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RESEARCH ARTICLE

HEMI-PARASITIC ESTABLISHMENT IN ROOT ZONE OF WHITE SANDAL (*SANTALUM ALNUM* L.): A DOCUMENTARY FROM WEST BENGAL

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ABSTRACT

The white sandalwood plant *Santalum album* L. is a tree species has been proved its ability to adopt various ecological conditions since ancient time. Like other terrestrial tree species *Santalum album* L. can grow in various soil conditions also though it requires hosts at least two years for up-taking nutrition for its proper establishment on soil. *Santalum album* L. has a special nutrient up-taking haustorial mechanism. It forms small campanulate haustoria on the roots of host plant to make parasitic relationship. The haustorial structures are not only found on the tap roots and rootlets of the host but also found on the tubers of the host. The haustorium is consists of a peripheral hyaline body and a central penetration peg like structure. This peg gives sufficient pressure and secrete cell wall degrading bio-chemical fluid to make a proper and sure relation with the host. The entire host parasite interface is made up of parenchymatous tissue (K.U.Tennakoon and D.D. Cameron, 2006). We could trace out a little bit relationship of *Santalum album* L. with different host plants. We could find three different host plants in this phase of work which were not recorded previously elsewhere. The aims and objects of this investigation were to prove the hidden relationship between *Santalum album* L. with different host plants for which the possible morpho-physiological and anatomical evidences have been illustrated in this context.

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INTRODUCTION

The white sandalwood plant *Santalum album* L. is a widely distributed plant belongs to the family Santalaceae. It is a tropical hemi-parasitic plant and can grow various ecological as well as various soil conditions with its require hosts. The hemi-parasitic characteristic made the plant somehow unique from other terrestrial tree species. *Santalum album* L. require host plants to draw nutrition at least it attain the age of two years. The plant has a special campanulate haustorial mechanism to uptake nutrient materials from its host. The haustoria are formed by the tap root and rootlets of the plant and get attached to the host. Haustoria are consist of a peripheral hyaline body and a central penetration peg which prove sufficient pressure and secretes biochemical fluid to make a proper and sure parasitic relationship with the host plant by degrading the host cell wall.

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After get reach of the vascular tissue of plant the penetration peg formed a disc like structure and entire host-parasitic interface is made up of parenchymatous tissue (K.U.Tennakoon and D.D. Cameron, 2006). Furthermore, it is also revealed the direct lumen to lumen xylem connection between the xylem of the host plant and parasite were absent (D. Rocha, PK Ashokan, AV Santhoshkumar, EV Anoop and P Sureshkumar, 2015). We have found 3 different host species viz *Coccinia indica* (Family: Cucurbitaceae), *Cayratia trifolia* (Family: Vitaceae) and *Lespedeza procumbens* (Leguminosae) to *Santalum album* L. made parasitic relationship by forming haustoria. A large number of haustoria were found in the tubers of Cayratia trifolia.

MATERIALS AND METHODS

Materials

- Seeds of *Santalum album* L.
- Different concentration of GA3 solution.

- Rough sand
- Hycopot
- Host plants

Methods

Sandal seeds were selected randomly and treated with different concentration of GA3 solution (500ppm and 700ppm) for 72 hours. After that seed were sown in the 4 inch thick nursery bed made up of rough sand. After 33 days of sowing seeds were sprouted and the germination data were recorded properly for further critical analysis. After 20 days of germination seedlings were hycopoted and kept the nursery racks carefully. Seedling were treated with N (Urea as a source of Nitrogen), P (Super-phosphate as a source of Phosphorus), and K (Potash as a source of Potassium) in a regular interval. Different metrical data were recorded properly. After an age of 2 months seedlings were planted in the ground along with their host plants such as Justicia adhatoda (family: Acanthaceae), Catharanthus roseus (family: Apocynaceae), Ocimum sanctum (family: Lamiaceae), Calotropis procera (family: Asclepiadaceae). After 3 years of growth and development of the seedlings we took a venture to study the root parasitic relationship. Ground soil of the white sandal wood sapling base were remove carefully and the roots were cleaned with water spray machine.

