Activity of Cytochrome Oxidase in the Haustoria of Stem Parasite *CASSYTHA FILIFORMIS L.* and Root Parasite *SANTALUM ALBUM L.*

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Abstract- In *Cassytha filiformis L.* the enzyme cytochrome oxidase activity was more pronounced at the tip of young haustorium, hence restricted to the terminal region and margin of the endophyte, but in mature condition it accumulated more in the vascular core. In young haustorium of *Santalum album L.*, the cytochrome oxidase activity was very less but it was more pronounced in mature haustorium at the region of parasite contact with the host and also in the vascular core. The sites of this enzyme activity appeared bluish-green in colour.

Keywords-*Cassytha filiformis L* , Endophyte , *Santalum album L* ,Cytochrome oxidase, Haustorium.

INTRODUCTION

Parasitic plants are of two groups *viz*., root parasites and stem parasites depending on the region of attachment on the host. Epiphytes are those which are attached to the aerial parts (branches and stem) and root parasites which are those attached to the root system of the host plant (Kuijt, 1969). Stem parasites can perhaps be better referred to as aerial parasites since they are also found sometimes on the leaves and fruits. Based on the nutritional requirements, parasitic plants are grouped into hemiparasites and holoparasites. The holoparasites are necessarily obligate parasites, while hemiparasites may sometimes be facultative.

Most of the biochemical reactions are governed through the enzymes. Study of localization of enzymes offers a procedure for tissue characterization. The importance of enzymes in the developing plant tissues helps to study tissue differentiation. Enzyme reactions are also activated in the cells when the tissue is sectioned. The end product of enzyme reaction is also detected. The enzymes like catalases, peroxidases, esterases etc., may become activated when tissue is damaged. The enzyme activity is partially or completely independent of cellular stability, but the activity of enzymes like dehydrogenases is associated with the cellular integrity, because these enzymes are destroyed partially or completely when the cell undergoes lysis.

In the present study qualitative localization of enzymatic activity during the development of haustorium of *Cassytha filiformis*, a stem parasite and *Santalum album* a hemiroot parasite were obtained through histochemical tests. Localization of cytochrome oxidase was investigated because of their importance in cellular reactions. The possible involvement of enzymes in the penetration of intrusive cells of the parasitic angiosperm *Orobanche* into host root tissues was studied by using cytochemical and immuno cytochemical methods by Goshen *et al.*, (1998). Host preference of the federally endangered hemiparasite *Schwalbera americana* of Scrophulariaceae was investigated by Helton *et al*., (2000).

Among the various nutritional modes displayed by flowering plants, parasitism represents one of the most successful mode of nutrition in Santalalean and mistletoe was reported by Nickrent and Garcia (2009). Mistletoes are a diverse group of parasitic plants. These heterotrophic plants have world wide distribution. The biology of mistletoe was studied by Watson (2001). The haustorial anatomy in case of root parasite *Agalinis* of Brazil, belonging to Scrophulariaceae was studied by Elais and Gloria (2001).

The occurrence of graniferous tracheary elements in the haustorium of *Cassytha filiformis*, a non-host specific stem parasite was reported for the first time by Rajanna and Shivamurthy (2001). The authors also convincingly recorded and reported the occurrence of phloem in the haustorium of Santalum album for the first time. *Pate et al* (2001) described the haustoria of *Olax phyllanthi* in relation to uptake, transfer and

metabolism of xylem-borne nitrogenous solutes derived from a host.

