when it contact with the host (Lee and Lee, 1989), which is highly correlated with the present study as well. In *Cassytha filiformis,* the endophyte primordium is compressed of digitate cells (Fig. 2). The

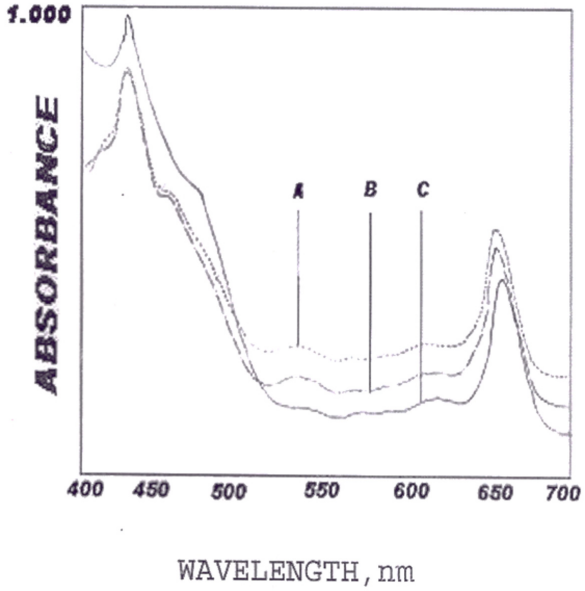

Fig. 3. Room temperature absorption spectra of chlorophyll extract from healthy *Morinda* leaves A: Parasitized *Morinda* leaves. B: and *Cassytha* stem. C: The spectra were normalized.

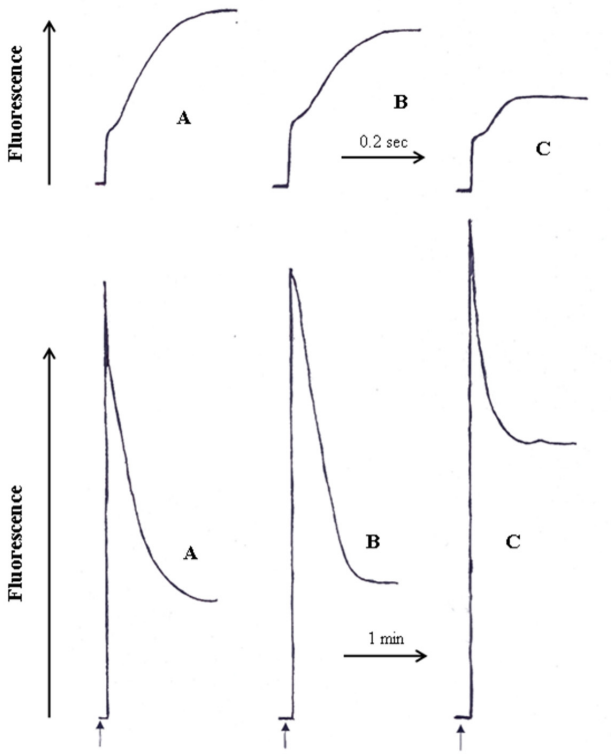

Fig. 4. Typical fast and slow fluorescence transients obtained with intact healthy *Morinda* leaves (A), parasitized *Morinda* leaves (B) and *Cassytha* stem (C). The samples were incubated in darkness for at least 15 min before measurement. The time indicates signal triggering time period. Short vertical arrows represent switching of excitation light.

digitate cells in primordium invade the host. Thus, the endophyte was established within the host tissues. In the first penetrating stage endophyte consists of axial and terminal cells that originate from the digitate cells of the endophyte in upper haustorium.

In the final maturing stage, the hyphal cells contact the host xylem and phloem eventually differentiates into xylary or phloic conductive hyphae (Lee and Lee, 1989). Structures corresponding to the endophyte primordium were reported in other parasites such as *Pedicularis* (Maybrook, 1971), *Cordylanthus* (Chuang and Heckard, 1971) and Scrophulariaceae parasitic members (Musselman and Dickison, 1975). While studying host-parasite relationship between *C. filiformis* and *Zizyphus jujuba* (host), Abubacker et al. (2005) reported that *C. filiformis* acquires the needed metabolites from the host vascular system rather than from a combination of host vascular translocates and nutrients gained by the destruction of host tissue. Contrastingly, in the present study, the host (*Morinda*) tissues including vascular bundles were severely damaged by the parasite *C. filiformis* (Fig. 2) during intrusive phase.

