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AN INVESTIGATION OF A MYCORRHIZAL ASSOCIATION ON OPUNTIA POLYACANTHA

A Thesis

Presented to the

Department of Botany

Brigham Young University

In Partial Fulfilment

of the Requirements for the Degree

Master of Science

by

R. Craig Stutz

August, 1969

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R. Craig Stutz

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INTRODUCTION

The eco-physiological relationship of fungi with the roots of higher plants can vary from a relatively indifferent saprophytic association to a severe pathogenic infection. In the rhizosphere saprophytic fungi decompose organic matter from dead roots or from tissue which is sloughed from growing roots. On the other hand, root pathogens invade living tissue and disturb the general metabolism of the root to a lesser or greater extent while using the organic materials of the host as a source of energy and growth substances. Between these extremes are relationships in which the association tends toward pathogenesis, but the host also benefits from the association. Relationships of this type are termed mycorrhizae.

The word "mykorhiza" (mycorrhiza) was coined by Frank (1887) to describe roots which had been modified morphologically by the presence of symbiotic fungi. He also divided mycorrhizae into two types which he called ectotrophic and endotrophic mycorrhizae. Ectotrophic mycorrhizae are often stunted and nodulated. The root tips may swell, and they are usually devoid of root hairs. The young roots are ensheathed in a fungal mantle, while intercellular hyphae form a reticulate net within the cortex. Endotrophic mycorrhizae have less pronounced external modifications. They are usually

recognized by their yellowish discoloration and their fleshy texture. The fungal symbiont penetrates the plasma membrane and develops arbuscles and vesicles within the host cell. There is little or no external hyphae in contact with the soil. A third type of mycorrhizae which shows characteristics of both types was classified by Doak (1935) as ectendotrophic mycorrhizae.

During the past forty years copious data have been compiled concerning various aspects of mycorrhizal associations. Fortunately, several excellent reviews are available. Kelly (1936) has reviewed and summarized over 700 early publications dealing with the historical development of the study of mycorrhizae. The physiology of the association has been treated by MacDougal and Dufrency (1946), Melin (1953), Garrett (1956), and Harley (1959). Zak (1964) and Meyer (1966) have summarized the anatomical studies. Although the bulk of mycorrhizal research has been with conifers (Trappe, 1964) and orchids (Ramsbottom, 1922; Arditti, 1967), mycorrhizae have been described in virtually every major group of vascular plants. Trappe (1962) described ectotrophic forms in 39 different genera of angiosperm trees and shrubs in two genera of ferns. He later (1964) summarized the distribution of ectotrophic mycorrhizae in eight plant families representing every continent but Antarctica. Henry (1933) found ectotrophic and endotrophic mycorrhizae in all 60 species of trees he examined. Laughton (1964) reported endotrophic mycorrhizae in "almost all trees" and many shrubs

indigenous to South Africa. In Colorado, Thomas (1943) found endotrophic mycorrhizae in 65 plant species representing 27 different families. Jones (1924) described endotrophic forms in 23 genera of crop plants and McDougall and Glasgow (1929) found mycorrhizae in 19 genera of weeds. The only major groups of North American seed plants for which mycorrhizae have not been adequately described are the Caryophyllales and Cactales.

The only previous report of mycorrhizae in Cactales was published by Johansen (1931) when he noticed that seedlings of Neomammalaria and Corypantha whose roots were infected with septate hyphae grew better than seedlings grown under aseptic conditions. The infected roots were described as being endotrophic mycorrhizae.

Nodulated roots have been found on Opuntia subterraneae Fries (Britton and Rose, 1919), O. polyacantha Haw. (Farnsworth and Hammond, 1968b), O. fragilis (Nuttall) Haw. (Farnsworth and Hammond, 1968a), and O. phaeacantha Engelmann (Farnsworth, personal communication, 1968). The nodulated roots of O. polyacantha were collected by Dr. Raymond Farnsworth and shown to Dr. David Hanks, a mycologist at Brigham Young University, who suggested that they might be mycorrhizal. This study was initiated to determine whether the root nodules on O. polyacantha are in fact mycorrhizal.