MATERIALS AND METHODS

TEST FOR CYTOCHROME OXIDASE ACTIVITY

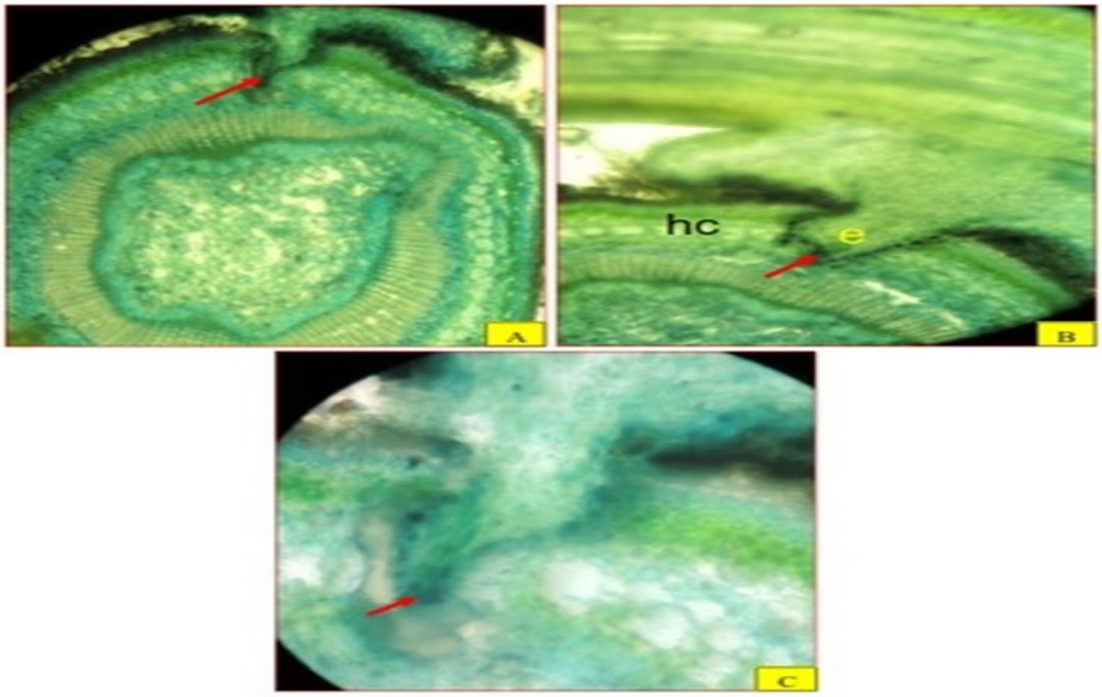
Free hand fresh sections of both the plant materials were taken and incubated for about 30 seconds in a reaction mixture at lab temperature. The reaction mixture consisting of 25 ml of 0.05 m phosphate buffer at pH 7.6, { prepared by dissolving A) 3.15 g of Sodium phosphate dibasic in 1000 ml of distilled water and B) 3.026 g of potassium phosphate monobasic dissolved in 1000 ml of distilled water. 172 ml of solution A and 27 ml of solution B were mixed}, 1% α-naphthol solution was added , (prepared by dissolving 1gram of α-naphthol in 40% alcohol) and 1ml of 1% solution of dimethyl paraphenylene diamine hydrochloride (prepared by 1 g of reagent dissolved in 100 ml of distilled water). Then the sections were rinsed in water and mounted in glycerine. In control, heat killed sections were placed in a reaction mixture. Localization of cytochrome oxidase activity was indicated by greenish blue colour.

Observations

Cytochrome oxidase activity in *Cassytha filiformis L.* appears to be present both in the host and the parasite. Its activity is indicated by bluish green colour. In the early stage of haustorial development, the cytochrome oxidase activity is confined to the epidermal layer of the host, the tip and margin of the endophyte at the region of penetration (Fig. 1A).