From the present results, it was found that though *Cassytha* depended on the *Morinda* as its host for food material, the level of photosynthetic pigments and also the ratio of chlorophyll and carotenoid, and carotene and xanthophyll were unaffected in *Cassytha* stem extract (Table 1). The level of chlorophyll *b* was lower than chlorophyll *a* in *Cassytha.* This could be attributed to poorly developed PS II complex, as it is more associated with chlorophyll *b* and xanthophylls content in the parasite stem. The change in Chl *a*/*b* ratio generally indicates physiological alteration in the biosynthetic pathway of molecules. A relatively higher ratio of chlorophyll *a/b* in *Cassytha* reveals that the ability of the parasitic plant to accumulate more of chlorophyll *a* than chlorophyll *b* despite being a leafless plant. Nonetheless, the amount of carotene and xanthophyll in *Cassytha* is comparatively low as compared to *Morinda.* This ascertains the fact both the photosystems (PS I and PS II) are intact in *Cassytha.* Moreover, the organization of the pigment species or the pigment-protein complex in *Cassytha* would be clear only from the electrophoretic separation of the chlorophyll-protein complexes. Further investigations are however warranted in this direction.

Chlorophyll (Chl) fluorescence is used as a quick probe in studying the preliminary photosynthetic events. Changes in the kinetics of Chl *a* fluorescence have been used to monitor several stress induced impairment of photosynthetic function (Karapetyan and Bukhov, 1986). Parasites can reduce host carbon fixation by lowering host stomatal conductance, impacting host photosyn-

Table 1. Photosynthetic pigments composition of the host leaves and parasite stem (n=5).

Pigments	*Cassytha*	*Morinda* (Parasitized)	*Morinda* (Healthy Host)
Chlorophyll *a* (mg g^{-1} fresh wt.)	0.141±0.02[a]	0.549±0.09[b]	0.745±0.08[c]
	(18.92)	(73.69)	(100)
Chlorophyll *b* (mg g^{-1} fresh wt.)	0.043±0.001[a]	0.195±0.01[b]	0.235±0.06[c]
	(18.29)	(75.91)	(100)
Total chlorophyll (mg g^{-1} fresh wt.)	0.184±0.03[a]	0.744±0.01[b]	0.980±0.23[c]
	(18.77)	(75.91)	(100)
Carotenoid (mg g^{-1} fresh wt.)	0.018±0.001[a]	0.110±0.02[b]	0.172±0.02[c]
	(10.46)	(63.95)	(100)
Carotene (μ mol. g^{-1} fresh wt.)	92.71±5.62[a]	163.35±14.56[b]	174.85±21.03[c]
	(53.02)	(93.42)	(100)
Xanthophyll (μ mol. g^{-1} fresh. wt.)	15.50±1.05[a]	49.06±3.97[b]	51.88±4.55[b]
	(29.88)	(94.58)	(100)
Chl *a*/*b* ratio	3.28±0.01[a]	2.86±0.01[b]	3.17±0.03[ab]
Chl / Carotenoid	3.00±0.01[a]	6.76±0.04[b]	5.69±0.02[ab]
Carotene / Xanthophyll	5.98±0.03[a]	3.32±0.02[b]	3.37±0.02[b]

