RELATION OF MYCORRHIZA TO CONIFERS
and
IMPORTANCE IN CONIFEROUS PLANTINGS

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PREFACE

It is not the intention of the writer to present new material on the subject of maycorrhiza in this thesis, but rather to present in as far as he is capable a fair interpretation of the subject through wide and judicious readings in this field. It is unfortunate that the writer does not possess the ability to read German and French as some of the best works relating to the subject are written in these languages.

The material used in writing this thesis was obtained through the facilities of the Oregon State College Library, supplemented by pertinent works loaned through the courtesy of Dr. Hatch of the Oregon State School of Agriculture, to whom the writer is indebted for much kind assistance.

Ivan W. Cowin

INTRODUCTION

The establishment of nurseries and the transplanting of timber and allied species of conifers in other than their natural habitat is becoming one of the major problems in forestry of today. This is illustrated by the Shelter Belt planting project in the United States and the wide-spread plantings that are being carried out in various countries throughout the world. That this operation is not as simple as once believed can be easily seen by a review of the current literature on the subject. The many failures resulting from attempted plantings and establishment of nurseries have been of value in adding to the meager store of knowledge relating to the survival of seedlings and transplants. It is true that very efficient methods of evaluating the site have been evolved, but these have in many cases been proved practically worthless through the failure to consider one factor. It was until recently believed that to determine the suitableness of any given site for a certain species required the evaluating of the following primary factors: climate, the character of the soil, and the adequacy of the cultural operations. However, plantings made upon this basis have in certain instances failed. The result is that a certain biological soil factor is coming to be viewed with suspicion as being accountable for the success or failure after the primary factors listed above have been carefully weighed and found to be present in the right degree. Many authorities on tree culture admit the vast influence of a certain biological soil factor, and several have become convinced that its identity is mycorrhiza.

The existence of mycorrhiza has been known for over half a century, but the belief of it being a large factor in seedling survival is of rather recent origin. Since the close of the 19th century there has been an ever increasing amount of research carried out in the attempt to prove the relationship of mycorrhiza to the host and to evolve practical methods that will be applicable to the problems of the forester engaged in this field. The surface in this line of endeavor has been barely scratched and each new method of approach to the problem reveals new factors that must be investigated in order that a practical solution with working results may be reached.

REVIEW OF MYCORRHIZAE

A. Introduction to Mycorrhiza

The easiest approach to an understanding of the role mycorrhiza play in seedling growth and survival was deemed to be in first presenting to the reader a review of the organism constituting this growth in order that he might have before him a clear picture of the plant phenomena discussed in this paper.

It was in 1885 that A. B. Frank first coined the word mycorrhiza to describe a root formation of plants possessing a regular and characteristic infection by fungal mycelium. Hence the word mycorrhiza in its derivation means fungus-root, or in other words, a fungus growing associated with a root. Thus mycorrhiza are structurally composed of the root of the host and a fungus mycelium. It may be recalled that fungi constitute that group in the plant kingdom which are characterized by being unable to manufacture their own food, owing to the lack of the green coloring matter known as chlorophyll. In other words they are dependent plants in that they have to depend upon either living or dead matter for food. The vegetative body of fungi is the mycelium. Mycelium is a term employed to designate collectively the vegetative hyphae of the fungus. Hyphae in turn are comparable to minute hairs or for the student of botany, more aptly to filaments or strands of some green algae whose tubes are characterized by the absence of crosswalls and lined with a continuous protoplasm containing many nuclei. For the benefit of the layman who may have become confused by this rather rapid broadside of terms, a homely illustration may be drawn by comparing a fungal mycelium to a piece of cloth in which the individual threads are thought of as the pipe-like structures called hyphae and the whole as being the mycelium.

In accordance with the position of the mycelium in relation to the root, mycorrhiza are classified into three groups, namely endotrophic, ectotrophic and ectendotrophic. The endotrophic type of mycorrhiza according to Kelley (7) is characterized by the fungus entering the root by means of the root hairs and passing through the cells of the cortex forming a zone of infected tissue. Individual hyphae may be scattered or twisted about one another within the cell, or they may be woven into skeins until they appear to be a mass of threads. Often the hyphae are broken into short fragments or have the appearance of large granular introcellular masses, which according to various authorities, represent hyphae that are being digested by the host cells. The individual hyphae are not confined to any one cell, but often extend from one root cell to another. The mycelium is usually considered in this case to be confined only to the cortex. Externally the roots are swollen at the tips and branch dichotomously (by forking) or they appear to have bead-like constrictions borne singly or in pairs. The distinguishing characteristic that should be borne in mind in regard to the endotorphic type of infection is that the hyphae penetrate into the interior of the root cells.