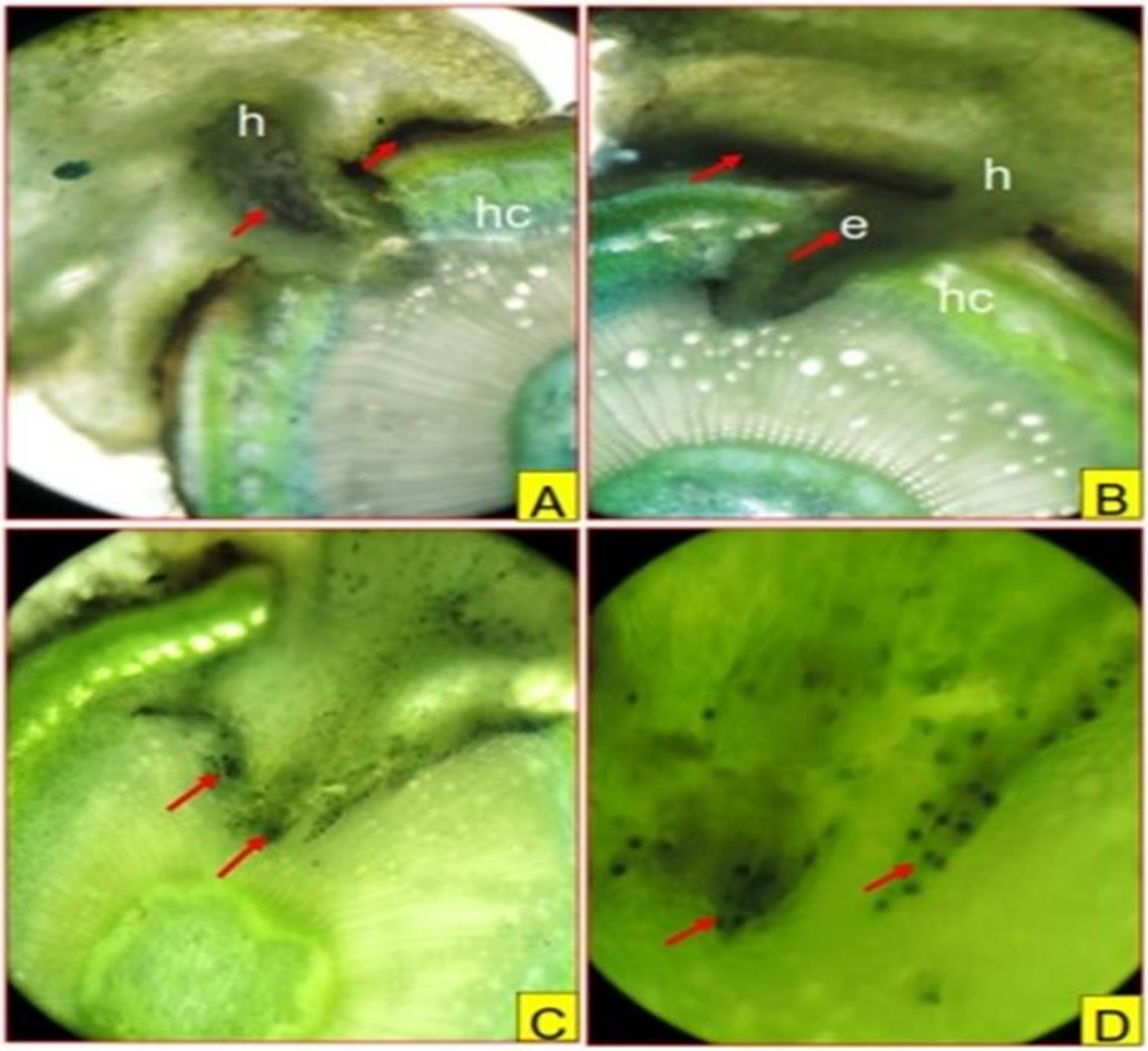
As the development proceeds, the concentration of the enzyme gradually appears to be more at the tip and at the margin of the endophyte. In the early stages of development, the enzyme activity is not noticed in the haustorium (Fig. 1B & C). As the haustorium matures, the concentration of the enzyme increases (Fig.2A & B), the endophyte penetrates the host cortex, in this condition the enzyme concentration appears to be more in the region of vascular core and upper portion of the haustorium. Cytochrome oxidase activity was clearly observed even at the region of cell division and growing part of the endophyte (Fig. 2 C & D).