RESULTS AND DISCUSSION

We have found significand host parasite relation ship with other weeds instead of that host plants which were planted along with the Sandal. Sandal saplings formed small campanulate haustoria in the roots of *Coccinia indica*, in case of *Lespedeza procumbens* the haustorial association is found in a large scale, where as in case of *Cayratia trifolia* haustoria were formed not only on the tap roots but also on the tubers. We have studied the haustorial anatomy also, and get all the structural cellular details as according to K.U.Tennakoon and D.D. Cameron, 2006. In all these three plants haustoria are formed by the Santalum album, consists of peripheral hyaline body and a central peg. It is also found that there is no direct xylem to xylem relationship between host and parasite as according to D. Rocha, PK Ashokan, AV Santhosh kumar, EV Anoop and P Suresh kumar, 2015.

Growth responses on S. album: The two N2-fixing species (Acacia confusa and Dalbergia odorifera) used in this study were better hosts than the two non-N2-fixing hosts (Bischofia polycarpa and Dracontomelon duperreranum) in promoting S. album growth. This is in accordance with previous studies, which concluded that xylem-tapping root hemiparasites grow better when associated with N2-fixing hosts, apparently as a result of higher N concentrations in the xylem of legumes compared with non-legumes (Radomiljac et al. 1999b, 1999c, Press and Phoenix 2005, Bell and Adams 2011). The data for the two N2-fixing plants in the present study clearly showed that D. odorifera was better at promoting the growth and photosynthesis of S. album than A. confusa, but was considerably poorer than the latter species when considering foliar N. Nevertheless, by the end of the 6-month study period, the growth of A. confusa was severely constrained under parasitism. Thus, our results indicate that S. album possibly parasitizes various angiosperm hosts, but some are more heavily infected than others.

An interesting finding from this study was that the growth of S. album in the absence of a host was greater than that of plants grown with non-N2-fixing host B. polycarpa and 'D. duperreranum supporting earlier studies suggesting a minimal benefit, if not disadvantage, in terms of competition for nutrients when the parasite associates with an inferior host (Radomiljac et al. 1999a). Our studies also found that the most suitable host quality index for S. album were the biomass production per haustoria and the total haustorial biomass production instead of the number of haustoria attached to the host's roots. This is in accordance with previous studies that not all species attacked by parasites act as suitable hosts because some attached haustoria are not able to penetrate their vascular tissues (Cameron et al. 2006, Cameron and Seel 2007, Suetsugu et al. 2012).

Nitrogenous solute flux from host to S. album: Since the xylem sap of host and parasite are linked by a haustorium, it has been suggested that organic N is acquired by the passive, non-selective flux of xylem sap from the host to the parasite (Pate et al. 1994, Radomiljac et al. 1998, Hibberd and Jeschke 2001, Pageau et al. 2003). Our results revealed substantial and consistent differences between the amino acid composition of the root xylem sap in the host species and associated S. album. The concentrations of amino compounds in the root xylem sap of the two N2-fixing hosts and associated S. album were higher than the two non-N2-fixing hosts and their associated S. album. Therefore, our results provide evidence that a direct bulk transfer of major nitrogenous solute did indeed take place from the xylem of N2-fixing hosts to S. album. This finding is consistent with the ‘nitrogen parasitism hypothesis’ that the primary physiological function of importing organic N compounds from the host xylem sap is to supply N to the parasite (Schulze et al. 1984, Marshall et al. 1994). However, a total of 13 or 19 amino acids with two distinctive organic acids (pipecolic acid and djenkolic acid) were detected (Tennakoon et al. 1997b, Radomiljac et al. 1998), while a total of 26 amino acids were found in this study. We assume these differences are mainly from the utilization of different plants species and tissues (stem sap vs root sap). Meanwhile, a new generation of amino acids analyzer was also employed in this study.