MATERIALS AND METHODS

Anatomy of Nodulated Roots

Nodulated roots of Opuntia polyacantha Haw. were collected in the spring and summer of 1968 from Juab County, Utah, Township 12 south, Range 4 east, Salt Lake meridian and base line, and were fixed in FAA (1:1:18). They were dehydrated through a t-butyl alcohol series (70%, 85%, 95%, 100%) and embedded in paraffin. Transverse and longitudinal sections (5-50 microns thick) of the nodulated roots were made on a rotary microtome. The sections were mounted with Haupt's adhesive and stained with safranin and fast green according to the techniques of Johansen (1940). Additional root material, both fresh and fixed, was sectioned (20 microns thick) on a freezing microtome and mounted in lacto-phenol with cotton blue according to Wastie (1965). The sections were examined microscopically to determine the nature of the nodules.

Epiphytic Fungi of Nodulated Roots

Plants of O. polyacantha were carefully dug up and the roots containing the nodules were cut into 4 cm lengths. Three lengths of root were placed in 250 ml of sterilized distilled water. Four such collections, each from a different

plant, were immediately taken to the lab where they were aseptically transferred to 250 ml of sterile distilled water. The solutions containing the roots were agitated for five minutes at high speed on a rotary shaker. The roots were transferred to another 250 ml aliquot of sterile distilled water and agitated for 15 minutes. The roots were washed seven more times with fresh 250 ml aliquots of sterile distilled water; three washes of 30 minutes, three washes of 60 minutes, and one wash of 120 minutes. After each washing 1 ml, 0.1 ml, and 0.01 ml aliquots of the wash water were plated on peptone dextrose agar (Table 1) containing 1:30,000 parts rose bengal to inhibit the growth of the more active fungi and streptomycin (30 ug/ml) to inhibit bacterial growth. After the final wash, the roots themselves were plated on the same type of agar. Ten days following inoculation, the fungal colonies on each plate were counted and isolated for identification.

Endophytic Fungi of Nodulated Roots

To isolate endophytic fungi, fresh nodulated roots were carefully washed in a mild detergent solution (Liquid Ivory) and were surface sterilized in 1-5% sodium hypochlorite (Clorox) for five minutes. Lengths of the roots 1-2 cm long were transferred aseptically to petri dishes (1 section/plate) containing autoclaved media. The media used were Czapek's sucrose nitrate agar, malt extract agar, Jensen's

agar medium, and peptone dextrose medium (Table 1). Rose bengal was added to all media, and streptomycin was added to one-third of the plates. Additonal plates were prepared using the four media listed above except that the media were modified by adding a polysaccharide which was easily extracted from Q. polyacantha (Spoehr, 1919) as the only source of carbon. Any fungus growing out from the root sections into the agar was isolated for identification.

Table 1. Composition of nutrient agars used in isolating endophytic fungi.

Ingredient	Agars			
	Czapek's	Malt extract	Jensen's	Peptone dextrose
Agar	15.00 g	25.00 g	15.00 g	20.00 g
Sucrose	30.00 g			
Dextrose		20.00 g	2.00 g	10.00 g
Malt Extract		20.00 g		
Peptone		1.00 g		5.00 g
Casein			0.20 g	
$NaNO_3$	2.00 g			
$MgSO_4.7H_2O$	0.50 g		0.20 g	1.50 g
K_2HPO_4	1.00 g		0.50 g	
KH_2PO_4				1.00 g
KCl	0.50 g			
$FeCl_3.6H_2O$			trace	
$FeSO_4.7H_2O$	0.01 g			
Water	1.00 l	1.00 l	1.00 l	1.00 l

Soil Analysis

Soil was collected from Township 12 south, Range 4 east, Salt Lake meridian and base line, and was sifted to remove debris. Some of it was autoclaved in three inch flats for five hours at 15 pounds pressure. Cactus stems of approximately equal size were washed in 1% NaOCl and placed on the soil to root. They were rooted in six inch clay pots under three different conditions. Some stems were placed on sterilized soil; some on unsterilized soil; and some on a 50/50 mixture of sterilized and unsterilized soils. All pots were brought to field capacity with tap water once every two weeks. After five weeks the roots which had developed were measured, washed in 1% NaOCl, and 1-2 cm sections of the roots were plated on agar as described above.