Figure 1
***Cassytha filiformis* L.**
Test for Cytochrome oxidase activity



A&B. V/s of the young haustorium showing cytochrome oxidase activity (arrow) Note: the endophyte (e) of the haustorium penetrated the host cortex (hc)
C. Cross section of mature haustorium shows cytochrome oxidase activity (arrow)

Figure 2
***Cassytha filiformis* L.**
Test for Cytochrome oxidase activity

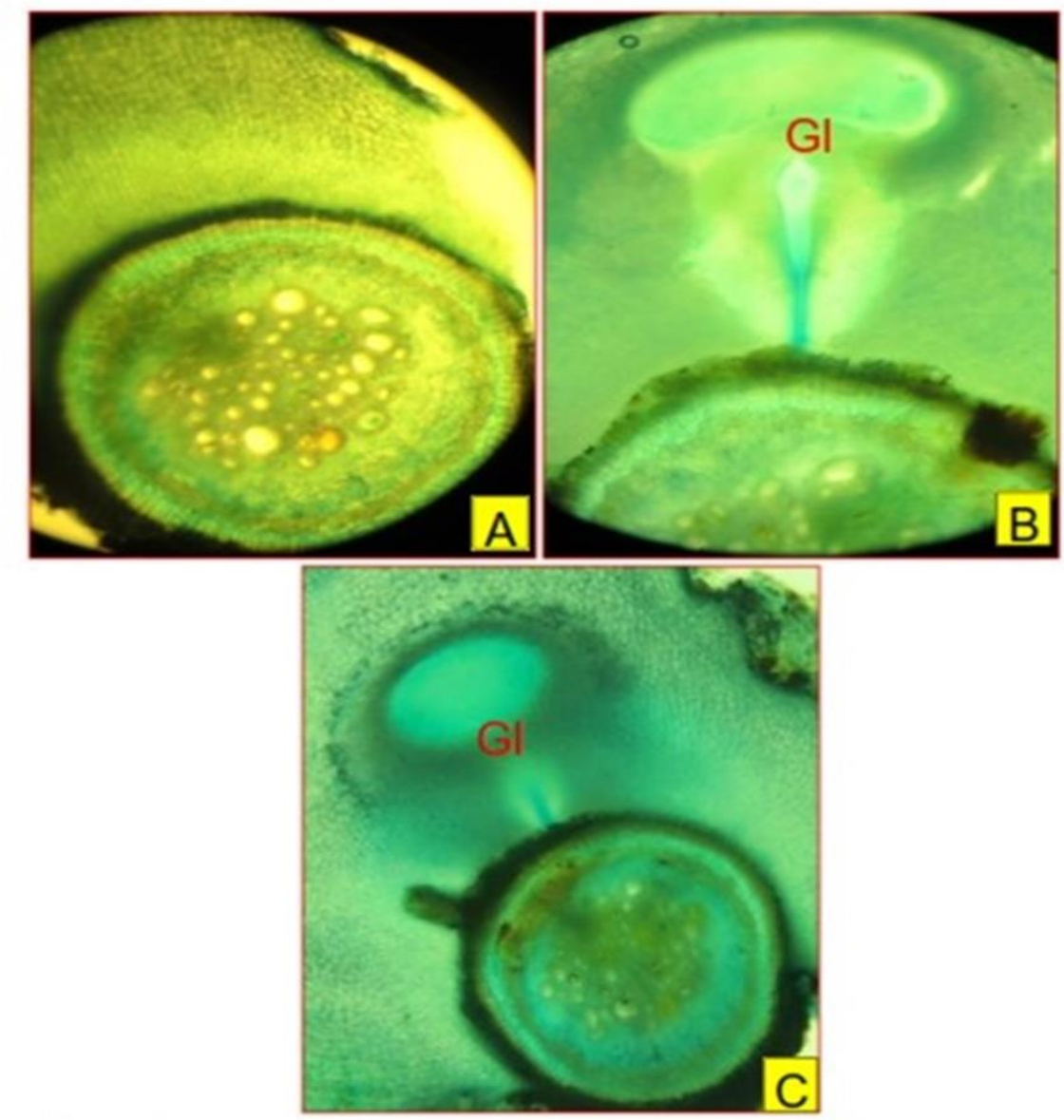


A & B. V/s of haustorium penetrated the host cortex (hc) shows cytochrome oxidase activity Note: The haustorium (h) is completely filled with the enzyme (arrows)
C&D) Cross section of matured haustorium enlarged to show the dividing cells possess enzyme activity (arrows)