The abundant nodulation of A. confusa and D. odorifera, a number of haustoria of S. album attached to both nodules and roots, and values of δ15N close to zero for both legumes and accompanying S. album provide evidence of a high dependence of host and parasite on fixed. N. For most annual or woody hemiparasites, the proportion of nitrogenous compound transferred from the host ranged widely, from low (0.2–18%) via non-N2-fixing hosts to high (56–70%) via N2-fixing plants (Tennakoon et al. 1997b, Jiang et al. 2004, Cameron and Seel 2007); in such studies there is little relevance in distinguishing between N2-fixation and N transfer. Bearing this in mind, the present study examines that D. odorifera with effective nodules do have enhanced N fluxes between host D. odorifera and S. album, suggesting that effective N2-fixation could supply more nitrogenous substances in the xylem sap to the S. album haustoria (Lu et al. 2013). Hence, N2-fixing legumes are assumed to be superior hosts by supplying N to parasites. In contrast, some studies have reported that N2-fixing species do not enhance the growth of parasites compared with non-N2-fixing hosts (Atsatt and Strong 1970, Kelly 1990, Marvier 1996, Matthies 1997). Recently, Jiang et al. (2008) suggested that N2-fixation does not influence the quality of legumes as hosts for the hemiparasite *Rhinanthus minor*, but rather the

