Santalum album–host plants interaction: an incomplete story of semi-root parasite

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Sandal (*Santalum album* L.) is one of the most valuable hemiparasitic tree species cultivated for its scented heartwood and oil. The economic yield from sandal depends on the hosts associated with it. Previous studies show that the sandal–host interaction is related to certain physiological, genetic and molecular mechanisms that enable them to identify host plants, to grow invasively into the hosts, and to establish connections to withdraw water and other resources from the hosts. However, the understanding of these mechanisms is still very vague. Our observations from the three-month-old sandal seedlings–host interaction study revealed the complex and multifaceted character of the host–parasite signalling mechanism. Besides, we found numerous unsolved questions and a significant knowledge gap in this field. Therefore, this article aims to correlate and contrast our observations with previous findings and to deliver some key questions to bridge the knowledge gap in future research.

Keywords: Haustoria, HIFs, host–parasite interaction, *Santalum album*.

INDIAN sandalwood (*Santalum album* L.; family: Santalaceae) is one of the most valuable woody plants, extensively cultivated for its scented heartwood and oil. The aromatic oil extracted from wood contains santalol, which is used to prepare perfumes, cosmetics and medicines[1–3]. The Santalales order, to which sandal belongs, consists of morphologically and physiologically diverse group of parasitic plants. For example, the families in this order, including Balanophoraceae, Mystropetalaceae, Loranthaceae and Santalaceae, are parasitic in nature. Sandalwood is considered a facultative root parasite since they partially depend upon other plants (called host plants) for the nutrients required for its survival and growth. However, the host is not obligated to complete their life cycle[4]. Usually, the facultative parasites contain chlorophyll (hence are photosynthetic) and take nutrient sap by connecting to the host xylem via haustorium. Haustorium is a specialized absorbing structure by which the parasitic plants penetrate host tissues and ultimately establishing the physiological conduit with the host. Water, sugar and nutrients, especially nitrogenous compounds, flow between the parasite and the host through this haustorium[5–7]. Approximately 4,500 parasitic plant species among angiosperms can form haustoria and attach their vasculatures to their hosts to obtain water and nutrients[8]. Numerous studies have been done to understand host–parasite interaction and its ecological and economic impacts[9–15]. However, excluding basic investigations on host–parasite interaction, the majority of studies were biased in favour of the host plant. 'Survival strategy and defense mechanism of host plant', 'development and improvement of resistant varieties of host' and 'management strategies to evade parasitic plant' are the areas mostly studied and discussed so far. The parasitic plants such as witchweeds (*Striga* spp.), boomrapes (*Orobanche* and *Phelipanche* spp.), mistletoes (*Loranthus* spp.) and dodders (*Cuscuta* spp.) are the most widely studied species, because, they are widely distributed and cause serious economic loss to the farmers[16,17]. In contrast, a parasitic plant (sandal) is important because of its high economic value in the sandal-host plant system. Hence, sandal is fostered by the management of the host plants. Until now, the host–parasite interaction, including its signalling mechanism and the major factors involved, has remained unclear or often unknown, especially in the case of tree root parasites. In this context, the Indian Council of Agricultural Research (ICAR)-Central Agroforestry Research Institute, Jhansi, Uttar Pradesh, India, initiated the sandal–host interaction study in the field. During the initial phase of the study, we had some exciting observations which led to many unsolved questions in addition to what we had learned. Hence, the present article aims to shed light on our observations with the help of previous findings in the same line and to identify the unexplored area of sandal–host interaction.

Materials and methods

Three-kilogram sandal seeds were purchased from Seed Centre, Kerala Forest Research Institute, Thrissur, India, in October 2020. The sowing of seeds was done in November 2020 after treatment with 500 ppm Gibberellic acid for 12 h at the ICAR-Central Agroforestry Research Institute ($25°30'19''$ lat., $78°32'36''$ long.). The sowing was carried

Table 1. List of host species (weeds) identified for *Santalum album* parasitism

Common name	Scientific name	Family
Host weeds		
Blue gum	*Eucalyptus globulus*	Myrtaceae
Indian goosegrass	*Eleusine indica*	Poaceae
Round-leaved dock	*Rumex obtusifolius*	Polygonaceae
Nut grass	*Cyperus rotundus*	Cyperaceae
Congress grass	*Parthenium hysterophorus*	Asteraceae
Yellow-flowered pea	*Lathyrus aphaca*	Fabaceae
Bhumi amla	*Phyllanthus neruri*	Phyllanthaceae
Common dandelion	*Taraxacum officinale*	Asteraceae
Non-host weeds		
Common nightshade	*Solanum nigrum*	Solanaceae
Sessile joyweed	*Alternanthera sessilis*	Amaranthaceae
Annual yellow sweet clover	*Melilotus indica*	Fabaceae
Unidentified A (grass)	–	Poaceae
Unidentified B	–	–

out on raised bed prepared by using red soil in an open condition as well as in a root trainer cup filled with different potting media in green net house condition. The observations of the present study were taken from three months old seedlings.

