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# *Cuscuta reflexa* Roxb. Parasitism: Structural Development of Adhesive Disk

**P. Chitralekha* and Anita Rani***
*Dyal Singh College, Lodhi Road, New Delhi–110 003*

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ABSTRACT

*Cuscuta reflexa* Roxb. (Convolvulaceae) is a total stem parasite that infects a large number of angiosperms. It grows and survives by parasitising host plants and extracting water and nutrients by developing and inserting into the host tissues, a haustorium. In general, *C. reflexa* stem infects the aerial parts of host plants. Field observations revealed that *C. reflexa* is found on the canopies of the plants well exposed to sunlight and often exhibits an annual cyclic pattern of growth on some trees such as *Holoptelea integrifolia*, *Cascabela thevetia* and *Ziziphus mauritiana.* It dries and withers in the months the hosts shed their leaves and regenerates after the hosts have sprouted new leaves. Moreover, *C. reflexa* is seen to forage and infect preferentially certain host plants such as *H. integrifolia*.

The first step in parasitisation by *C. reflexa* is to attach tightly to the host plant by developing an adhesive disk at the site of contact with the host. The nutrient-sucking parasitic organ, the haustorium, forms in the center of the disk and penetrates the host tissues. Since the formation of adhesive disk is an important process in the parasitisation by *Cuscuta,* and there is a paucity of information on the subject, the process was investigated in a variety of host plants. The structural development of the adhesive disk of *C. reflexa* was studied in the widely related host plants, *Alstonia scholaris* (L.) R.Br., *Bougainvillea spectabilis* Willd., *Volkameria inermis* L. and *Senna siamea* (Lam.) H.S. Irwin & Barneby, using light microscopy. The process during parasitisation of the different host plants appears to be similar. At the site of contact with the host, the epidermal cells of the parasite along with a few underlying cortical cells enlarge and form the swollen adhesive disk. The epidermal cells elongate radially towards the host surface. They are vacuolated and possess hypertrophied nuclei. The outer apical surface of the cells in contact with host epidermis is highly invaginated/infolded and lobed. A layer of cementing material is found between the lobed epidermal surface of the disk and the outer surface of the host at the site of contact, binding the two surfaces tightly. The nature of the cementing material appears to be different from that of the primary cellulosic walls of the epidermis. The invaginated surface of the epidermal cells provides a larger interface for secretion of the cementing material enabling a tighter adhesion to the host.

**Key words: Adhesive disk, Annual growth pattern, Cementing material, Dodder, Forage, Lobed epidermal cells**

***Authors for correspondence:** P. Chitralekha, Anita Rani; e-mail: pchitralekha22@gmail.com, anitarani@dsc.du.ac.in

## Introduction

*Cuscuta* is a genus of over 200 species (Albert et al., 2021; Zhang et al., 2021) of rootless shoot parasites belonging to the family Convolvulaceae. Its leaves are reduced to vestigial scales (McNeal et al., 2007). It is one of the most widespread and successful parasitic weeds parasitising a number of angiosperms (Kujit, 1969; Malik & Singh, 1979; Dawson et al., 1994; Vaughn, 2002; Shimizu & Aoki, 2019). Some *Cuscuta* species are "specialists" with a narrow host range while others like *C. reflexa* Roxb. and *C. chinensis* Lam. which can infect numerous species from different families are considered "generalists" (Dey & Mukherjee, 2013). In nature, a single *Cuscuta* plant often parasitises two or more neighboring host plants simultaneously (Koch et al., 2004; Hettenhausen et al., 2017; Li et al., 2020; Těšitel et al., 2021; Zhang et al., 2021) and materials are exchanged between different host plants connected through the *Cuscuta* bridge enabling a natural interspecies grafting. The stem of *Cuscuta* twines around host organs, attaches tightly to the host by forming adhesive disks and penetrates the host tissues via specialized absorptive organs, the haustoria. Within the haustorium, conducting cells differentiate which connect the host vascular tissue with that of the parasite for translocation of water, nutrients and other substances from the host to parasite (Chang & Lynn,1986; Dawson et al., 1994; Hibberd & Jeschke 2001; Birschwilks et al., 2006; Birschwilks et al., 2007; David-Schwartz et al., 2008; Lee, 2009; Smith et al., 2013; Yoshida et al., 2016; Brun et al., 2021; Park et al., 2022). A large number of haustoria are

formed laterally from a single *Cuscuta* stem (Yoshida et al., 2016).

Parasitic plants including *Cuscuta* cause substantive loss of yield when they infect crop plants. Since *Cuscuta* lacks roots and exhibits limited or negligible photosynthesis, it draws most of its nutrients from the host for its survival and thus, is a powerful sink competing with host for assimilates (Wolswinkel, 1974; Jeschke & Hilpert, 1997). It has been seen to reduce dry matter production and flowering in *Ricinus* (Jeschke & Hilpert, 1997), prevent fruit development in parasitised faba bean plants (Wolswinkel, 1974) and severely limit nitrogen fixation (Jeschke et al., 1994b). Disease-causing viruses (Greber, 1967; Hosford,1967; Marchoux et al., 1970; Birschwilks, 2006) and phytoplasmas (Heintz, 1989; Kaminska & Korbin, 1999) have been transferred from one host plant to another connected through *Cuscuta* bridges. Moreover, parasitisation by *Cuscuta* appears to compromise host defense responses. *Cuscuta*-parasitised tomato plants exhibit weakened resistance to beet armyworm (Runyon et al., 2008). As a result, in many parts of the world, *Cuscuta* species are serious pests.