The ectotrophic type as contrasted to the endotrophic is characterized by the hyphae penetrating the root through the epidermal cells and advancing between the cell walls of the primary cortex until a network (known as the Hartig net) is formed around the cortical cells; the infection seldom progressing inward beyond the endodermis of the root. The root cap is reduced to a few cells owing to the fungal mat preventing further growth in length, this in turn giving rise to the development of lateral roots which in turn are infected. Externally this type is characterized by the mycelium forming a sheath in a manner to completely cover the root except for the growing tip, with individual strands of hyphae protruding from the main mass in a manner closely resembling root hairs. Owing to the effect of the sheath, root hairs are absent, making it appear that the sheath and the protruding hyphae carried on the functions of absorption. When viewed with the unaided eye, there may be seen groups of many short roots at the tip of a larger one, giving the appearance of a cluster of corals, from which is derived the term coralloid for this form. However the outstanding characteristic of this type of association is that the hyphae nearly always grow between the cells of the cortex, never penetrating the cell walls as was the case in the endotrophic mycorrhiza.

The presence of a third type of mycorrhiza is disputed by some authorities. It was named ectendotrophic by the investigators that are inclined to believe in its existence. This type represents a gradation between the endoctorphic and ectotrophic in that it grows inside of some cortical cells while between the walls of others. The opponents to this third class base their contentions on the fact that a distinct line cannot be drawn between the two types that are accepted by all, and for this reason the third type is not worthy of a classification due to the various gradations that are to be found. From this it may be concluded that the third form is to be accepted tentatively until agreement is reached on whether or not it is a type distinct to the extent of warranting classification.

There is in addition to the three forms discussed another class worthy of note. This is pseudomycorrhizas or false mycorrphiza. The mantle is usually thinner than in true mycorrhiza, and the Hartig net is absent.

B. Causative Factors in Forming Mycorrhiza Types.

The study of mycorrhiza types is not complete without viewing the factors concerned with the formation of the respective types, i.e. endotrophic, ectendotrophic or ectotrophic

However there are several conflicting beliefs as to the nature of the factor that is responsible for the variance of fungus roots. It was therefore deemed wise to present the more outstanding theories without attempting to arrive at any conclusions. Melin, an investigator in this field, carried out experiments on pine, spruce, and larch . From his findings he arrived at the conclusion that the different types of mycorrhiza represented different stages in the infection by the same species capable of forming these types. The order of succession was found to be that the initial infection gave rise to the endotrophic form. This was replaced by the transitional stage of ectendotrophic infection which carried through to the final stage or ectotrophic. The physiological explanation of this phenomena is the activity of the root cells in digesting the hyphae and consequently elimination them until all that remains is the external and intercellular investment of mantle and Hartig net.

The theory of "virulence" is another notable view as relating to the type of infection formed. This contends that the type of infection is determined by the strength of the fungal strain. Fungal strains that have been weakened by continual growth under unfavorable conditions such as in sterilized humus or on a substratum of unsuitable H-ion concentration, can cause only endotrophic infection. The more vigorous strains that are the result of better growth conditions are capable of producing the intercellular net together with a well developed external mycelia sheath or mantle. The conclusion to be drawn from thesetwo theories is that definite facts relating to the explanation of a particular type of infection are not at present forthcoming, and will not be available until sufficient research on this question has been accomplished to allow the investigators to reach an agreement.

C. Functional Relation of Mycorrhiza to Host.

The most important as well as the most interesting phase in the study of mycorrhiza, both from the standpoint of the researcher and the forester engated in tree planting, is the relation of mycorrhiza to the tree or host. The question of the character assumed by this relationship has been the subject of mucy speculation and experimentation, the results of which have been rather diverse and have given rise to a variety of conclusions. The claims of various workers as pertaining to the true nature of the relationship existent may be roughly classified as : (1) that all cases of infection are a relation of one-sided parasitism in favor of the fungus; (2) that there exists a relationship of mutual benefit between the two organisms, and (3) a partial combination of one and two in that one-sided parasitism and mutual benefit are confined to a given mycorrhizal type. The more recent investigators appear to be acclaiming the third view as describing the true nature of the role played by mycorrhiza. In view of this fact it is assumed that the third condition is the proper one to accept in dealing with the question.