Samples of the soil were analyzed for total nitrogen using the Kjeldahl method (Lepper, 1945), for phosphorous using a molybdate reaction according to Truog (1930), and for potassium using the procedures of Volk and Truog (1934) which involves the precipitation of di-potassium sodium cobalt nitrate. The amount of organic matter was estimated from total nitrogen composition and from weight loss on combustion when the soil was heated to 650° for one-half hour. Mechanical analysis was obtained by means of a hydrometer.

RESULTS

Opuntia polyacantha Haw. typically has two types of roots. One type, large lateral roots, are only slightly branched and may never penetrate the soil any deeper than 10 cm, while reaching lengths up to several meters. They are covered with a thick, flaky periderm. These roots often have glochids produced in areole-like arrangement and, according to Harvey (1936), are capable of propagating stem shoots. Some secondary tissues develop around a polyarch protostele. The cortex is composed of large parenchyma cells which are with a mucilaginous material. Many intracellular crystals, presumably of calcium oxalate (Metcalf and Chalk, 1950), are also present in aggregates which measure 50-75 u in diameter.

Smaller, highly branched roots develop from stems or from lateral roots. The smaller roots penetrate deeper into the soil than do the lateral roots, and are, according to Preston (1900), responsible for most of the absorption of water and minerals. These roots have tetrarch protosteles and very little, if any, secondary tissue. The phloem is opposite the primary xylem points instead of alternate as is common in most dicotyledons (Fig. 1).

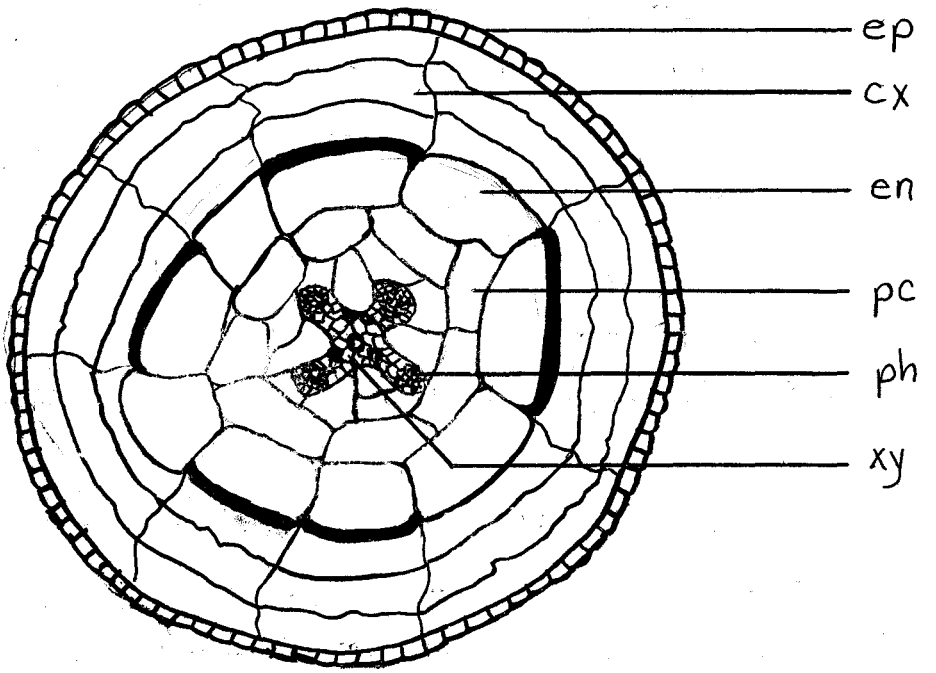

Fig. 1. Transverse section of a small root of Opuntia polyacantha showing epidermis (ep), cortex (cx), endodermis (en), pericycle (pc), phloem (ph), and xylem (xy).

Anatomy of Root Nodules

Nodules were found only on the smaller absorptive roots (Fig. 2). They were present on every cactus observed, and they persisted throughout the year. The nodules were all quite uniform in size, ranging in diameter from 0.3 to 1.0 mm and from 0.5 to 1.5 mm in length. The nodules contained a vascular trace which was connected to the vascular system of the main root and which was surrounded by large parenchymaceous cells. Small cells with large nuclei formed an apical cap. Calcium oxalate crystals were also evident (Figs. 3, 12).