On the flip side, several reports have indicated that parasitism by *Cuscuta* has a positive effect on the ecosystem. Some host plants infected with *Cuscuta* showed increased photosynthesis (Jeschke et al., 1994b; Jeschke et al.,1997; Jeschke & Hilpert, 1997), higher accumulation of nitrogen (Jeschke et al., 1997; Saric-Krsmanovi et al., 2019), potassium (Saric-Krsmanovi et al., 2019), and leaf chlorophyll (Jeschke et al., 1997), delayed leaf senescence (Jeschke & Hilpert, 1997), and higher acquisition of defense-related phenolic compounds such as quinic acid, gallic acid, caffeic acid, hyperoside, quercetin, and naringenin (Surmus Asan & Özen, 2016). Induction of new vascular elements in *Cuscuta*-parasitised hosts has been reported by Dawson et al. (1994). Such changes in nutrient content along with host preference shown by *Cuscuta* can facilitate species coexistence, regulate invasiveness, and thus, increase biodiversity affecting the composition of plant communities (Pennings & Callaway, 1996; De Deyn et al., 2004; Yu et al., 2009; Těšitel et al., 2021). *Cuscuta* has also been used in biological control of invasive plant species (Lian et al., 2006; Yu et al., 2011; Wu et al., 2019).

Interspecies trafficking of mobile substances between different host plants connected through the *Cuscuta* bridges has been found to regulate developmental and stress responses in both the host and the parasite. Biotic and abiotic stress signals, including herbivory, water and nutrient deficiency are transferred to multiple hosts via *Cuscuta* bridges. Warning signals generated against insect attack (Hettenhausen et al., 2017; Zhuang et al., 2018; Qin et al., 2019), salt stress (Li et al., 2020) and soil nitrogen deficiency (Zhang et al., 2021) have been shown to be transferred from the affected hosts to the unaffected hosts, upregulating expression of resistance genes in the latter and preparing them to face the stress better. It is likely that *Cuscuta* facilitates interplant communication of multiple stress-induced signaling among different hosts, reshaping the ecology of *Cuscuta*-infested plant communities (Hettenhausen et al., 2017). Given the range of ecological interactions, there is a need to study the interaction of *Cuscuta* with a larger number of host plants to better understand ecological consequences.

A functional haustorium does not develop without the presence of an adhesive disk and attachment of the parasite to the host (Heide-Jørgensen, 1987; Lee & Lee, 1989; Tada et al., 1996; Lee, 2008). Hence, formation of adhesive disk is important in the process of parasitisation. Information on the development of adhesive disk can be useful in the regulation and control of *Cuscuta* infestation of economically important plants. Most of the studies on *Cuscuta* parasitism have focused on the structure, development and physiology of the nutrient absorbing haustorium. There is little information on the development of the adhesive disk during *Cuscuta* infection. Thus, the present study, to investigate the anatomical process of adhesive disk formation in a wide variety of host plants, was undertaken to bridge that gap in our knowledge.

## Materials and Methods

***Field observations:*** Roadside trees, shrubs and herbs in the city of Delhi, India, were observed for *Cuscuta reflexa* infection. In April, 2013, a *C. reflexa* infected *Holoptelea integrifolia* Planch. (Ulmaceae) tree was observed with withered and dry strands of the parasite hanging from its bare branches as the tree had shed its leaves. Within a month (in May, 2013), new yellow-green strands of *C. reflexa* appeared on the same tree which had by then sprouted new leaves. By September, the tree was covered with the parasite. Subsequently, similar phenomenon was observed in *C. reflexa* infected trees (3 of each) of *Cascabela thevetia* (L.) Lippold (Apocynaceae) and *Ziziphus mauritiana* Lam. (Rhamnaceae) growing in different

parts of the city. These infected trees were observed almost every month for the next six years (2013-2019) and photographed.

***Anatomical study:*** Stems of *Alstonia scholaris* (L.) R.Br. (Apocynaceae), *Bougainvillea spectabilis* Willd. (Nyctaginaceae), *Volkameria inermis* L. (Lamiaceae) and petiole of *Senna siamea* (Lam.) H.S. Irwin & Barneby (Fabaceae/Caesalpiniaceae) parasitised by *C. reflexa* were collected and cut into 5 mm pieces. The pieces were fixed in FAA and processed for glycol methacrylate embedding (Feder & O'Brien, 1968). Semi-thin sections (2-5 µm thick) were cut using glass knives, stained either with 0.05% aqueous toluidine blue O (TBO) or first with PAS (periodic acid-Schiff) reaction and then counter-stained with TBO (Feder & O'Brien, 1968), and mounted in D.P.X.