In Santalum album enzyme activity appear bluish-green in colour. The activity of this enzyme appears both in host and parasite. When haustorium is young the concentration is less when compared to mature haustoria. During the early stages of development of the haustorium, cytochrome oxidase activity is noticed between the epidermal cells of the host and the parasite (Fig. 3 A), but after the formation of gland the activity gradually increases. The entire gland is surrounded by the accumulation of Cytochrome oxidase. It is assumed that the Cytochrome oxidase enzyme is synthesized and released from the gland (Fig. 3B & C). This enzyme appears to be present both in the parasite haustorium and the host with which it establishes

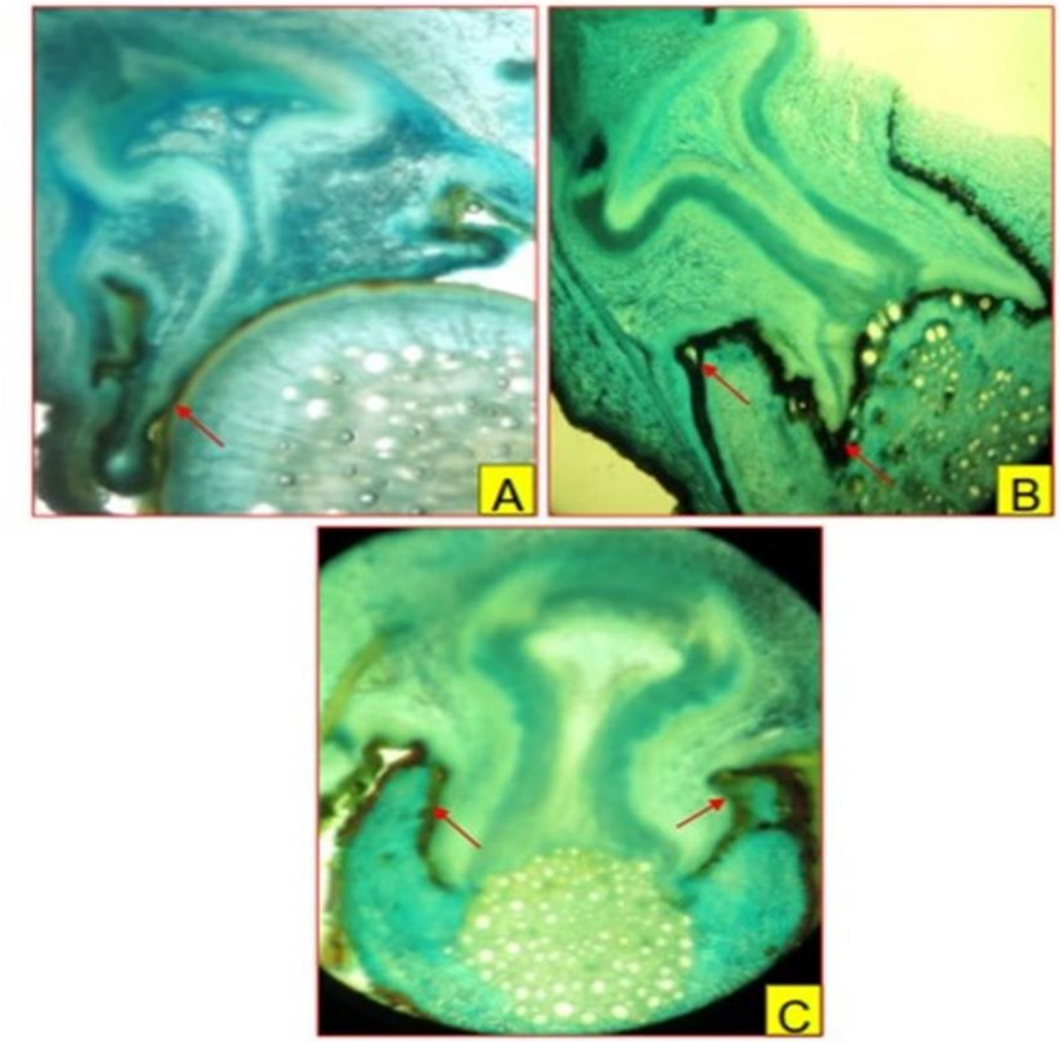
contact. The enzyme activity is more in the parasite than the host (Fig. 4A). The mature haustorium of *Santalum album* is richly filled with Cytochrome oxidase at the region of vascular core and the tip of the endophyte (Fig. 4 B & C). As the development of haustorium continues the terminal region of the endophyte loses its activity and accumulated more at the region of clasping folds and even in the cortex region of the host tissue (Fig. 4 B & C).