The mycorrhiza types believed to result in mutual benefit to the tree and to the fungus organism are endotrophic, ectendotrophic, and ectotorophic; the degree of benefit being increasingly greater with order of listing the types. The type that is directly harmful to the host through its one-sided parasitism is the pseudomycorrhiza.

The side of the question that appears to best withstand the test of experimentation is that mycorrhiza are related to the host in a manner analogous to the relationship existing between the leguminous plants and the bacteria contained in the nodules on their roots. In the case of mycorrhiza the fungus organism makes available or fixes certain soil nutrients in a form that enables or facilitates their utilization by the host, combined with the fact that in the case of the ectotrophic type a more efficient absorbing organ than the rootlet is formed. This of course results in improved growth of the host plant, especially when growing on a soil whose character makes the obtaining of mineral nutrients a somewhat difficult function. In turn for its activity the fungus organism receives food from the tree. As fungi do not contain chlorophyll it is essential that they obtain food for continued activity either from living or dead matter. Thus is seen to be illustrated the case of mutual existence, with one organism giving and receiving benefit from the other.

The organ produced by the ectotrophic type might well be worthy of discussion. It may be recalled that in the growing tip of the normal root there is a relatively small area which bears root hairs. This region moves progressively forward with the growing root tip: the root hairs on the older portion of the root dying, so there is at any one time only a relatively small area of actively functioning root hairs. It may also be recalled that the ectotrophic infection formed a sheath completely enclosing the root, and that certain individual hyphae protruded from it in a manner resembling root hairs. In contrast to the uninfected root structure the advantage of infection by the ectotrophic type of mycorrhiza can be readily seen. In the first place the mantle and individual hyphae are believed to be as efficient absorbing structures as a comparable area of root hairs. Secondly this structure does not follow a series of new growth regions but remains alive on the older portion of the root while growing with the root in the newer portion. It must be admitted that this activity results in curtailing the growth of each individual rootlet which in turn causes a new one to appear in a manner analogous to the branching of deciduous tree species that lack a terminal bud; and in addition to this that only the roots in the top six inches of soil are infected. However, if this phenomena works in itself as a detriment to the host, the other benefits of infection appear to overbalance this disadvantage as has been found by improved growth in the presence of infection. From the standpoint of the surface for absorption alone, the advantage of the mantle may be demonstrated in view of the above facts. First there is a continual living sheath that occupies a much larger area for absorption that the root hairs, and secondly individual hyphae protrude from the sheath and are believed to carry on absorption.

The physiological factor relates to the ability of the membrane to allow certain nutrients to pass through it.

The membrane is believed to have a higher degree of effeciency in absorbing certain soil solutes; namely, nitrogen, potassium, and phosphorus, than the root hairs. It is without doubt needless to state that if any of these elements are not available to the tree in sufficient and usable quantities inferior growth will result. The theory of "fixation" of certain elements in a manner comparable to the nitrogen-fixing bacteria on the leguminous plants is a tentative consideration of the role played by mycorrhiza. However the general census of opinion appears to be that if mycorrhiza do carry on this function, it is relatively of minor importance as compared to the two listed above.

It can therefore be concluded that the functional relation of mycorrhiza to the tree-host is an association of mutual benefit with a distinct advantage for growth. This is brought about through a greater expanse of absorptative surface and the presence of a membrane that is more permeable to certain essential soil solutes than root hairs.

EFFECT OF MYCORRHIZA IN NURSERY PLANTINGS

The criticism may be justly made that the theories relating to the functional role of mycorrhiza have been proven under the controlled conditions of the laboratory and the results are therefore not in keeping with what might be expected to take place in the natural habitat. It is true that abnormalties have developed in the laboratory experiments which have given rise to different growths than found in nature, but if the subject is looked at in the broad light of "do mycorrhiza benefit their host?" the answer will be interpreted to favor the affirmative by the following review of nursery and plantation failures in various widely separated regions throughout the world.