## Results

***Field observations:*** The shoot parasite, *C. reflexa,* was found to infect aerial parts of host plants almost throughout the year. It parasitises many plants in Delhi, India, including both dicotyledons such as *Aegle marmelos* (L.) Corrêa, *Alstonia scholaris* (L.) R.Br. (Fig. 1A)*, Casuarina equisetifolia* L. *Ehretia laevis* Roxb., *Ficus benjamina* L*., Holoptelea integrifolia* Planch.(Fig. 1B,C)*, Cascabela thevetia* (L.) Lippold (Fig. 1D), *Milletia peguensis* Ali*, Senna siamea* (Lam.) H.S. Irwin & Barneby*, Syzygium cumini* (L.) Skeels, *Ziziphus mauritiana* Lam. (Fig. 1E)*, Bougainvillea spectabilis* Willd. (Fig. 1F)*, Duranta erecta* L*., Hamelia patens* Jacq*., Lantana camara* L*., Volkameria inermis* L. (Fig. 1G), *Amaranthus viridis* L., *Phyllanthus amarus* Schumach. & Thonn., and monocotyledons such as *Cynodon dactylon* (L.) Pers. (Fig. 1H) and *Brachiaria ramosa* (Vogel) H.S. Irwin & Barneby (Fig. 1I). Strands of *C. reflexa* were observed forming thick mats mostly on the upper canopy of the trees (Fig. 1A, B, D, F). Interestingly, the growth pattern of *C. reflexa* parasitising a woody deciduous tree, *Holoptelea integrifolia,* exhibited an annual cycle, as observed over a period of six years. The greenish yellow strands of *C. reflexa* (Fig. 1B) are present on the tree from May to next February, after which they begin to dry. In April, the withered strands of the parasite can be seen hanging from the bare tree which has shed its leaves (Fig. 1C). New yellow-green strands of the parasite reappear in May on the tree which, by then is covered with leaves. A similar phenomenon of drying and regeneration of *C. reflexa* was observed on host plants *Cascabela thevetia* (Fig. 1D) and *Ziziphus mauritiana* (Fig. 1E). Though *C. reflexa* infects *Syzygium cumini* (image not included), the parasite appears to prefer *H. integrifolia* as a host as it was not observed to parasitise an adjacent *S. cumini* tree (Fig.1C), apparently exhibiting host preference and differential foraging behaviour.

***Formation of adhesive disk:***

*C. reflexa* parasitises host plants by twining anticlockwise around the host stem (Fig. 1F, H, I), making a tight contact with host surface and producing lateral haustoria which penetrate into host tissues. The tight contact is found to be established through the formation of mostly round and sometimes elongated swollen adhesive disks by the parasite at the region of contact with the host (Fig. 1F, H, arrows).

The stem of *C. reflexa* consists of an outer layer of epidermis enclosing a few layers of cortex and a ring of collateral vascular bundles (Fig. 2A). The structure and development of the adhesive disks that formed on the four widely-related hosts, *Alstonia scholaris*, *Bougainvillea spectabilis*, *Volkameria inermis* and *Senna siamea,* was found to be similar. As *C. reflexa* stem makes contact with the host surface, the epidermal cells of the parasite at the site of contact begin to elongate radially and enlarge (Fig. 2A). An increase in the size of their nucleus is also apparent (Fig. 2A). The cortical cells just below the elongated epidermal cells, too, enlarge, especially those present at the outer protruding edges of the disk (Fig. 2B) to bring the epidermal cells in close contact with the host surface. Thus, the swollen adhesive disk surrounding the central haustorium is formed of the enlarged cortical and highly elongated epidermal cells of the parasite (Fig. 2B). The elongated epidermal cells are vacuolated with a thin layer of peripheral cytoplasm and prominent hypertrophied nuclei (Fig. 2C, F). Their walls in contact with the host are deeply invaginated or infolded creating a lobed contact surface (Fig. 2 C-F). The lobes of the adjacent cells are found to project into spaces between each other and interlock to form a compact surface (Fig. 2C arrows, E, F). A continuous layer of cementing material is clearly visible between the epidermal cells of the parasite and the host (Fig. 2E, F). The layer appears to fill in all the gaps and crevices between the host and the infolded/ lobed surfaces of parasite epidermal cells. As a result the contours of the layer facing the parasite appears highly convoluted corresponding to the lobed surface of the parasite epidermal cells (Fig. 2E, F, arrow). The