Under certain conditions, the apices of the nodules became very active, producing one to several branch roots (Figs. 4-8). Older branches were found with remnants of nodulation.

Fungal mycelium was associated with the nodules. The hyphae were easily distinguished from the root hairs in that the hyphae were smaller (3 u compared to 8 u for the diameter of root hairs), much branched and septate. Also, the bases of the root hairs were much inflated (up to 40 u) whereas no such feature was associated with the fungus (Figs. 9, 10). The mycelium formed a mantle around the nodule which was 100-300 u thick (Figs. 11, 12).

Fig. 2. Nodulated roots of Q. polyacantha (natural size).

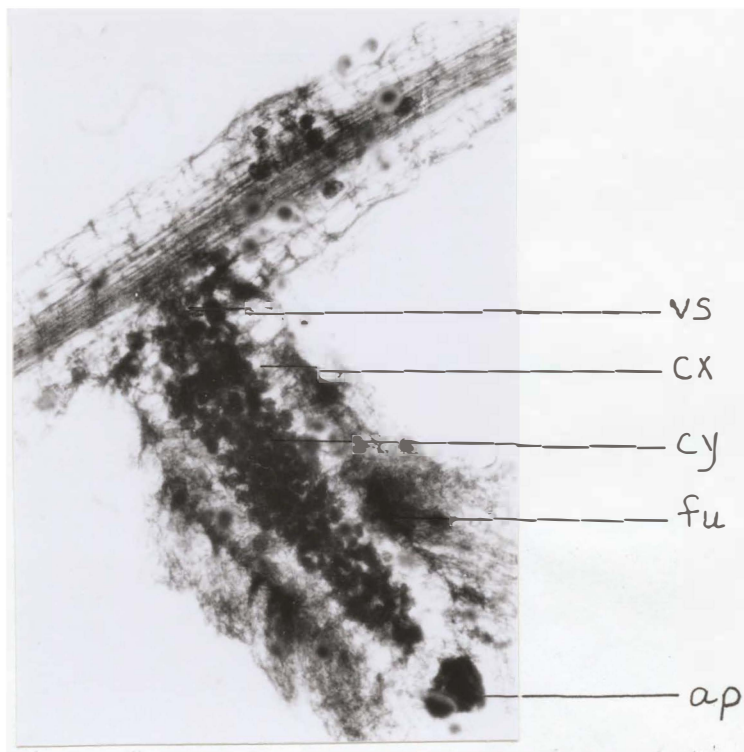

Fig. 3. Root nodule of O. polyacantha showing vascular system (vs), cortex (cx), apical cap (ap), crystals (cy), and fungal mycelium (fu). (x 90).

Fig. 4. Root nodule of O. polyacantha which has become meristematic. (x 50).

Fig. 5. Base of branch root of O. polyacantha showing remnants of nodule. (x 50).

Fig. 6. Branching habit of O. polyacantha root nodules. (x 50).

Fig. 7. Root nodule of O. polyacantha with two branch roots. (x 50).

Fig. 8. Mature roots of O. polyacantha showing four branch roots originating from a common area. (x 50).

Fig. 4

Fig. 5.

Fig. 6

Fig. 7.

Fig. 8.

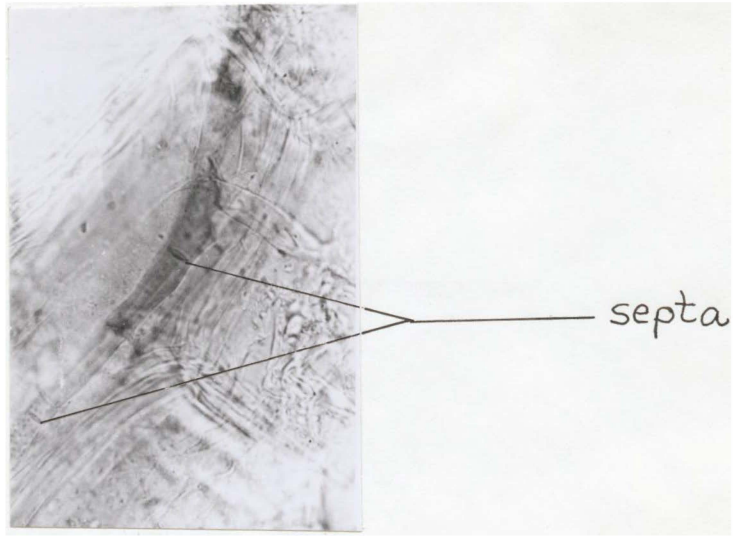

Fig. 9. Epiphytic hyphal strand on nodulated root of Q. polyacantha showing septations. (x 1,600).