Observations

The uprooted sandal seedlings showed a haustoria connection (seen on the lateral side of primary and lateral roots) with 8 weeds (Table 1 and Figure 1) out of 13 weeds identified in the seedbed. Both monocot and dicot plants were found among the host (host means the weeds associated with the sandal). The host plants were from taxonomically different families. Interestingly, the sandal–sandal haustoria connection was observed several times, around 5–6 times. The number and size of the haustoria varied from species to species. The haustoria were bell-shaped and varied in diameter from 1 to 3 mm ([Supplementary Figure 1](#)). Tap roots of the round-leaved dock (*Rumex obtusifolius*) and rhizome of the nut grass (*Cyperus rotundus*) had large-sized haustoria (Figure 1). In the fibrous roots of Indian goosegrass (*Eleusine indica*), a large number of small haustoria were observed. No haustoria development was seen in seedlings cultivated in root trainer cups. In open and green net house conditions, there was no discernible difference in height or dry biomass between seedlings with and without weeds (Table 2). In contrast to earlier research, we did not find a haustoria connection between sandal and *Alternanthera sessilis* (*A. sessilis:* a tiny shrub that is thought to be the best sandal host plant).

Discussion

The types of host plants included monocots and dicots, annuals and perennials and short-term and long-term hosts (in plantation). Earlier reports state that at the nursery stage, *A. sessilis*, a small bushy ornamental plant, is considered a good primary host, while *Crotalaria juncea* and *Cajanus cajan* act as 'bridging agents' between early and long-term hosts for promoting the growth of *S. album*[18–20]. In addition, more than 150 short and long-term hosts were identified in India[21,22]. Previous studies and reports on sandal plantation establishment reported the need for weeding for the survival and better growth of the sandalwood[21]. However, our findings reveal that sandal may use a variety of weeds as a natural host plant without any detrimental effect on its growth and survival (Table 2). The growth attributes of the sandal seedlings grown in open beds along with weeds and grown in greenhouse conditions shown in Table 2 substantiate the same. But, in the later stages, what effect weeds would have on the economic quality of sandals? Whether good or harmful, it must be investigated. The weeds observed in the plot belonged to diverse taxa, including monocots and dicots from different families and in different forms (trees and shrubs). The root structure of these weeds was also of different forms, i.e. fibrous and tap root systems, which significantly influenced the size and number of haustoria connections. In the case of a fibrous root system of a host plant like *E. indica*, sandal formed many haustoria connections, but the haustoria size was small. Larger haustoria were found to be associated with the taproot of *R. obtusifolius* (Figure 1 *f*), but the number of haustoria was less compared to other hosts having fibrous root systems. It was found that larger the haustoria, the lesser the number and vice versa (Table 3). Comparatively, less haustoria observed in other weeds might be due to low preference by the sandal or high resistance by the host or simply due to low root density and smaller root structure. The number and size of haustoria connection with sandals were different for different weeds. In some cases, sandal may not have any connection with nearby weeds. This indicates the hierarchy of preference by sandal. The absence of haustoria connection with previously reported host *A. sessilis* also indicates the distinct hierarchy preference maintained by sandal to select suitable host plants from a diverse group of plants/weeds. In our study, the distinct hierarchy

Figure 1. Haustoria connection of sandal (indicated by yellow arrow) with weeds like (***a***) *Eucalyptus globulus*, (***b***) *Eleusine indica*, (***c***) *Taraxacum officinale*, (***d***, ***e***) *Parthenium hysterophorus*, (***f***) *Rumex obtusifolius*, (***g***) *Lathyrus aphaca*, (***h***) *Cyperus rotundus*, (***i***) *Phyllanthus neruri*, (***j***) Dead root of host species, (***k***) Sandal to sandal haustoria connection, (***l***) Long and extensive roots of *Solanum nigrum*, a non-host weed which was not found associated with sandal (insight pictures: full view of sandal-weed association).