Fig. Host parasite relationship between Santalum album and Coccinia indica

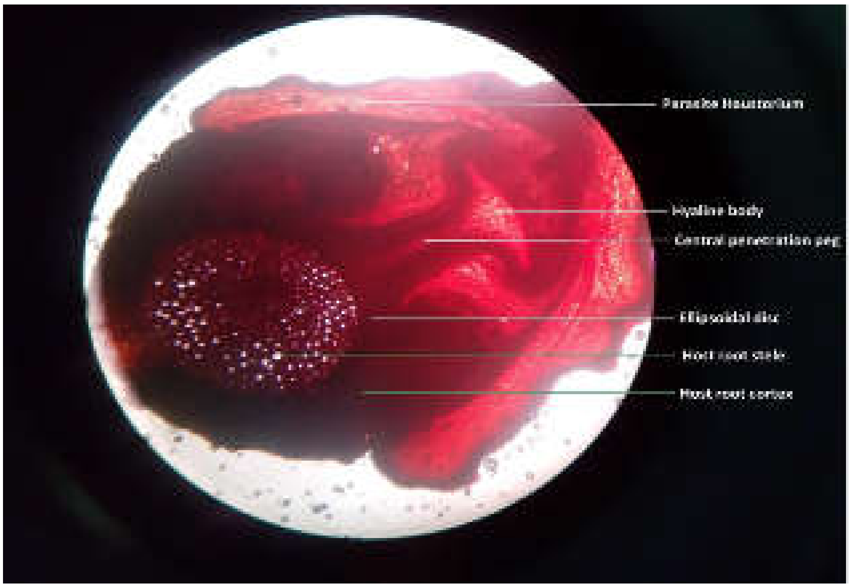

Fig: Anatomy of a haustorium

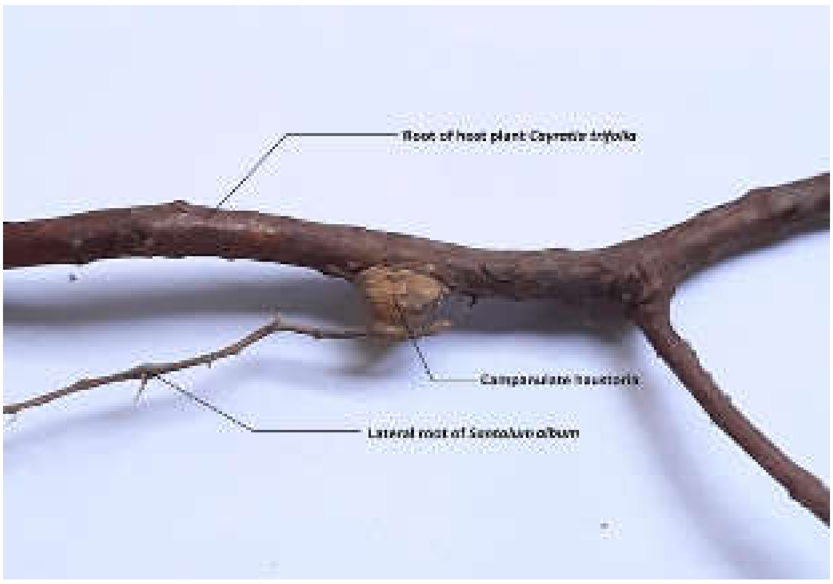

Fig. Host-parasite relationship between *Santalum* album and *Cayratia trifolia*

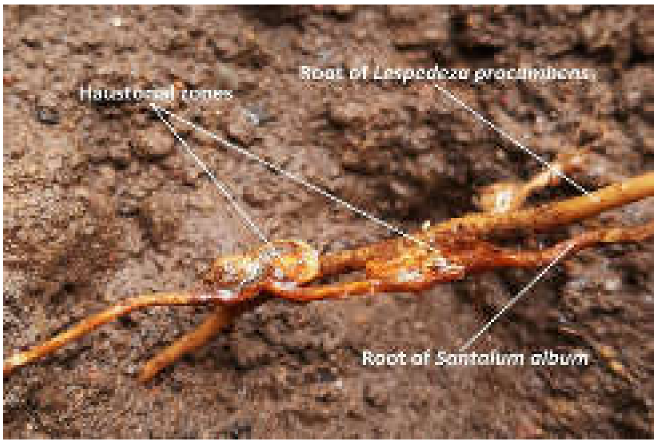

Fig. Host-parasite relationship between *Santalum* album and *Lespedeza procumbens*

well-developed haustorium formed by the parasite, coupled with the lack of defensive mechanism of the host, and the presence of ample nitrogenous compounds in the xylem sap accessible to the parasite's haustorium, govern the host quality of legumes. Our results show that the comparison of δ15N signatures of the parasite and its potential hosts gives a good indication of the N2-fixing plants likely to act as principal N sources to *S. album*.

ABA concentrations in parasite and host: Parasitic plants are known to accumulate high concentrations of ABA (Jiang et al. 2010), but its function in such unprecedented concentrations remains unclear. In any case, parasitization may significantly influence the associated host metabolism to favor nutrient acquisition by the parasite, such as elevated levels of ABA in host tissues (Taylor et al. 1996, Frost et al. 1997, Pageau et al. 2003). In common with other hemiparasites, such as *Striga* and *Rhinanthus* species, the foliar ABA concentration in S. album was found to be significantly higher than in its associated hosts. In addition, the foliar ABA concentration in all four hosts was significantly higher after attachment by *S. album*, as shown earlier for *Striga* and *Rhinanthus* by Taylor et al. (1996) and Frost et al. (1997). Taylor et al. (1996) suggested three possible sources for the extra ABA following host/parasite association: (i) a wounding response by haustorial attachment; (ii) a water deficiency of the host after parasitizing; (iii) ABA synthesis in the parasite and transport into the host. A recent study found another mechanism by which haustoria of S. album could synthesize phytohormones (e.g., ABA and GA), which was likely to be used for cell division and differentiation during haustorial development (Zhang et al. 2012). In this study, a strong positive relationship was observed between S. album biomass and amounts of ABA ($r2 = 0.83$, $P = 0.00$, $n = 12$, see Figure SIC available as Supplementary Data at Tree Physiology Online), suggesting that ABA content might be a reliable indicator of host quality. Zhang et al. (2012) verified that the ABA and GA contents of S. album were three times higher in attached haustoria than in non-attached haustoria, suggesting that endogenous hormones (e.g., indole-3-acetic acid, GA and ABA) might be involved in the haustorial formation of S. album and in water and nutrient transport for the host–parasite association (Zhang et al. 2012). Based on the haustorial research, our explanation for the high concentration and amounts of ABA in S. album grown with superior hosts is that it is possible that S. album may form more effective haustoria with suitable hosts (*A. confusa and D. odorifera*) than with inferior hosts (*B. polycarpa and D. duperreranum*). Several studies have indicated that hormones (e.g., ABA, jasmonic acid) could be responsible for initiating the heartwood transformation (Davison and Young 1973, Shain and Hillis 1973, Taylor et al. 2002). Thus, we would intend to investigate whether such an effect is responsible for accelerating the heartwood formation of *D. odorifera* after parasitization by S. album.