Fig. 10. Root hairs of Q. polyacantha. (x 600).

Fig. 11. Whole mount of root nodule showing mantle and extended hyphae (x 50).

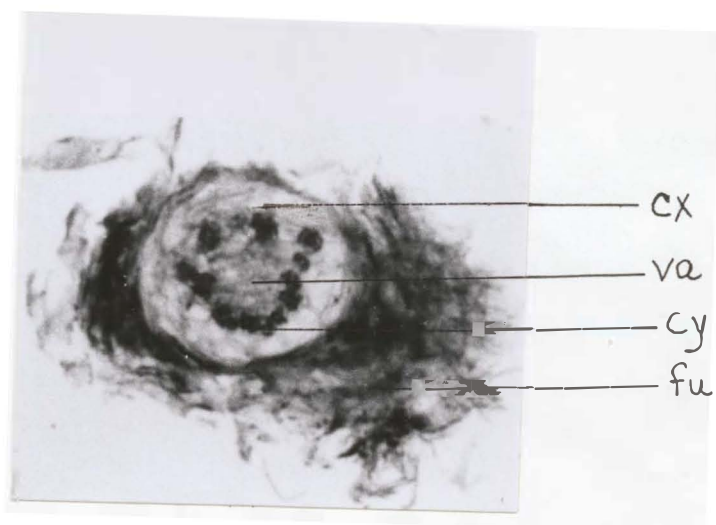

Fig. 12. Transverse section of root nodule showing mycelial mantle (fu), crystals (cy), vascular tissue (va) and cortex (cx). (x 50).

Endophytic Fungi of Nodulated Roots

Inasmuch as neither fruiting structures nor spores of the endophytic fungus were observed while it was in association with the roots, attempts were made to isolate the fungus so that it could be identified. Roots which were surface sterilized with sodium hypochlorite consistently yielded two types of fungus regardless of the medium used. The fungus most commonly isolated produced a woolly white mycelial mat on all media, and was bright red on the bottom. It produced a slightly pigmented sporodocium. Terminal and intercalary chlamydospores were produced. Large sickle shaped conidia with three transverse septae and smaller single celled oval conidia were produced in the sporodocium. The macroconidia were 35-40 u long and 4.5-6.0 u wide. The microconidia were 7-10 u long and 4.5-6.0 u wide. This fungus fits the description given by Gilman (1966) for Fusarium poae (Peck) Wollenweber except that the macroconida from the endophyte were somewhat wider than the dimensions (3.5-5.0 u) given by Gilman for the macroconidia of F. poae.

The second fungus which was isolated with some consistency from the surface sterilized roots formed a dark spreading mycelial mat on all media. The colony was black on the reverse side. Pigmented conidia with three transverse septae and one or two longitudinal septae were produced terminally on short septate conidiophores. The conidia were 22-30 u long and 8-10 u wide. Gilman's description of Stemphylium

piriforme Bonorden fits the endophytic fungus except S. piriforme is reported to have conidia which are 13-15 u wide.

It is assumed that the fungi isolated from the roots of O. polyacantha are Fusarium poae and Stemphylium piriforme. Positive identification, however, must await the opinion of an expert mycological taxonomist.

Roots which were initiated in unsterilized soil or in a mixture of sterilized soil and unsterilized soil all yielded Fusarium poae and Stemphylium piriforme, while none of the roots which were initiated in sterile soil yielded either.

Ephiphytic Fungi of Nodulated Roots

When roots were washed thoroughly, and no surface sterilant was used on them, only Fusarium poae was isolated from the roots which were plated on agar. The roots themselves were plated when the number of organisms washed from the roots per unit of time reached a minimum.

Soil Analysis

Roots which were initiated in sterilized soil were 10-15 cm long at the end of the five week period, while those initiated in unsterilized soil, or in sterilized soil which had been inoculated with unsterilized soil never grew over 3 cm long.