Table 2. Sandal seedling growth attributes in different media in green net house condition and in open soil. (In open field weeding has not been done)

Condition	Potting media used	Plant height (cm)	Root length (cm)	Plant dry weight (g)
In mist chamber, root trainer seedlings	Potting media 1	12.42 (0.766)	10.94 (0.375)	0.347 (0.072)
	Potting media II	12.70 (0.459)	11.68 (1.438)	0.305 (0.040)
	Potting media III	12.00 (1.121)	11.34 (1.022)	0.296 (0.036)
	Potting media IV	10.98 (0.519)	8.04 (0.872)	0.210 (0.018)
In field (on seed bed)	Open soil	11.00 (0.729)	9.78 (1.120)	0.200 (0.072)
Average		11.82 (0.341)	10.356 (0.499)	0.272 (0.021)
Significant level		ns	ns	ns

ns, Not significant.

preference of sandal with weeds was in the order (from high to low): *Rumex obtusifolius* > *Eleusine indica* > *Phyllanthus neruri* > *Eucalyptus globulus* > *Taraxacum officinale* > *Parthenium hysterophorus* > *Lathyrus aphaca* > *Cyperus rotundus*. But the factors influencing this hierarchy preference by sandal are not known. Finding these factors will help to manipulate the host and to identify the best sandal–host combination which yields multiple benefits (both from sandal and host). The number of haustoria connection is the only criterion for determining the best suitable host of sandal[23,24]. We believe that, in addition to this, the number of active haustoria, their size, the amount of

Table 3. Haustoria characteristics of the host plant

Species	No. of haustoria	Size of haustoria (mm)
R. obtusifolius	6	4–6
E. indica	11	2–3
P. neruri	6	3–5
E. globulus	5	3–4
T. officinale	6	2–3
P. hysterophorus	4	2
L. aphaca	3	2–3
C. rotundus	5	2–3

water and other nutrient transported through haustoria, and ultimately the dry biomass increment in sandal must be considered to identify the most suitable host.

Host plant growth performance is equally important, like sandal growth performance, to decide the best sandal–host combination. Sandalwood is a generalist parasite and can have many hosts. The performance of each host will be different with sandal. The quality and quantity of resources offered by the host and the duration (how long the association will be) are the factors that determine the suitability of the host species. The defensive ability of the host species also determines the sandal and host plant association[25,26]. A study by Jiang *et al.*[27] on hemiparasite *Rhinanthus minor* suggested that factors like the well-developed haustorium of the parasite, the lack of defensive mechanism of the host, and the presence of ample nutrients in the xylem sap accessible to the parasite's haustorium, govern the quality of the host. Sometimes sandal can have detrimental effects on host plants, which may lead to suppressed growth or even death of the host plant. Earlier studies also reported that the excess parasitism of the sandal on other plants could suppress the biomass and photosynthesis of the associated host plants or sometimes lead to their death[28–31]. Root hemiparasites can effectively decrease the growth rate of their host and hence decrease its competitive ability, which ultimately results in a high negative effect on the host performance[25,32,33]. For example, citrus plant is not considered as a good host for sandal because the over exploitation of resources by sandal lead to their death after 2–3 years of association (unpublished data). In our study, we observed dead roots of some weeds like *C. rotundus* associated with sandal root, which indicates the competition between weed and sandal or the defensive mechanism of the weeds. To avoid the negative effects of parasites, some host plants perform defensive actions like the degradation or necrosis of their roots to avoid the haustoria connection (discussed below).

'Complete avoidance' is the first level of defensive or inhibitory mechanism performed by the host plant to prevent the attack of the parasites. How the parasites perceive host-derived signals for their development, similarly, the host is also able to sense and respond to the presence of a parasite nearby in the rhizosphere. In our study, the five species – common nightshade (*Solanum nigrum*), sessile joyweed (*Alternanthera sessilis*), annual yellow sweet clover (*Melilotus indica*), unidentified A (grass species) and unidentified B, seen very close to sandal had no haustoria connection with them. This kind of host resistance, called as 'pre-attachment resistance', includes different strategies like (a) no or reduced production of germination stimulant(s); (b) production of germination inhibitors; (c) delay, reduction, or complete inhibition of haustorium formation leading to attachment incompetence; and (d) development of preformed mechanical or structural barriers on the host surface to impede attachment. Though there are various models explaining the defence mechanism of host plants against parasites, complete knowledge is still lacking, particularly for this kind of host–parasite combination. Involvement of complex genetic, molecular, biochemical and physiological factors makes the research challenging. Recent findings show that host–parasite defence mechanism is similar to pathogen–host plant interaction[34,35]. During host–pathogen interaction, the host's complex defence system uses a range of receptors to detect pathogens. At the same time to circumvent the resistance of host, pathogens will produce or secrete virulence proteins and metabolites called effectors. This type of pathogen–host plant interaction was conceptualized by Harold H. Flor in 1942, who proposed a gene-for-gene model[36]. He stated that during a pathogen–host plant interaction, a pathogen avirulence (*Avr*) gene and the corresponding host resistance (*R*) gene initiate a cascade of defence responses, often leading to a hypersensitive response (HR) or programmed cell death that consists of localized cell necrosis at the host infection site. A similar mode of action might be the reason for the dying of roots of some host species (in *E. globulus* and *C. rotundus*) in the case of sandal–host association.