In Western Australia difficulty was experienced in raising pine on new nursery sites (8). The germination of seed was excellent but the seedlings were found to grow poorly after reaching a height of from one to three inches. The foliage was characterized by "an unhealthy yellow color with dwarfed needles". An explanation was sought through investigating the influence of the season of sowing, irrigation, shade, soil acidity or alkalinity, and fertilizers. These were found to have little effect on bringing forth better growth. The possibility of disease was eliminated by microscopical examination of the seedlings. The possibility that young pine might depend on a certain soil organism was next investigated. In connection with this, it had been noted that healthy pine seedlings taken from older nurseries showed on their roots the coral-like development of mycorrhiza, and that the nurseries growing this successful stock had a network of fungus mycelium extending throughout the top layers of the soil and closely associated with the pine roots. An experimental plot was set aside on a newly established nursery that showed all signs of failing. This plot was inoculated with soil taken from old pine nursery. "This treatment resulted, after several months in all the remaining pines gradually assuming a healthy green color and later showing virourous growth. No deaths occurred in the second summer". It will be noticed that this example does not conslusively prove mycorrhiza to be the controlling factor although it does indicate that the success of the experiment was due to the infection of the soil with a species of fungus acting together with the seedling roots.

The Rhodesian nursery failure (15) offers another example similar to those of Western Australia. In this the pines never attained a height over 4 inches, characterized by being yellowish and weakened. Remedies attempted along the same lines as those in the Australian nurseries resulted in little if any improvement in growth. The seed beds were then inoculated with soil from successful sites; the results obtained being comparable to those in the Australian nurseries. To further test the soundness of this procedure, seedlings bearing mycorrhiza from the treated seedbeds were transplanted to the plantations and grown adjacent to non-mycorrhizal seedlings planted two years earlier. In nine months the seedlings bearing mycorrhiza had attained a height of 13 inches while the nearby non-mycorrhizal plants were still less than 4 inches in height. Small quantities of soil known to contain mycorrhizal fungi were then worked into the seedbeds containing the seedlings left over from previous plantings, and in the short space of a month these treated plants changed to a dark green color and began rapid growth.

In addition to the two preceeding cases a still more striking example is seen in the attempts to extend the range of Pinus insularis in the Phillippine Islands. (13) This species of pine which is the most valuable softwoods in the islands, grows normally at a high altitude. In 1909 the first attempts were made to extend its range to the lowlands by planting seeds in a nursery at Los Banos. Normal germination was obtained but the growth of seedlings was poor, resulting eventually in one hundred per cent mortality. The attempt was repeated at intervals with the same results. Seeds of this species were sent to South Africa and the Hawaiian Islands where the same failures were encountered with lowland plantings, although success was obtained by planting at higher elevations. In the years of 1919, 1922, 1927 and 1929 potted seedlings were transported from the natural highland habitat to the lowland. These seedlings grew vigorously, averaving over a meter a year or nearly twice that of the species in its natural habitat. The inoculation of seedbeds in the Los Bonas nursery with soil taken from around the roots of these original potted seedlings has brought forth success in subsequent plantings.

It must be admitted that due to the lack of research in these cases, the phenomena observed in the effect of soil inoculations cannot be laid directly to mycorrhiza in the sense of excluding all other soil organisms. However, as mycorrhiza have been found in other instances to be of benefit to certain tree species, and owing to the fact that mycorrhiza were found to exist in these nurseries together with the fact that no other soil organism is known to have similar relations to the tree, it is only logical to conclude that mycorrhiza were the determining factor in the success or failure of these plantings.

MYCORRHIZA INOCULATIONS

It might be well to give a few "hints" on the manner in which seedlings may in the future be given the aid of mycorrhiza. The methods outlined should be tentatively considered as at present there has not been enough work accomplished in this line to give any cut and dried procedure. The possible methods that may be brought forth in the future fall roughly into two groups. In the first group the spores or fruitifications mycorrhizal fungi would be introduced into the new sites either by inoculating the soil before planting or by introducing the fungal bodies with the seed. The second group would be that in which the uninfected sites are incoluated with the vegetative part of the fungus such as mycelium through some such means as soil mixing. However only through future research will the best methods of introducing mycorrhizal infections be obtained.

CONCLUSION

In concluding it should be remembered that mycorrhiza bear a definite relation to the tree species and that this relation is of a beneficial nature in all cases of true mycorrhiza. Also, that there is still a great deal of conflict between the various authorities as to the extent of benefit derived from mycorrhiza, but which appears to be rather great if one stops to consider the practical data given in the material relating to nursery studies. It can be readily seen that the field of mycorrhizal studies as practically applied to the problems of forestry has been barely scratched, and that only intensive and extensive research in the future will place in the hands of the forester a useable instrument for insuring success in his plantations. If this work continues at its present rate, not many years should pass before an essential part is supplied to the knowledge of tree planting.

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