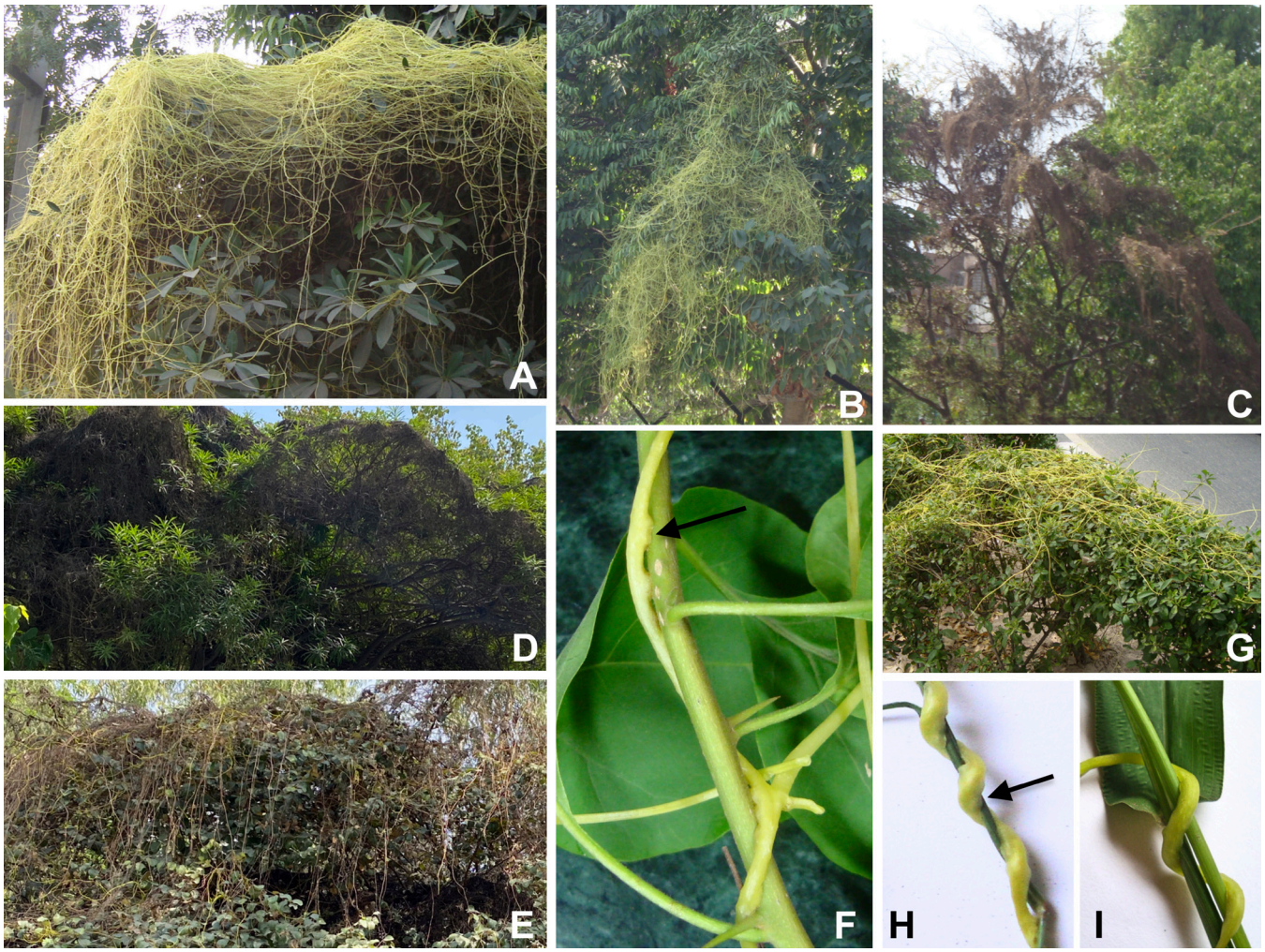


**Figure 1.** ***Cuscuta reflexa*** **parasitising host plants (A)** ***Alstonia scholaris.*** **(B-C)** ***Holoptelea integrifolia.*** **(B) September. (C) April; note the absence of the parasite on the nearby** ***Syzygium cumini*** **tree on the right. (D)** ***Cascabela thevetia.*** **(E)** ***Ziziphus mauritiana.*** **(F)** ***Bougainvillea spectabilis.*** **(G)** ***Volkameria inermis.*** **(H)** ***Cynodon dactylon.*** **(I)** ***Brachiaria ramosa.*** **Arrows point to adhesive disks.**

cementing layer stained blue with PAS-TBO staining indicating a composition different from the magenta-stained (PAS reaction) cellulosic walls of both the host and the parasite (Fig. 2E). The host epidermal cells in contact with the adhesive disk do not show any infoldings or irregular surfaces (Fig. 2E, F).

## Discussion

*Cuscuta reflexa* parasitising perennial trees, *C. thevetia*, *H. integrifolia* and *Z. mauritiana,* shows a yearly cyclic pattern of growth; it appears to wither and die during the period of March to April, the months the host trees shed their leaves, and reappears soon after the trees are covered with new leaves in May. The first host species exhibits a thinning of leaves between March and April, while the latter two possess a deciduous habit during these months (Krishen, 2006). Such a growth pattern of the parasite vis-a-vis the phenological changes exhibited by the host trees is interesting as it seems to indicate an adjustment of the growth of the parasite with that of the host. A similar growth pattern was not observed in evergreen trees or shrubs such as *Alstonia scholaris, Casuarina equisetifolia, Ficus benjamina, Bougainvillea spectabilis, Duranta erecta, Hamelia patens, Lantana camara* and *Volkameria inermis.* According to Dey and Mukherjee (2013), the majority of *Cuscuta* species are typical annuals. However, when they grow on perennial hosts (especially woody plants), a small vegetative part of the parasite after completion of its life cycle, survives within the host plant and the rest dies off. The embedded part in the host produces a new vegetative body in the next growing season and *Cuscuta* thrives as a perennial on the arboreal host plants. This phenomenon of *Cuscuta*

