MODERATOR FURUTA: Our first speaker will be Dr. Robert Linderman, USDA plant pathologist of Corvallis, Oregon, who will tell us something of his work on mycorrhizal fungi. Dr. Linderman.

POTENTIAL USE OF MYCORRHIZAL FUNGI TO ENHANCE GROWTH AND ADAPTABILITY OF ORNAMENTAL PLANTS

ROBERT G. LINDERMAN

Ornamental Plants Research Laboratory USDA/ARS - Oregon State University Corvallis, Oregon 97331

Healthy rootlets of most vascular plants grown in natural soil are inhabited by non-pathogenic, probably beneficial, fungi living in a state of symbiosis with the plant root. Roots so inhabited are called mycorrhizae, "myco" meaning fungus, and "rhiza" meaning root. Such mycorrhizal associations in nature are the rule, not the exceptions and further, in ornamental horticulture, we have not paid attention to these associations which most mycorrhizologists feel are indispensible for the survival and well-being of the host plant (not to mention that of the fungus).

The first objective in this discussion is to present a brief explanation of what mycorrhizae are. Then we will consider how mycorrhizae function and what they can do for a plant. Lastly, we will consider mycorrhizae in terms of the propagation and growth of ornamental plants.

What are mycorrhizae? A mycorrhiza is a symbiotic association between a non-pathogenic (or weakly pathogenic) fungus and living, primarily cortical cells of a root. It is this symbiotic association, i.e., the living together (and benefit derived therefrom) of these two unlike organisms, which is the core of this discussion. In a broad sense, these root-fungus associations fall into the same physical and biological realm with all other root infections, including those by pathogens. The main differences are that pathogenic root infections are the exception, rather than the rule, and result in deleterious effects, whereas in nature rootlets not invaded by fungal or bacterial symbionts suffer deleterious effects. Nevertheless, there are certain parallels between pathogenic and symbiotic root infections.

The presence of mycorrhizae or mycotrophic rhizomes predates higher plants, according to the fossil record. These early nutritional systems apparently have evolved differently with different hosts. A higher dependency on mycorrhizae evolved with the development of a higher shoot: root ratio, and with a decrease in root hairs, i.e., plants with less profuse root hairs or root hairs that do not persist have become more dependent on mycorrhizae. The extreme in dependence on mycorrhizae is seen in the achlorophyllous plants such as Monotropa.

If we look, then, at the result of evolutionary selection of mycorrhizal symbionts with their hosts, we note that three major types of mycorrhizae have evolved. There are ectomycorrhizae where the mycorrhizal fungus is confined exclusively to intercellular spaces of root cortex. These mycorrhizae typically have a thick mantle of fungus around the root tips, and often have hyphal strands extending out into the soil. By contrast, the fungal symbiont of endomycorrhizae is confined exclusively to the intracellular spaces of root cortical cells. Some of these fungi are called vesicular-arbuscular because they form vesicles and arbuscules within the cells. Members of the genus Endogone (or Glomus) make up the majority of the known endomycorrhizal associations. These fungi have an extensive mycelial system extending out into the soil surrounding the root and usually form abundant chlamydospores near the surface of the root. A third group, the ectendomycorrhizae combine some features of the first two groups. Here the mycorrhizal fungus occupies inter-cellular spaces of the root cortex, but also may penetrate some of the adjacent cells and may have some hyphae in a loose mantle around the root.

How do mycorrhizae function? In order to establish an association with a compatible host, a fungal symbiont must go through the same process that a potential fungal pathogen must in order to parasitize its host. As James Trappe has pointed out, "The formation of a given mycorrhiza is the end product of a selective process in which the total number of potentially successful fungi is reduced to one successful symbiont (or occasionally a few), provided that the susceptible root is not first attacked by a pathogen". The potential symbiont must first produce viable mycelium in the root vicinity. This usually would involve germination of spores or resting hyphae. This mycelium must make its way through the rhizosphere, which is the region of soil surrounding the root in which the microflora is influenced by the root. This region is the most critical to any prospective root invader in that it may contain the needed stimulants and nutrients to sustain the invasion, but it also contains the highest number of competitors capable of suppressing the invasion. Finally, if the mycelium of the potential symbiont gets through the rhizosphere, it must invade the root tissue. Prior to penetration and to a balanced extent after penetration, the host may produce metabolites which prevent infection or result in the fungus and host arriving at a state of symbiosis. From that point on, the partners must give and receive benefit from their association.

In general it is thought that the fungal symbiont benefits from its association with a host plant by getting carbohydrates produced by the plant and translocated to the roots. In addition, it benefits by having a protected place to live and complete its life cycle which may involve production of resting spores or its fruiting structures (mushrooms).

More important to our discussion, however, is how the plant may benefit from its association with a fungal symbiont. The literature in this area is extensive, and my intent is only to draw attention to these benefits in a general way. I visualize plants benefiting from mycorrhizae in several categories: 1) water and nutrient uptake, 2) detoxification of soils, 3) altered root morphology and physiology, 4) protection against root pathogens, and 5) other benefits as yet undiscovered. Admittedly, these accomplishments are tremendous, and, to be sure, no one fungal symbiont can contribute all these benefits to its plant associate. Rather, certain fungal symbionts can do one thing well, and others, something else.