It is hypothesized that the host's defence signalling mechanism upon the perception of molecular determinants from parasites is similar to plant–microbe interactions where cell surface pattern recognition receptors (PRR) will help the host plant to recognize pathogen-associated molecular patterns (PAMPs) from their surveillance. In support of this hypothesis, recently, a PRR named CuRe1 identified from tomato recognized a potential PAMP from the stem of the parasitic plant *Cuscuta reflexa*. In addition, the role of immune receptor in identifying parasitic plants, *Striga gesnerioides* was reported in cowpea, which also strengthens

this hypothesis. They identified a cowpea *R* gene *RSG3-301* encoding a nucleotide-binding domain and leucine-rich repeat-containing (NLR) receptors[37]. The identification and characterization of parasitic plant-derived molecules and their cognate receptors will provide a significant step towards the prediction and elaboration of resistance in hosts.

It is found that the defensive mechanism of the host plant against the parasite is originated from the co-ordinated actions of genes (induction of immunity-related genes), molecular (effector and receptor protein actions, reactive oxygen species (ROS) production), physiological (transport of solutes and enzymes), biochemical (origin of haustoria inducing factors (HIFs)) and anatomical responses (vessel occlusion, thickening of cortex tissues)[38–40]. A study by Delavault[35] provided valuable, albeit incomplete, evidence that root parasitic plants, as is the case with many phytopathogenic organisms, can produce effector proteins to lure and knock down the immunity response of their host plants. He demonstrated that the *SG4z* gene effectively produced a protein effector, suppressor of host resistance 4z (SHR4z) in its haustorium that, once transferred to the host, interfered with the signalling pathway normally triggered during a resistant interaction. To date, no other parasitic effectors have been clearly characterized.

It is accepted that most of these resistances are quantitative, which are controlled by several genes. However, in a few cases, the host–parasite interaction is characterized by a host HR, which is a central feature of gene-for-gene based plant disease resistance resulting in race-specific resistance. Botanga and Timko[41] reported the resistance of the cowpea cultivar B301 to a specific race of *S. gesnerioides* by host tissue necrosis at the point of parasite attachment corresponding to an HR-type response. Studies on hemiparasite *R. minor* showed that Fabaceae always serves as good hosts for *R. minor* because of the absence of obvious defensive structures[26,27], but the poor host *Plantago lanceolata* exhibited strong reactions (e.g. releasing toxic secondary compounds and host cell disintegration) against the haustorial tissues[26]. In addition, the recent development of transcriptomic and proteomic approaches revealed that most classical biotic stress-related defense pathways play crucial roles in host defence against parasitic plants[40]. In our study, the defensive mechanism observed by *Solanum nigrum* is needed to be studied further based on these available findings and hypothesis. *S. nigrum* can be considered a model plant to study plant–parasite resistance mechanisms.

Next, if the resistance or defence mechanism of the host fail or in the absence of such mechanism, parasites can make use of nearby host in two ways. First, for certain parasites, seed germination requires specific signals (the germination stimulants) produced by host roots, and second, the development of a specific organ, the haustorium, which is also triggered by host signals HIFs[40–42]. For obligate root parasitic plants of the Alectra, Striga, Orobanche and Pheli-panche genera, the signal from host is obligatory for their germination and further survival[43]. In connection to *S. album*, previous studies have reported that seed germination and early seedling growth are independent of the host stimulus, but host plants are required for their later survival. Aseptically grown seedlings survived only with a host plant where the seeding readily established a haustoria connection[44]. The early-stage development of haustoria was observed in almost 70% of one-month-old seedlings[45] and in all 3 months old sandalwood seedlings that grew in washed sand (to avoid the effect of any external biochemical factors) supplied with full nutrient regime[36]. Barrett and John[46] stated that sandal could generate haustoria without HIFs originating from the host plant. Similarly, Meng *et al.*[47] reported that sandal could undergo a non-parasitic phase in the absence of a host and could develop a regular root system with haustoria. In contrast to this, our observation in six months old sandal seedlings grown in root trainer indicated that though the seed germination was independent of the host stimulus, the host plant was obligatory to initiate haustoria in sandal seedlings. However, seedlings with and without haustoria not showed any difference in morphological attributes and early seedling growth. In haustoria developed seedlings it was found that the sandal preference over host plants varied between weed species. Though the earlier studies reported a high preference of sandal on nitrogen-fixing species (e.g. Acacia, Casuarina and Sesbania)[18,48], we did not observe any association with nitrogen-fixing weeds. Some earlier studies demonstrated that host nitrogen was not always a reliable predictor of parasite performance[26,48–50]. This indicates that multiple factors govern the host–sandal root association.