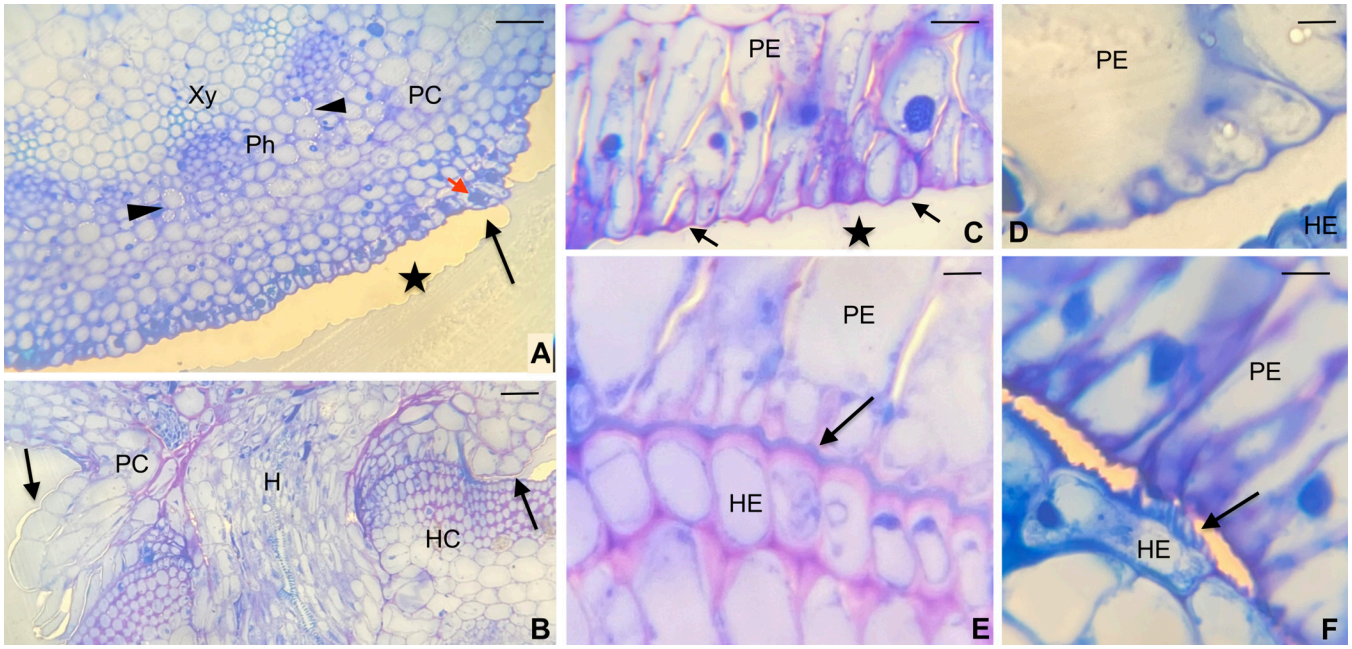


**Figure 2. Transverse section of stems of parasite and host (A) T.S. *Cuscuta reflexa* stem showing a layer of outer epidermis enclosing parenchymatous cortex and a ring of collateral vascular bundles. Black arrow points to the elongating epidermal cells with hypertrophied nuclei (red arrow) at the region of contact with the host; arrowheads point to starch-containing cortical cells; bar = 50 µm. (B) Section of the swollen adhesive disk (arrows) and the haustorium in the center; note the enlarged epidermal and cortical cells of the disk; bar = 50 µm. (C, D) Sections showing the epidermal cells of the adhesive disk with invaginated and lobed surfaces at the site of contact with host; in (C) the interlocked lobes (arrows) of the adjacent epidermal cells can be seen; epidermal cells possess hypertrophied nuclei; bar in C = 10 µm, bar in D = 2.5 µm. (E, F) Sections showing the layer of cementing material (arrows) between the epidermal cells of host and the adhesive disk at the site of contact; in (F), the convoluted surface of the layer facing the parasite epidermis is clearly visible; parasite epidermal cells have hypertrophied nuclei; bar = 5 µm. Hosts A-C, E: *Bougainvillea spectabilis* Willd.; D, F: *Senna siamea* (Lam.) H.S. Irwin & Barneby. Staining: A, D, F with TBO; B, C, E with PAS-TBO. H - haustorium, HC - host cortex, HE - host epidermis, PC - parasite cortex, PE - parasite epidermis, Ph - phloem, Xy - xylem; star indicates the position of the dislodged host.**

haustorium perennating within the tissues of the host and regenerating new shoots in the following spring/ growing season is well-documented (see Truscott, 1958; Sandler, 2010). According to Alakonya et al. (2012), the region of *Cuscuta* stem from which the meristem for haustorium development is derived has sufficient indeterminate meristematic activity to be able to form vegetative as well as flowering branches, and thus, may be involved in the regeneration of new shoots.