Gas exchange between S. album and host: The results of this study showed that increased N derived from the xylem stream of the two N2-fixing hosts resulted in an increase of N concentration in S. album tissue and high photosynthetic performance and ultimately, improved biomass production. Improved rates of photosynthesis in S. album when grown in association with N2-fixing *A. confusa and D. odorifera* provide circumstantial evidence that S. album has a lower dependence on such hosts for carbon compared with non-N2-fixing *B. polycarpa and D. duperreranum.* However, S. album clearly appears to optimize root xylem sap extraction from its hosts in the same way as the obligate hemiparasite *Striga hermonthica* (Taylor et al. 1996) and facultative hemiparasite *Rhinanthus minor* (Jiang et al. 2003), by having higher transpiration rates and lower WUE values than in the host. However, notable exceptions include '*S. acuminatum* (Tennakoon et al. 1997a), *Olax phyllanthis* (Pate et al. 1990) and mistletoe (Press et al. 1993, Seel et al. 1993). Due to elevated parasite transpiration, xylem sap is drawn through the haustorium, providing vascular continuity between *Striga* and its host, and into the parasite via cohesion (Press and Graves 1995). But there is no vascular continuity between the haustorium of *S. album* and its host *Tithonia diversifolia*, instead the presence of massive interfacial parenchyma was found at the host–parasite interface (Tennakoon and Cameron 2006).

Host responses to parasitism: It has long been known that parasitism can suppress the biomass and photosynthesis of the associated host plant (Hibberd et al. 1996, Watling and Press 2001, Cameron et al. 2005, 2008, Fisher et al. 2013). In *Dalbergia*, significant decreases in photosynthesis, transpiration and N concentration of root were noted compared with unparasitized plants, suggesting that S. album sequesters significant amounts of N from the host plant. These decreases were mirrored in *Acacia*, except for the N concentration and transpiration. In contrast, in the two non-N2-fixing plants *B. polycarpa and D. duperreranum*, intraspecific competition had a worse influence on the growth of unparasitized plants than parasitism by *S. album*. From an evolutionary perspective, in order to acquire large amounts of xylem sap from hosts, parasites may have evolved by improving their attraction to potential hosts rather than by their absorbing ability. The hemiparasite *S. album* competed poorly with hosts *B. polycarpa and D. duperreranum* for available nutrients in pot studies, and thus both non-N2-fixing hosts parasitized by *S. album* grew consistently better than their unparasitized treatments. However, differences in defensive ability have been indicated to underpin these differences in host quality and the associated parasite-induced host damage (Cameron et al. 2006, Cameron and Seel 2007, Rümer et al. 2007). Because of the absence of obviously defensive structures, Fabaceae have always served as good hosts for R. minor (Rümer et al. 2007, Jiang et al. 2008). Nevertheless, poor host *Plantago lanceolata* exhibited strong reactions (e.g., releasing toxic secondary compounds and host cell disintegration) against the haustorial tissues (Rümer et al.

2007). Therefore, in investigations addressing *S. album*–host interactions, anatomical surveys on host defense may be important to get a complete picture of the complex interactions.

Conclusion

Form the study it is found that *Santalum album* L. can make relationship with a large number of host plants belong to different families. We have found relationship with three different plant species viz *Coccinia indica, Cayratia trifolia* and *Lespedeza procumbens* belongs to the family Cucurbitaceae, Vitaceae, and Leguminosae which were not recorded previously elsewhere. Among these plants host-parasite relationship found stronger in case of *Lespedeza procumbens* belongs to the family Leguminosae, moderate relationship is found in case of *Cayratia trifolia* belongs to the family Vitaceae and the relationship with *Coccinia indica* belongs to the family Cucurbitaceae is quite low. In conclusion, the results on the physiology of the root hemiparasite S. album presented in this study collectively provide an insight into the complex interactions between the parasite and the host during the early growth stage of S. album. A range of questions remain concerning the heartwood development of both S. album and its suitable host *D. odorifera.* Further research in this area is needed to allow the development of a superior methodology for the concurrent plantation of these two valuable timber species.

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