The mechanism of initiation of haustoria development in root parasites is still very vague. The question 'who produces signals or factors responsible for the haustoria development, whether host or parasite?' needs to be answered. In our view, based on the observations from root trainer and seedbed seedlings (the seedlings grown along with weeds showed a haustoria connection, but it was absent in root trainer seedlings), the biochemical signal from the host plant is the precursor for haustoria development in the roots of sandalwood. This biochemical signal may be in the form of secondary metabolites or some volatile compounds or any other unknown compounds. The parasitic plants have mechanisms to locate the host plants in their vicinity by catching these biochemical signals. Several previous studies also reported similar as well as contradictory views regarding this. Some say the root exudates like cytokines and flavonoids, directly or indirectly via soil beneficiary microorganisms, 'induce' (host initiated) signals to sandal for haustoria development, while others say sandal 'sends' signals to nearby host plants via the same mechanism. Delavault[35] reported that the parasite receives the host-derived signals, HIFs, which trigger the development of a specific organ, the haustorium. But still, the identification of the specific active components of HIFs in host exudates,

the mechanism of HIF production, its transport, and its mode of action remain largely unknown. However, previous studies reported that HIF activity was related to the pectin fraction of host cell walls[51], and the structures of HIFs were more closely related to those of lignin monomers. Experiments on HIFs in the parasitic Orobanchaceae family (weed species like Striga, Orobanche and Phelipanche) by Goyet *et al.*[52] revealed that prehaustorium (haustoria formation before host attachment) development was provoked by host-derived signal molecules, collectively called the HIFs. Cell wall-related quinones and phenolics, and the plant hormone cytokinins, which are structurally distinct from phenolic compounds were the biochemical molecules which triggered prehaustorium formation in Orobanchaceae. In addition to this, another study in Orobanchaceae plants proposed that the ROS produced by the root parasitic plants converted host-derived phenolic precursors of HIFs like syringic acid into active HIFs, such as 2,6-dimethoxy-p-benzoquinone (DMBQ, commonly recognized HIF). In this way, parasitic plants can identify the proximity of the host for haustoria connection. The role of quinones in haustoria formation was also reported. Studies on *Triphysaria versicolor* reported that quinones are reduced by the NADPH-dependent oxidoreductase to produce reactive semiquinones, which activate downstream signalling pathways. Though the mechanism by which semiquinones transduce the signal remains unknown, it is believed that this could occur via a ligand–receptor interaction in a structure-dependent manner. In connection to this, based on the studies on endogenous hormone levels of haustoria in *S. album* L. seedlings, Zhang *et al.*[31] presumed that the hormones might act as a web-like set of interactions to regulate the haustorial development of *S. album*. In particular, endogenous auxin production and accumulation are the key factors associated with haustoria development. The negative response of haustoria development by the application of auxin activity inhibitor (p-chlorophenoxyisobutyric acid) and auxin efflux inhibitor (2,3,5-triiodobenzoic acid) and positive response to DMBQ by auxin-inducible-promoter construct in *T. versicolor* provided the conclusive evidence of involvement of auxin in haustoria development process[53]. Additionally, auxin biosynthesis was also found to be essential for haustoria formation in *Phtheirospermum japonicum*, a root parasitic plant. In this regard, a recent study by Meng *et al.*[47] confirmed the involvement of auxin in haustoria development in *S. album*. They found that auxin biosynthesis inhibitor L-Kyn and the polar auxin transport inhibitor N-1-naphthylphthalamic acid (NPA) negatively affected haustoria formation and development.

The biochemical molecules can act as precursors or stimuli during the signalling process between host and parasite. In general, these biochemical molecules released by hosts can be categorized into two groups: (1) which initiate and enhance haustoria development; (2) which act as a defensive mechanism to avoid sandal parasitism (as mentioned earlier). Even in discussions about host–parasite relationships,

sandal to sandal haustoria connection observed in the seedlings, reported earlier by Hamilton and Conard[54], makes these theories or concepts increasingly complex. Previous studies reported the specificity of HIF to determine host ranges and avoid spontaneous haustorium formation on a parasitic plant's roots, as well as a non-productive association (e.g. with congeneric or conspecific plants)[55,56]. In this context, the signalling mechanism and the cause of sandal–sandal connection needs to be investigated.

Understanding the mechanism of biochemical signalling and succeeding interaction via haustoria between sandalwood and host plant may help to understand the nutrient flow, induction of haustoria (artificially), and selection of suitable host plant which limit the detrimental effects on both sandalwood and the host species. Hence, the future studies should be focused on understanding: (1) Bio-chemical and physiological mechanism responsible for the specific host selection/preference by *Santalum album*; (2) Common and specific signalling pathways between different host species employed in response to *S. album* parasitism; (3) Specific compounds of HIFs by which parasitic plants sense the presence of a host and begin their parasitic lifestyles; (4) Quality of sandalwood with respect to different host nutrition factors.