The anticlockwise twining of *C. reflexa* stem around the host organs observed in the present study is also reported by Tada et al. (1996), Albert et al. (2008), Dey and Mukherjee (2013) and Shimizu and Aoki, (2019), and appears to be a consistent feature. Thick mats of yellow-green stands of *C. reflexa* are found generally on the terminal exposed branches of the trees with dense canopy such as *Holoptelea integrifolia, Cascabela thevetia, Ziziphus mauritiana, Aegle marmelos*, *Alstonia scholaris* covering large parts of host tree; very few strands are present on the lower branches. On shrubs with patchy canopy as in *Hamelia patans* and *Duranta erecta*, strands are seen all over the plant. The observation that *C. reflexa* strands are consistently present on canopies, exposed to sunlight, indicates that, in all probability, the parasite accesses light energy for some kind of metabolic activity; as suggested by previous work on its physiology.

In its infective stage, *Cuscuta* is considered to be an obligate holoparasite (Machado & Zetsche, 1990; Parker & Riches, 1993; Jeschke et al., 1994a; Dawson et al., 1994; Kaiser et al., 2015), dependent, more or less, completely on the host for supply of assimilates and water (Van der Kooij et al., 2000; Birschwilks et al., 2001; Kumar & Amir, 2021). According to Jeschke et al. (1994b), 99% of the carbon that *C. reflexa* uses comes from the host plant. Moreover, despite the presence of functional photosynthetic genes in *Cuscuta* (Haberhausen, et al., 1992; Haberhausen & Zetsche, 1994; McNeal et al., 2007), a distinct down regulation in the expression of the genes during infective stages

of *C. pentagona* was found by Ranjan et al. (2014) underscoring the fact that *Cuscuta* carries out negligible photosynthesis during the parasitic phase.

On the contrary, low rates of light-stimulated assimilation of $^{14}CO_2$ in *C. campestris* and *C. gronovii* (MacLeod, 1961), *C. indecora*, *C. campestris* and *C. approximata* (Pattee et al., 1965) and *C. australis* (Baccarini, 1966) have been detected. Panda and Choudhury (1992) reported operation of Hill reaction in *C. reflexa.* Plastids in adult plants of *C. reflexa,* though lacking grana and possessing fewer thylakoids than normal chloroplasts (Machado & Zetsche, 1990), are reported to contain small amounts of chlorophyll (Machado & Zetsche, 1990; Hibberd et al., 1998) and active rubisco (Machado & Zetsche, 1990). Hibberd et al. (1998) found the presence of both rubisco enzyme and chlorophyll localized to a band of cells adjacent to the vascular bundles. The authors are of the opinion that under the reduced $CO_2$ conductance found in the parasite stem, the photosynthesis in these cells is restricted to refixing carbon dioxide released through respiration. Thus, *Cuscuta* appears to be cryptically photosynthetic (Funk et al., 2007; McNeal et al., 2007) carrying out limited photosynthetic activity (Dawson et al., 1994; Hibberd et al., 1998). However, the low levels of carbohydrate fixation in spite of presence of active rubisco and chlorophyll strongly implies an alternative role for rubisco and the harnessed light energy, probably in lipid biosynthesis as suggested by McNeal et al. (2007).

The first step in the process of parasitism is to find a suitable host and attach to it. In the present investigation, foraging behaviour of *C. reflexa* is clearly apparent as the parasite is found mostly on the host plant *Holoptelea integrifolia* but not on the nearby *Syzygium cumini* though it can infect the latter when no other suitable host is available. Experiments have shown that *Cuscuta* can move towards any vertically elongated object (Dawson et al., 1994) such as plastic rods (Furuhashi et al., 2011), dead twigs and metal rods (Kaiser et al., 2015). It is suggested that in the absence of choice, the parasite will coil round any nearby support but that light and host released-chemicals enable it to forage for hosts. Reports since the 19th century indicate that dodders can forage and choose the host best for their survival (see Parise et al., 2021). Kelly (1992) through elegant experiments was able to establish that *Cuscuta* species can distinguish differences within as well as among host nutrient categories, and are more likely to accept and invest energy and resources in coiling around more rewarding hosts of high nutritional quality. Moreover, they may invest substantially into parasitising a poor quality host if a better one is not available (Koch et al., 2004). Nickrent and Musselman, (2004) too, have reported that though *Cuscuta* parasitises many hosts at the same time, they are found on a few select hosts indicating foraging behaviour.

One of the reasons enabling dodders to forage could be their ability to measure red/far-red light. They are attracted to regions with a low ratio of red/far-red light (Furuhashi et al., 2011; Orr et al., 1996; Benvenuti et al., 2005) which is indicative of presence of healthy leaves with abundant chlorophyll (Parise et al., 2021). Another mechanism of detection of specific hosts by dodders could be through electrical signaling. Parise et al. (2021) performed elaborate experiments and demonstrated that the dynamics of *C. racemosa* electrome (the totality of the electrical activity occurring in any organism or part of it during an amount of time) changed consistently when presented with different kinds of hosts. They suggest that the changes are triggered by specific volatile organic chemicals emitted by the hosts, supporting the observations of Runyon et al. (2006) that dodder can distinguish between different hosts mediated by the volatiles released by them.