Values in parentheses have been expressed in percentage.
Different letters (a, b, c, ab) indicate that means are significantly different at α=0.05

thetic metabolism or changing host biomass, biomass allocation or architecture (Graves, 1995; Press et al., 1999; Watling and Press, 2001). The healthy leaves of *Morinda* showed ODIPST pattern, which corresponds to the various phases in the fast transient (Fig. 4). The rate of D–P rise could be correlated to the efficiency of the PS II electron transport (Bose, 1980). In contrast to the fast transient, the slow fluorescence signal is interpreted as the energy dissipation from PS II to PS I. The points PST in slow transient refers to efficient transfer of exciton energy from PS II to PS I and S–T stands for the quenching of fluorescence by the PS I, in which T refers to stationery state. From the data obtained, it is clear that the photosynthetic machinery is quite efficient in *Morinda* (healthy leaves) and least efficient in *Cassytha* stem. The D–P rise was slow in the case of affected leaf of *Morinda* and *Cassytha* and corresponds to slow rate of photosynthetic electron transport in PS II. This is substantiated with the values obtained for F_v/F_m (Fig. 5). Low value indicates the reduced rate of photosynthesis. Similarly, De La Harpe (1981) and Prider et al. (2009) also observed such severe impact of *Cassytha ciliolate* and *Cassytha pubescens* on photosynthetic efficiency of

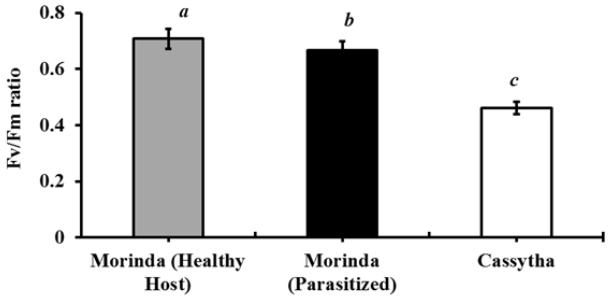

Fig. 5. Fv/Fm ratios (fast fluorescence transients) of the host (healthy and parasitized) and parasite stem. Different letters on the vertical bar indicates that means (n=5) are significantly different at α=0.05.

different host species in South Africa and Southern Australia respectively.

Lingakumar and Kulandaivelu (1993) observed such low F_v/F_m ratios in short-term UV-B irradiated leaves of *Vigna*. In case of slow fluorescence, parasitized *Morinda* and the parasite *Cassytha* samples exhibited a fast S–T decline which ascertains the incomplete energy transfer

from PS II to PS I. The attainment of early T state has been correlated to the reduced energy quenching by PS I (Lingakumar and Kulandaivelu, 1993). The present study provides the first ecophysiological impact of *Cassytha* on *Morinda tinctoria*. Unlike other species of *Cassytha* which does not damage their host, *Cassytha filiformis* was found to have ability of choosing its host plant and cause death to its host at final stage of infection. So far, there are no any adaptive mechanisms of *Morinda* to parasitism of *Cassytha*. Being an economically important plant in South Asia, *Morinda tinctoria* population is affected majorly due to the hostage of *Cassytha*. However, it is important to understand the ecological implication of such plant associations that could possibly help decrease the damage inflicted by seedy parasitic plants such as *Cassytha*.

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無根草與其宿主黃木巴戟在解剖與生理構造上的適應

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摘要：本研究試圖釐清無根草與黃木巴戟在解剖學與生理學上的宿主－寄生物關係。在解剖構造上，無根草的吸器由兩大部分構成：上部吸器及內部吸器；前者為停留在宿主器官外部的吸器，後者則會穿透宿主器官至其組織內部。同時實驗也觀察到宿主會啟動一種讓皮層薄壁細胞去分化的機制，好讓薄壁細胞發展更濃密的細胞質，並使細胞核更明顯及產生比平常更多的澱粉粒，這些細胞反應會在寄生物的上部吸器附著時開始發生。若將無根草與黃木巴戟相比較，會發現它的葉綠素b比葉綠素a及葉黃素都要來得少。為確定光合作用的活化情形，實驗使用了葉綠素a螢光誘導曲線，發現被寄生的植物組織及寄生物的莖，兩者的光合作用效率都同樣低落，這可能是光合系統II發育不佳所導致。

關鍵詞：解剖學、無根草、葉綠素、內部寄生植物、螢光運動學、半寄生生物、吸器、光系統II。