Figure 3
***Santalum album* L.**
Test for Cytochrome oxidase activity



A. Vertical section of haustorium with the host root cut transversely showing the initiation of haustorium
B&C. Vertical section of young haustorium with gland (Gl) shows cytochrome oxidase activity

Figure 4
***Santalum album* L.**
Test for Cytochrome oxidase activity



A, B & C. V/s of mature haustorium showing cytochrome oxidase activity (arrows)

DISCUSSION

Cassytha filiformis. L. is a rootless sprawling, perennial, viny total stem parasite of Lauraceae which grows clasping over the host plant forming large tufts .The stem bears small scale like leaves. Stems are very long and chord like and *Cassytha* species have much higher levels of chlorophyll and are generally yellowish green to green in colour. The plants are perennials and easily spread from one host to another. *Santalum album* L. a famous sandal wood tree is a member of family Santalaceae. The family is a reminiscent of the mistletoes except for five anomalous entities. The taxon grows as a hemi root parasite. It is moderate sized tall branched ever green tree. Host range has been a matter of discussion in the past among different parasitic angiosperms. Sandal wood tree grows better with luxuriant green foliage when associated with some hosts belonging to Fabaceae such as *Crotalaria juncea, Erythrina indica, Clitoria ternatia, Pongamia glabra, Dalbergia sissoo and Abrus precatorius.* While with others the growth is slightly retarded. This might be associated with nitrogen metabolism as there is no indication of any

sort of host specificity. In some cases the occurrence of hyperparasitism has been reported, this clearly demonstrates that the angiosperm parasites do not have any host specificity (Rajanna *et al*., 2010). Self parasitism was common in *Cassytha filiformis.*

Haustorium is one of the most important specialized organ among parasitic angiosperms. It forms an anatomical and physiological bridge between the parasite and its host. Normally, two kinds of haustoria are recognised on the basis of their origin (Kuijt 1977). If the root apical meristem of the embryo gets transformed into a haustorium, it is referred to as "primary haustorium". This is observed among the members of Orobanchaceae, Loranthaceae, Viscaceae and *Striga orobanchoides* of Scrophulariaceae. On the other hand, haustoria developing from regions other than the radicular apex of embryo are called "Secondary haustoria". Both the taxa selected for the present study developed only secondary haustorial contacts with their hosts. A peculiar kind of haustoria is the leaf haustoria formed directly from the scaly leaves in *Hyobanche* of Scrophulariaceae (Kuijt *et al*., 1978).

The size of the haustoria of root parasitic angiosperms normally very small organs, measuring in mm or at the most few cms in diameter. Haustoria of *Santalum album* measures about the size of pin head to a hazel nut (Corylus), whereas the haustorium of *Scleropyrum wallichianum* measures about 16 mm in diameter. The *haustoria of Cassytha filiformis* can be said to be almost 2 to 5 mm in diameter, the *haustoria of Exocarpus* are very small. The perennial species of parasites have large haustoria than the annual ones; the life span of parasitic plant may indeed be one of the factor which determines the size of the haustoria (Musselman and Dickinson 1975). In *Santalum album* and *Cassytha filiformis* the haustoria are firmly anchored to the host plant.