***Formation of Adhesive disk***

Attachment of *Cuscuta* to host tissue is facilitated at the region of contact with the host, through the development of adhesive disks (Dörr, 1968; Heide-Jørgensen, 1991; Dawson et al., 1994; Fathoulla & Duhoky, 2008), also called holdfasts (Shimizu & Aoki, 2019) or pre/upper haustoria which include the haustorial meristem (Kujit, 1977; Lee & Lee, 1989; Vaughn, 2002; Lee, 2008; Hong, 2011; Alakonya et al., 2012; Kaiser et al., 2015). Although coiling of *Cuscuta* stem and haustorial initiation including prehaustoria formation can occur on plastic rods (Furuhashi et al., 2011), dead twigs and metal rods (Kaiser et al., 2015), according to Fathoulla and Duhoky (2008), adhesive disks form only on contact with a live host.

The adhesive disks, in this study, are formed of elongated and enlarged epidermal and underlying cortical cells of the parasite present around the haustorium. They appear to develop through a simple reorganization of cells at the region of contact with the host, as also reported by L´opez-Curto et al. (2006)

in *C. jalapensis*. The cortical cells enlarge to bring the epidermal cells of the disk into close contact with the host surface. Neither division of the epidermal or cortical cells nor differentiation of a meristem-like structure is seen to be involved in the formation of the adhesive disk. A similar observation was made by Heide-Jørgensen (2008). On the contrary, anticlinal division of the epidermal cells of parasite have been observed during the formation of adhesive disks in some species of *Cuscuta* (Vaughn, 2002; Lee, 2008; Costea et al., 2015, Yoshida et al., 2016, Shimizu & Aoki, 2019). A differentiation of a meristem during the development of prehaustorium/adhesive disk has been reported by a number of investigators (Dörr, 1968; Heide-Jørgensen, 1991; Christensen et al., 2003; Saric-Krsmanovi et al., 2019). However, it is not clear whether the cells forming the adhesive disk are derived from the meristem. Unlike in the present study where adhesive disks are found to be comprised of cells of both epidermis and cortex, most other structural studies report involvement of only the enlarged epidermal cells in the adhesion of the parasite to the host at the site of contact (Lyshede, 1985; Heide-Jørgensen, 1991; Vaughn, 2002; Lee. 2008).

Two mechanisms are suggested to be adopted by dodder haustorium/adhesive disk to attach tightly to the host (Vaughn, 2002; Lee, 2008; Albert et al., 2008). First is through the formation of epidermal cells with extensively modified malleable walls allowing them to elongate, form an invaginated/infolded apical surface as well as conform to the outer surface of host epidermal cells, and the second is through excretion of a cementing material by these epidermal cells at the region of contact with the host. Both the mechanisms are initiated in the parasite epidermal cells prior to contact with the host. In the present study, the adhesive disk contains elongated epidermal cells whose outer apical ends in contact with the host epidermis are deeply invaginated and lobed with numerous toe-like branches or projections. The disk surface also conforms to the outer contours of the host epidermis indicating the highly flexible nature of the walls of the epidermal cells making up the disk.

Adhesive disks comprised of similar elongated epidermal cells having invaginated or infolded surfaces with toe-like projections have been described in *C. reflexa* (Heide-Jørgensen, 1987; 1991), *C. pentagona* (Vaughn, 2002), *C. japonica* (Lee, 2008), and *C. monogyna, C. chinensis* and *C. campestris* (Fathoulla & Duhoky, 2008). The projections from neighbouring cells interlock at the crevices (Lee, 2008, present study). Hong et al. (2011) report that in *C. campestris,* the host epidermal cells too, at the contact interface, invaginate and protrude between the lobes of the parasite epidermal cells to form a tight seal. According to Heide-Jørgensen (1991), contact with the host surface prevents the extension of the elongating epidermal cells of the disk. This results in the growing apical surface of the cells to fold inwards giving rise to the invaginations and lobes at the site of contact (Vaughn 2002; Lee 2008). The infoldings of the epidermal cells play an important role by creating spaces in which the adhesive/cementing material is deposited to ensure tight adhesion to host surface.