Ethics approval: This study does not contain any experiments with human participants or animals performed by any of the authors.

Conflict of interest: The authors declare that they have no conflict of interest.

1. Kim, T. H., Ito, H., Hayashi, K., Hasegawa, T., Machiguchi, T. and Yoshida, T., Aromatic constituents from the heartwood of *Santalum album* L. *Chem. Pharm. Bull.*, 2005, **53**, 641–644.
2. Ochi, T., Shibata, H., Higuti, T., Kodama, K. H., Kusumi, T. and Takaishi, Y., Anti-*Helicobacter pylori* compounds from *Santalum album. J. Nat. Prod.*, 2005, **68**, 819–824.
3. Bhaskar, D., Viswanath, S. and Purushothaman, S., Sandal (*Santalum album* L.) conservation in southern India: a review of policies and their impacts. *J. Trop. Agric.*, 2010, **48**, 1–10.
4. Lu, J. K., Xu, D. P., Kang, L. H. and He, X. H., Host-species-dependent physiological characteristics of hemiparasite *Santalum album* in association with N_2-fixing and non-N_2-fixing hosts native to southern China. *Tree Physiol.*, 2014, **34**(9), 1006–1017; doi.org/10.1093/treephys/tpu073.
5. Pate, J. S., Haustoria in action: case studies of nitrogen acquisition by woody xylem-tapping hemiparasites from their hosts. *Protoplasma*, 2001, **215**, 204–217.
6. Bell, T. L. and Adams, M. A., Attack on all fronts: functional relationships between aerial and root parasitic plants and their woody hosts and consequences for ecosystems. *Tree Physiol.*, 2011, **31**, 3–15.
7. Yoshida, S., Cui, S., Ichihashi, Y. and Shirasu, K., The haustorium, a specialized invasive organ in parasitic plants. *Annu. Rev. Plant Biol.*, 2016, **67**, 643–667.
8. Westwood, J. H., Yoder, J. I., Timko, M. P. and Depamphilis, C. W., The evolution of parasitism in plants. *Trends Plant Sci.*, 2010, **15**, 227–235.
9. Radomiljac, A. M., McComb, J. A. and McGrath, J. F., Intermediate host influences on the root hemi-parasite *Santalum album* L. biomass partitioning. *For. Ecol. Manage.*, 1999, **113**, 143–153.

10. Press, M. C. and Phoenix, G. K., Impacts of parasitic plants on natural communities. *New Phytol.*, 2005, **166**(3), 737–751; doi:10.1111/j.1469-8137.2005.01358.x.

11. March, W. A. and Watson, D. M., Parasites boost productivity: effects of mistletoe on litterfall dynamics in a temperate Australian forest. *Oecologia*, 2007, **154**(2), 339–347; http://www.jstor.org/stable/40213084.

12. Watson, D. M., Parasitic plants as facilitators: more Dryad than Dracula? *J. Ecol.*, 2009, **97**(6), 1151–1159.

13. Demey, A., De Frenne, P., Baeten, L., Verstraeten, G., Hermy, M., Boeckx, P. and Verheyen, K., The effects of hemiparasitic plant removal on community structure and seedling establishment in semi-natural grasslands. *J. Veg. Sci.*, 2015, **26**(3), 409–420.

14. Těšitel, J., Mládek, J., Fajmon, K., Blažek, P. and Mudrák, O., Reversing expansion of *Calamagrostis epigejos* in a grassland biodiversity hotspot: *Hemiparasitic rhinanthus* major does a better job than increased mowing intensity. *Appl. Veg. Sci.*, 2015, **21**(1), 104–112.

15. Těšitel, J., Li, A. R., Knotková, K., McLellan, R., Bandaranayake, P. C. G. and Watson, D. M., The bright side of parasitic plants: what are they good for? *Plant Physiol.*, 2021, **185**(4), 1309–1324; doi:10.1093/plphys/kiaa069

16. Watson, M., Richard, C., McLellan, F. and Fontúrbel, E., Functional roles of parasitic plants in a warming world. *Annu. Rev. Ecol. Evol. Syst.*, 2022, **53**(1), 25–45.

17. Christopher, R., Clarke, M. P., Timko, J. I, Yoder, M. J. and Axtell, J. H., Westwood molecular dialog between parasitic plants and their hosts. *Ann. Rev. Phytopathol.*, 2019, **57**(1), 279–299.