The soil in which the cacti naturally grew and which was used for initiating roots was 65% sand, 30% silt, and 5% clay. Weight lost on combustion was 1.5%. The soil analyzed contained 1.10% N., 0.08% P., and 2.03% K.

DISCUSSION

The evolution of ectotrophic mycorrhizae has generally been considered from two view points. Harley (1959) interprets the "mycorrhizal phenomena as a special case of rhizosphere effect." He wrote: "We are dealing, then, in ectotrophic mycorrhizae with a special case where, on a given root, one species of fungus in particular is so affected by local conditions as to become dominant in the root-surface zone." The mycorrhizal fungi, then, according to this view, are highly advanced saprophytes, able to compete in the rhizosphere to the exclusion of all other organisms. There is much evidence to support this view. The fact that there is virtually no intracellular penetration by the fungus suggests a saprophytic association rather than a parasitic one. Mycorrhizae are known to prevent further infection by root pathogens (Zak, 1964). Most of the fungi which are known to be mycorrhizal are also known to be saprophytic under certain conditions, and are often easily cultured in vitro.

An alternate point of view concerning the nature of ectotrophic mycorrhizae is proposed by Garrett (1956) who regards the association as a highly advanced parasitic one. He reasoned: "The efficiency of a parasite can thus be correlated directly with the degree of symbiosis that the parasite achieves with its host; amongst the root-infecting fungi, the

most successful parasites are the mycorrhizal fungi and especially, perhaps, the ectotrophic mycorrhizal fungi." A primitive parasite, according to this view, infects juvenile tissues, and is very destructive to the host. A specialized parasite infects the host after it has achieved some degree of maturity, and the destruction of host tissue is reduced and somewhat delayed. Ectotrophic mycorrhizal fungi have specialized even more. They may cause hypertrophy, but do not otherwise disrupt host tissue.

If mycorrhizal fungi are in fact highly specialized or obligate parasites rather than specialized saprophytes, it becomes necessary to reconcile this habit to the ease with which they are cultured in vitro. Garrett reasoned that the term "obligate parasite" as it is commonly used is not so much an objective biological definition as a subjective admission of human failure to culture an organism in vitro. Perhaps a better concept of a specialized parasite would be one of an "ecologically obligate parasite." An ecologically obligate parasite can become saprophytic in vitro only in the presence of certain essential elements and in the absence of competition from more active saprophytes. Mycorrhizal fungi may be obligate parasites in nature and still be induced to grow saprophytically in vitro.

The view points of Harley (1959) and Garrett (1956) are not necessarily incompatible. It is very likely that mycorrhizae represent a transitional stage between a sapro-

phyte and a root parasite. Any evidence which would indicate such a transition would be both enlightening and novel. For this reason the study of nodulated roots on Opuntia polyacantha is of particular interest.

Root nodulation as the result of mycorrhizal infection is not unknown. Under Melin's classification of ectotrophic mycorrhizae (see Harley, 1959) Type C mycorrhiza was described as "nodules formed of short root branches which are enclosed in a sheath system, yellow-grey in color. From the sheath trailing hyphae run into the soil. This type of mycorrhiza, even when relatively little developed, is characterized by the thick yellowish mantle." The nodules on O. polyacantha fit this description very well in that not only are they branch roots, as is evidenced by the vascular system, but they are covered with a fungal mantle from which hyphae trail into the soil. Cross sections of the nodules show striking resemblance to the photographs of Fagus mycorrhiza published by Clowes (1951, 1954). Anatomically the nodules on O. polyacantha resemble ectotrophic mycorrhizae.

Mycorrhiza, as a symbiotic association, is a physiological concept. It denotes that the root and the fungus both receive mutual benefit from the association. Such physiological relationships were not investigated in this study. However, the data from this study are not disharmonious with the hypothesis that the nodules are actually mycorrhizae.