For the elongation and the extensive invaginations to occur, the walls of the dodder epidermal cells need to be flexible. Vaughn (2002) found the outer walls of the secretory-type trichome-like epidermal cells to be rich in de-esterified pectins. In addition, a large number of Golgi-derived wall loosening or osmiophilic particles, thought to be associated with the loosening of wall material and elongation of the cell walls, is found in the epidermal cells of the disk at the host contact site (Vaughn, 2002; Lee 2008). One of the components of the osmiophilic particles is suggested to be the protein expansin involved in making cell walls malleable and expandable (Vaughn et al., 2001). Enrichment of epidermal walls with de-esterified pectins which can then be attacked by pectinases to loosen the walls (Wakabayashi et al. 2003), and accumulation of the large number of wall loosening complexes are suggested as reason for making the walls flexible (Lee, 2008). In addition, reports indicate participation of enzymes in the wall remodelling process during attachment of *Cuscuta* to host surface. Olsen et al. (2016) detected high expression of two genes coding xyloglucan endotransglucosylase/hydrolase enzymes during the initial stages of haustorium formation in *C. reflexa*. The function of these enzymes is to loosen the cell walls. The activity of the enzymes was most pronounced in the swollen (disk) area of the parasite facing the host. The authors proposed that such remodeling of parasite walls prepares the parasite for host infection. L´opez-Curto et al., (2006) found presence of peroxidase enzyme mostly in the cell walls of the epidermis and

sub-epidermis of *C. jalapensis* haustorial cushion/ adhesive disk and suggest that peroxidase may be involved in the processes necessary for attachment to host such as in the degradation and/or rearrangement of wall components to loosen the walls. According to them it is one of the first enzymes to interact with and break the defense barriers of the host, enabling penetration and growth of the haustorium. Svubova et al. (2017) too, report a dramatic increase in the peroxidases content on both sides of the host-*Cuscuta* contact site. The accumulation of peroxidases by parasite may be a mechanism to make host cell walls flexible and penetrable, whereas in the host, it appears to be a defense mechanism.

In the present study, a clear layer of cementing material is observed between the epidermis of the host and the parasite adhesive disk at the contact site. The nature of the material appears to be different from the primary cellulosic walls of the epidermal cells. Deposition of a cementing material produced by host and/or parasite at the interface of the host and parasite adhesive disk is well-documented (Shimizu & Aoki, 2019). The nature of cementing material has been variously described as cuticular (Weinert & Barckhaus,1975), sticky secretion from epidermal cells of parasite (Heide-Jørgensen, 1987), pectinaceous containing primarily de-esterified pectin residues (Vaughn, 2002, Svubova et al., 2017) or low-esterified homogalacturonan (Shimizu & Aoki, 2019), electron dense homogeneous substance deposited by dodder trichomes (Lee, 2008), phenolic derivatives (Fathoulla & Duhoky, 2008), arabinogalactan proteins (Albert et al., 2006, Hozumi et al., 2017), and mucilaginous substance (Shen et al., 2006). Shimizu and Aoki (2019) suggest that enzymes such as pectin methylesterases are probably secreted by the epidermal cells of the adhesive disk to de-esterify the pectin-rich cementing material which leads to a tighter adhesion of *Cuscuta* to the host. The de-esterified pectin used by dodder to secure a tight attachment with the host is similar to the pectin of middle lamella responsible for the cementing of plant cells. Thus, according to Albert et al., (2008), the adhesive material generally used to bind cells of a species is also recruited to attach cells belonging to different species with slight modifications, during *Cuscuta* parasitism.

Infection by *C. reflexa* also appears to induce expression of arabinogalactan proteins (AGPs) at the site of attachment. Whereas Albert et al. (2006) and Striberny and Krause (2015) found these proteins to be expressed in the host cells in response to infection, Hozumi et al. (2017) detected expression of three genes coding for AGPs in the holdfast/adhesive disk of *C. campestris* and suggest that AGPs synthesized by the parasite cells play a critical role in the adhesion of *Cuscuta* to the host epidermal cells. The low-esterified pectins (Sala et al., 2019) and arabinogalactan proteins (AGPs) (Bowling & Vaughn, 2008; Huang et al., 2016) have been shown to be involved in the tight adhesion of cells at the graft junctions and the adhesion of clinging plants to their support, respectively.

Thus, the epidermal cells of the adhesive disk in contact with the host appear to undergo extensive structural modifications to ensure a tight binding with the host surface (Vaughn, 2002; Lee, 2008). The cells elongate radially and acquire hypertrophied nuclei (Lee, 2008; present study). Their apical ends in contact with host surface, are infolded and lobed and contain dense cytoplasm (Lyshede, 1985; Lee, 2008). The cytoplasm possesses numerous organelles especially dictyosomes, dictyosome-derived secretory vesicles, r-ER, and polysomes, and appears to be well equipped for the high rate of biosynthetic and secretory activities associated with the production and secretion of enzymes, wall-loosening complexes and the cementing material at the apical ends of the cells (Lee, 2008). The extended membrane surface created by the invaginations at the apical ends of the cells is well suited for secretion of large amounts of these materials between the host and the parasite, and provides a larger interface to bind with the cementing material securing tighter adhesion with the host epidermis. The increased contact surface area of the convoluted ridged outer surface of the cementing layer, created by the lobed surface of the epidermal cells is shown for the first time in the present study.

The tight attachment of *C. reflexa* to the host surface with the help of the adhesive disk is a prerequisite for successful parasitisation. However, the molecular signals generated at the site of the contact between parasite and host, along with their receptors triggering the process of attachment are yet to be discovered. Identification of genes active in the process of formation of the adhesive disk may shed light on the molecular mechanisms involved in the initial establishment of parasitism by *Cuscuta*. The information can be used to regulate and control the growth of the parasite.

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