The haustoria are normally globose, conical, oval and hemispherical or button shaped structures in *Santalum album.* Similar shapes of haustoria have been observed in *Exocarpus* (Fineran 1963), *Comandra umbellata* (Kuijt 1969) of Santalaceae, *Gaiadendron punctatum* and *Atkinsonia ligustrina* (Fineran and Hocking 1983) both are root parasites of Loranthaceae and *Olax phyllanthi* (Pate *et al* 1990) of Olacaceae.

Chain like haustoria formation between parallely lying parasite and host organ has been observed in both the parasites and they were capable of forming a haustorial connections simultaneously on different hosts.

In *Santalum* and *Cassytha* the haustoria are initiated just behind the apex of growing roots. Such observations have been made by Fineran (1965) in *Exocarpus bidwillii*, Tooth and Kuijt (1976) in *Comandra umbellata*, Musselman and Dickinson (1975) in some Scrophulariaceae. In *Cassytha filiformis* haustoria are formed by narrower haustorial shoots which surrounds the host branches.

In both the taxa haustorial formation initiated by the meristematic activities of cortical cells of the root in *Cassytha filiformis*, prior to the initiation of haustorial primordium an adhesive disk from the epithelial cells developed into a secretary epithelium, which latter produces finger like projections from their tips. Similar type of haustorial formation has also been reported in *Cuscuta* (Heidejorgensen 1989). Exogenous origin of haustoria has been reported in many taxa belonging to Santalaceae (Rao 1942, Fineran 1965, Warrington 1970, Kuijt and Tooth 1976). Similarly the exogenious origin of haustoria in some members of Scrophulariaceae was studied by Chaung and Heckard (1971), Stephens (1912), Musselman and Dickison (1975) and in members of Lauraceae by Kuijt (1963, 1969).

The function of root is augmented by the haustorium involved in absorption of water and nutrients from the host root, its exogenous origin has been a matter of interesting discussion (Kuijt 1964) and it was concluded by Kuijt (1969) that haustorium represents a root in form and evolutionary in origin.

A well marked gland is organized within the developing haustorium just before the penetration of the host root in *Santalum album*. While in *Cassytha filiformis* gland formation was not observed. This unique feature is reported in the developing haustorium of only *Santalum* members so far. A structure similar to gland organization and function has not been described in any other parasitic angiosperms outside the santalales. The gland is reported to be absent in the aerial members of Loranthaceae (Kuijt 1969). In contrast to this work, Rao (1942) reported that an internal gland is formed in the developing haustorium only if a hard and woody root has to be penetrated. He was of the opinion that if the host root is soft and delicate, no such structure was formed. In the latter case, he attributed glandular

function only to the outer most layer of cells of the haustorium that were in contact with the host root

Rao (1942) described schizogenious origin for the cavity of the gland while Tooth and Kuijt (1976) assign a lysigenous origin. *Santalum album* of the present study supports Rao's view, while *Cassytha filiformis* of the present investigation agrees with the view of Tooth and Kuijt. The separation of the host root from the duct by a few layers of cells, as noted in both *Santalum* and *Cassytha o*f present investigation has also been reported in *Comandra umbellata* by Tooth and Kuijt (1976). Based on electron microscopic studies Tooth and Kuijt (1976) further reported that there is a distinct zone where the cavity of the gland ended and the duct begins.

Early reports about the penetration process, based on low resolution light microscopy, claimed that cell contents of the host cortical parenchyma is by means of a secretion from the intrusive cells and that the parasite is able to feed on dissolved substances. Histological observations clearly showed that only a combination of mechanical and enzymatic mechanisms exerted by a parasite to separate host cells, allows penetration (Joel and Goshen 1994; Neumann *et al*., 1998).