As Garrett (1956) pointed out, the mycorrhizal fungi are sugar-parasites. They are most likely to be successful in attacking a root when excess soluble sugar is available in the root. O. polyacantha roots have abundant carbonhydrate. The cortical cells are filled with a mucilaginous polysaccharide, probably the same as was found in stem tissue of Opuntia sp. by Spoehr (1919).[1]

Mycorrhiza are most likely to be formed in soils which are deficient in nitrogen, phosphorous, potassium, or calcium, or which have an imbalance of these nutrients (Melin, 1953). The desert soils of Juab County, being poor in nitrogen and phosphorous, would certainly predispose O. polyacantha to fungal attack.

It is doubtful that the fungal association on O. polyacantha is wholly pathogenic when one considers the relatively little damage which the fungus imposes on the host tissue, and especially that the cactus plant as a whole appears healthy even when severely infected with the fungus. The very fact that every cactus plant in the area is able to grow successfully and complete its life cycle while supporting the fungus also suggests that the association is mycorrhizal.

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[1]Spoehr (1919) reported a polysaccharide in species of Opuntia which upon hydrolysis yields d-galactose and l-xylose. He reports for l-xylose $[\alpha]^{20}_{D}$ +20.0°. Merk Index, 8th ed. reports l-xylose as being levorotatory, but for d-xylose $[\alpha]^{23}_{D}$ +18.6°. The mucilaginous carbonhydrate reported, therefore, is probably a polysaccharide of d-galactose and d-sylose.

There are, however, several aspects of the cactus-fungus association which are not strictly characteristic of ectotrophic mycorrhizae. Firstly, Fusarium poae which was consistently isolated from the nodules of O. polyacantha is not known to form ectotrophic mycorrhizae. Indeed, there are no Deuteromycetes other than a few Mycelia Sterila known to form ectotrophic mycorrhizae. Fusarium, however, is notorious as a root pathogen. Secondly, while mycorrhizal fungi typically stimulate root growth, the micro-organisms associated with the roots of O. polyacantha tend to retard root development. With these organisms removed from the soil the roots may develop five times more rapidly than when the organisms are present. Thirdly, when the nodules resumed growth by producing several branches, their growth habit was more suggestive of certain pathogenic growths than of normal mycorrhizae.

Inasmuch as F. poae has not been shown to be the same fungus seen on the nodules, and because the nodular fungus is not necessarily the organism which retards root growth, one could still properly identify the nodule as an example of mycorrhiza. Nevertheless, the third problem is real and significant. Never has an example been reported of a mycorrhiza recovering from the fungal attack by producing adventitious roots. Root elongation is usually attributed to the apical meristems of uninfected roots. On the other hand, such growth is not typical of root diseases. Hypertrophy is reported in hairy-root and crown gall, both of which are bacterial diseases, but neither of these resemble the growth

habit on cactus. Furthermore, unlike typical root pathogenic associations, there are no intracellular hyphae.

It is not improbable that the fungus-root relationship found on Opuntia polyacantha represents a stage in the development of mycorrhizal associations where a weak facultative parasite and a host tissue approach a symbiotic equilibrium. The fungus, attacking the young branch root, is unable to penetrate the host's defense system. Nevertheless, it exerts enough influence to temporarily arrest the growth of the root. When the root is in this condition, it is mycorrhizal. Only when the cactus is grown under ideal conditions, such as occurs in the spring and early summer, or is provided in a green house environment, can the roots overcome the fungal inhibition and resume growth. When the conditions are no longer optimal for the host, the fungus is able to reinfect.

It is possible that many ectotrophic mycorrhizae result from the stabilization of a relationship wherein the fungal symbiont is not able to completely penetrate the host's defense system, but the vascular symbiont is unable to completely escape infection. The stabilization of such a relationship is accomplished by each symbiont developing means by which it can benefit from the association.

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ABSTRACT

Roots of *Opuntia polyacantha* Haw. from Juab County, Utah were found to be nodulated. An anatomical study of the nodulated roots showed them to be ectotrophic mycorrhizae. *Fusarium poae* (Peck) Wollenweaver was found associated with the nodules both as an epiphyte and an endophyte. However, reinfection with this organism failed to induce subsequent nodulation.

Under certain conditions the roots of *O. polyacantha* are able to overcome the mycorrhizal infection and elongate. It is not uncommon for several branch roots to originate from a single nodule. It is suggested that the fungus-root association found in *O. polyacantha* represents an early stage in the evolution of ectotrophic mycorrhizae.