18. Satoko, Y., Songkui, C., Yasunori, I. and Ken, S., The haustorium, a specialized invasive organ in parasitic plants. *Ann. Rev. Plant Biol.*, 2016, **67**(1), 643–667.

19. Nagaveni, H. C. and Vijayalakshmi, G., Growth performance of sandal (*Santalum album* L.) with different host species. *Sandalwood Research Newsletter*, 2003, vol. 18, pp. 1–4.

20. Annapurna, D., Rathore, T. S. and Joshi, G., Modern nursery practices in the production of quality seedlings of Indian sandalwood (*Santalum album* L.)-stage of host requirement and screening of primary host species. *J. Sustain. For.*, 2006, **22**, 33–55.

21. Barbour, L., Analysis of plant-host relationships in tropical sandalwood (*Santalum album*). Rural Industries Research and Development Corporation, 2008, p. 35.

22. Institute of Forest Genetics and Tree Breeding, Sandal (*Santalum album* Linn.). *Envis Bulletin*, 2012, p. 7.

23. Ouyang, Y., Zhang, X., Chen, Y., Teixeira da Silva, J. A. and Ma, G., Growth, photosynthesis and haustorial development of semiparasitic *Santalum album* L. penetrating into roots of three hosts: a comparative study. *Trees*, 2016, **30**, 317–328; https://doi.org/10.1007/s00-468-015-1303-3.

24. Rocha, D., Ashokan, P. K., Santhoshkumar, A. V., Anoop, E. V. and Sureshkumar, P., Anatomy and functional status of haustoria in field grown sandalwood tree (*Santalum album* L.). *Curr. Sci.*, 2017, **113**, 130–133.

25. Cameron, D. D., Geniez, J. M., Seel, W. E. and Irving, L. J., Suppression of host photosynthesis by the parasitic plant *Rhinanthus minor*. *Ann Bot.*, 2008, **101**, 573–578.

26. Rümer, S., Cameron, D. D., Wacker, R., Hartung, W. and Jiang, F., An anatomical study of the haustoria of *Rhinanthus minor* attached to roots of different hosts. *Flora: Morphol. Distrib. Funct. Ecol. Plants*, 2007, **202**, 194–200; https://doi.org/10.1016/j.flora.2006.07.002.

27. Jiang, F., Jeschke, W. D., Hartung, W. and Cameron, D. D., Does legume nitrogen fixation underpin host quality for the hemiparasitic plant *Rhinanthus minor*? *J. Exp. Bot.*, 2008, **59**, 917–925.

28. Hibberd, J. M., Quick, W. P., Press, M. C. and Scholes, J. D., The influence of the parasitic angiosperm *Striga gesnerioides* on the growth and photosynthesis of its host, *Vigna unguiculata*. *J. Exp. Bot.*, 1996, **47**, 507–512.

29. Watling, J. R. and Press, M. C., Impacts of infection by parasitic angiosperms on host photosynthesis. *Plant Biol.*, 2001, **3**, 244–250.

30. Cameron, D. D., Hwangbo, J. K., Keith, A. M., Geniez, J. M., Kraushaar, D., Rowntree, J. and Seel, W. E., Interactions between the hemiparasitic angiosperm *Rhinanthus minor* and its hosts: from the cell to the ecosystem. *Folia Geobot.*, 2005, **40**, 217–229.

31. Zhang, X., da Silva, J. A. T., Duan, J., Deng, R., Xu, X. and Ma, G., Endogenous hormone levels and anatomical characters of haustoria in *Santalum album* L. seedlings before and after attachment to the host. *J. Plant Physiol.*, 2012, **169**(9), 859–866.

32. Fisher, J. P., Phoenix, G. K., Childs, D. Z., Press, M. C., Smith, S. W., Pilkington, M. G. and Cameron, D. D., Parasitic plant litter input: a novel indirect mechanism influencing plant community structure. *New Phytol.*, 2013, **198**, 222–231.

33. Shen, H., Prider, J. N., Facelli, J. M. and Watling, J. R., The influence of the hemiparasitic angiosperm *Cassytha pubescens* on photosynthesis of its host *Cytisus scoparius*. *Funct. Plant Biol.*, 2010, **37**, 14–21.

34. Su, C., Liu, H., Wafula, E. K., Honaas, L., de Pamphilis, C. W. and Timko, M. P., SHR4z, a novel decoy effector from the haustorium of the parasitic weed *Striga gesnerioides*, suppresses host plant immunity. *New Phytol.*, 2020, **226**, 891–908.

35. Delavault, P., Are root parasitic plants like any other plant pathogens? *New Phytol.*, 2020, **226**, 641–643; https://doi.org/10.1111/nph.16504.