Renaudin (1977) detected cellulolytic and proteolytic activity at the site of penetration in *Lathraea clandensiana* by using tissue impressions on photographic cellophane films. A few works presented *in vitro* evidence about pectolytic, cellulolytic and proteolytic enzymes being secreted by seedlings of *Phelipanche aegyptica* before penetration (Shomenn-Ilan 1992, 1993, 1999). Singh and Singh (1993) also studied the presence of cell-wall degrading enzymes such as cellulose, xylanase and protinase. They could also be involved in establishing haustorial connections with the host. However, neither of these work presented conclusive routes as to the actual enzymes that are active *in situ* within host roots.

The first proof of direct involvement of enzymatic activity during the invasion process came from the work by Goshen *et al*, (1998). The authors showed the presence of methylesterase at the penetration site using cytochemical and immunocytochemical methods with specific antibodies. In addition, the presence of pectin methylesterase was associated with the appearance of De- methylated pectins, galacturonic sequences with less than 50% esterification in the cell walls adjacent to intrusive cells, which is in accordance with the enzyme activity. This enzyme was previously identified and purified from calli and germinating seeds of *Orobanche* (Ben –Hod *et al*, 1993; Nun *et al*, 1996) other enzymes have been identified in *Orobanche calli*, such as polygalacturonase, but its involvement in host penetration still has not been proven (Ben- Hod *et al*, 1997). The endodermis with its cutinized or subarised casparian strips is another obstacle which the haustorium needs to cross its way to host conductive tissues. Indeed a combined anatomical and immunocytochemical study revealed that penetration of the *Phelipanche aegyptica* haustorium takes place between host and epidermal cells by the dissolution of cutin of the casparian strips (Joel *et al*, 1998) Similarly penetration through host endodermis by *Striga hermontheca* caused damage to endodermal cells. In the latter case the haustorium was described to advance between the primary and secondary wall of the endodermis (Neumann 1999). A substance diffusable therefore seems to exist between the parasite and their mode of penetration, but this issue needs further research. Putative cutanase activity was also found at the endodermis penetration point by means of immunocytochemistry by Joel *et al*, (1998).

Occurrence of enzymatic studies on the haustorium of parasitic phanerogams are infrequent and fragmentary, only few reports on the histochemical localization of few Enzymes were made on only few parasitic angiosperms such as *Orobanche aegyptiaca*, *Tapinanthus bangwensis* and *Comandra umbellata* to localize the acid phosphatase activity. But no work has been done on the localization of cytochrome oxidase. Hence the present study represents first time in the localization of cytochrome oxidase activity in the haustorium of Cassytha *filiformis* and *Santalum album*.

SUMMARY AND CONCLUSIONS

In both the taxa of present investigation, the haustorial formation was initiated by the meristematic activities of cortical cells. A well marked gland was organized within the developing haustorium just before the penetration of the host root in *Santalum album*. While in both *Cassytha filiformis* gland formation was not observed. This unique feature has been reported in the developing haustorium of only *Santalum* members so far.

Cytochrome oxidase enzyme activity in *Cassytha filiformis* appears to be present both in the host and the

parasite. Its reaction is indicated by bluish green colour. In the early stage of haustorial development, the enzyme activity is confined to the epidermal layer of the host, the tip and margin of the endophyte at the region of penetration

As the development proceeds, the concentration of the enzyme gradually increases at the margin and tip of the endophyte. In the early stages enzyme concentration is very poor, as the haustorium matures, the concentration of the enzyme gradually increases. In the vascular core of matured endophyte the activity is very much noticed.

In Santalum album the enzyme activity appears bluish green in colour both in host and parasite. When haustoria is young the activity is less when compare to mature haustoria. Initial states the activity is restricted only to the epidermal cells of the host and the parasite but after the formation of gland the enzyme activity gradually increases, The enzyme appears to be present both in the haustorium and the host. The matured haustorium of *Santalum album* is richly filled with Cytochrome oxidase at the region of vascular core and the tip of the endophyte. As the development of the haustorium still continues the terminal region of the endophyte loses its activity and accumulated more at the region of clasping folds.

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