36. Flor, H. H., Inheritance of pathogenicity in *Melampsora lini*. *Phytopathology*, 1942, **32**, 653–669.

37. Li, J. and Timko, M. P., Gene-for-gene resistance in striga-cowpea associations. *Science*, 2009, **325**, 1094–1094; https://doi.org/10.1126/science.1174754.

38. Swarbrick, P. J., Huang, K., Liu, G., Slate, J., Press, M. C. and Scholes, J. D., Global patterns of gene expression in rice cultivars undergoing a susceptible or resistant interaction with the parasitic plant *Striga hermonthica*. *New Phytol.*, 2008, **179**, 515–529; https://doi.org/10.1111/j.1469-8137.2008.02484.x.

39. Yoshida, S. and Shirasu, K., Multiple layers of incompatibility to the parasitic witchweed, *Striga hermonthica*. *New Phytol.*, 2009, **183**, 180–189; https://doi.org/10.1111/j.1469-8137.2009.02840.x

40. Mutuku, J. M. *et al.*, The WRKY45-dependent signaling pathway is required for resistance against *Striga hermonthica* parasitism. *Plant Physiol.*, 2015, **168**, 1152–1163; https://doi.org/10.1104/pp.114.256404.

41. Botanga, C. J. and Timko, M. P., Genetic structure and analysis of host and nonhost interactions of *Striga gesnerioides* (witchweed) from central Florida. *Phytopathology*, 2005, **95**, 1166–1173.

42. Pérez-de-Luque, A. *et al.*, Understanding Orobanche and Phelipanche–host plant interactions and developing resistance. *Weed Res.*, 2009, **49**, 8–22.

43. Bouwmeester, H., Li, C., Thiombiano, B., Rahimi, M. and Dong, L., Adaptation of the parasitic plant lifecycle: germination is controlled by essential host signaling molecules. *Plant Physiol.*, 2021, **185**, 1292–1308; https://doi.org/10.1093/plphys/kiaa066

44. Sahai, A. and Shivanna, K. R., Seed germination, seedling growth and haustorial induction in *Santalum album*, a semi-root parasite. *Proc. Plant. Sci.*, 1984, **93**, 571–580.

45. Nagaveni, H. C. and Srimathi, R. A., Germinative capacity of floating and sinking sandal seeds. *Indian For.*, 1985, **111**(8), 615–618.

46. Barrett, D. R. and John, E. F., *Santalum album*: kernel composition, morphological and nutrient characteristics of pre-parasitic seedlings under various nutrient regimes. *Ann. Bot.*, 1997, **79**(1), 59–66.

47. Meng, S., Ma, H. B., Li, Z. S., Yang, F. C., Wang, S. K. and Lu, J. K., Impacts of nitrogen on physiological interactions of the hemiparasitic *Santalum album* and its N_2-fixing host *Dalbergia odorifera*. *Trees*, 2021, **35**(3), 1039–1051.

48. Li, Y. L., Study on introduction of Sandalwood (*Santalum album* L.). Science Press, Beijing, China, 2003.

49. Atsatt, P. R. and Strong, D. R., The population biology of annual grassland hemiparasites. 'The host environment'. *Evolution*, 1970, **24**(2), 278–291.

50. Marvier, M. A., Parasitic plant–host interactions: plant performance and indirect effects on parasite-feeding herbivores. *Ecology*, 1996, **77**, 1398–1409.

51. Keyes, W. J., O'malley, R. C., Kim, D. and Lynn, D. G., Signaling organogenesis in parasitic angiosperms: xenognosin generation, perception, and response. *J. Plant Growth Regul.*, 2000, **19**, 217–231; https://doi.org/10.1007/s003440000024

52. Goyet, V. *et al.*, Haustorium inducing factors for parasitic *Orobanchaceae*. *Front. Plant Sci.*, 2019, **10**, 1056.

53. Tomilov, A. A., Tomilova, N. B., Abdallah, I. and Yoder, J., Localized hormone fluxes and early haustorium development in the hemiparasitic plant *Triphysaria versicolor*. *Plant Physiol*., 2005, **138**, 1469–1480; doi:10.1104/pp.104.057836.

54. Hamilton, L. and Conrad, C. E., In Proceeding of the Symposium on Sandalwood in the Pacific, Honolulu, Hawaii, US Forest Service General Technical Paper PSW-122, 9–11 April 1990, p. 84.

55. Yoder, J. I., A species–specific recognition system directs haustorium development in the parasitic plant Triphysaria (Scrophulariaceae). *Planta*, 1997, **202**, 407–413; https://doi.org/10.1007/s00425-0050144

56. Jamison, D. S. and Yoder, J. I., Heritable variation in quinone-induced haustorium development in the parasitic plant *Triphysaria*. *Plant Physiol.*, 2001, **125**, 1870–1879; https://doi.org/10.1104/pp.125.4.1870