· In terms of water and nutrient uptake, mycorrhizal plants are more efficient than non-mycorrhizal plants. This is due, in large part, to the increased opportunity for uptake by mycorrhizae because of the increased absorptive surface area. The surface area of mycorrhizae themselves is greater than non-mycorrhizal roots; but in addition, the hyphal network extending out from the roots into the soil to more distant sources of available nutrients or moisture, makes the mycorrhizal root system very efficient. Many experiments have been performed which demonstrate the increased efficiency of mycorrhizae for nutrient uptake from nutrient-deficient soils in terms of growth responses or using the quantitative measure of radioactively labeled nutrients. On nutrient-rich soil, the establishment of mycorrhizae and the subsequent growth benefits are much less striking. Ectomycorrhizae are known to absorb especially phosphate, but also potassium and alkali metals more efficiently than non-mycorrhizal roots. Endomycorrhizae, at least the vesicular-arbuscular types, are thought to also be efficient in P uptake, but also in uptake of copper, iron, and calcium.

In recent years, mycorrhizal plants have been grown on extremely nutrient-poor soils. But even more striking is the establishment of mycorrhizal conifer seedlings on soils too toxic to support any vegetation. The work of Don Marx in the southeastern U.S., using the ectomycorrhizal fungus, *Pisolithus*, to establish pine trees on mining-spoil sites, is a classic example of the ability of at least one mycorrhizal fungus to de-toxify soils too toxic for non-mycorrhizal plants to survive in.

Another major benefit resulting from many mycorrhizal infections is the altered physiology and morphology of the roots. Various researchers have demonstrated, though indirectly, that ec-

tomycorrhizae produce growth hormones and growth regulators when in association with the plant, and these substances are responsible for the altered metabolism and growth of mycorrhizal roots compared to non-mycorrhizal roots. These substances, auxins and cytokinins, can mimic the physiological and morphological changes which occur in mycorrhizal roots; i.e., bifercation of root tips, proliferation of roots, enhanced rooting of cuttings, cytological changes (hypertrophy), etc.

The last function of some mycorrhizae, which has received more attention in recent years, is the capacity of ectomycorrhizae to resist attack by certain soilborne fungus pathogens. Several mechanisms of protection have been proposed and explored by Zak and by Marks in recent years. These mechanisms are: 1) production of antibiotics by the fungal symbiont which inhibit or retard potential root pathogens; 2) mechanical barrier created by the fungal mantle of ectomycorrhizae; 3) production of chemical inhibitors by the host; 4) differences in chemical root exudation by mycorrhizae; and 5) establishment of protective microbial rhizosphere populations. Without delving deeply into any of the evidence supporting each of these mechanisms, let me say, as did Marks (3), that in all probability, most of the proposed mechanisms of root protection of mycorrhizae against root pathogens may be functioning simultaneously since several are inseparable. The evidence suggests that ectomycorrhizae are more resistant to attack than are non-mycorrhizal roots, but there is still insufficient knowledge to say precisely how the system works. In addition, there is no evidence to suggest any protection of endomycorrhizae against root pathogens.

I believe there are still many other functions of mycorrhizae which are as yet undiscovered. The number of findings probably is a function of the number of interested hunters.

I would now like to address the problems of introducing the concept and then the mycorrhizae into the culture of ornamental plants. During the last year, I have developed a growing enthusiasm for the whole idea of using mycorrhizae to benefit growth and adaptability of ornamental plants. That enthusiasm originated in my desire to understand mother nature's way of doing things relative to the ecology of soilborne fungi. Our whole approach has focused strictly on what to do to hold down the harmful fungi, but at the same time we have ignored our potential allies, the mycorrhizal fungi, which are true soil inhibitants just as are many fungus pathogens. My point is that if we are intent upon growing healthier, more adaptable plants, then we must broaden our view to those organisms which are good for the plants as well as those that are bad. The result is that we must alter our cultural practices to take both good and bad organisms into account. We have two alternatives: 1) eliminate the pathogens from soil without eliminating the mycorrhizal fungi, or 2) eliminate all organisms from the soil and then re-introduce only the mycorrhizae

(or other beneficial organisms). Since many nursery pathogens are the same types of fungi as some of the mycorrhizae, it is difficult to eliminate one and not the other. The second choice of eliminating all organisms and then inoculating with beneficial organisms like mycorrhizae seems the more fruitful choice. But let me explore the state of the art relative to inoculating soils used to grow ornamental plants.

Several techniques have been proposed or used to inoculate nursery soil with mycorrhizae. We could introduce mycorrhizae into nurseries by adding soil from natural forests, plantations, or old nurseries, any of which would contain mycelium or spores of one or several ecto- or endo-mycorrhizae. One could also introduce seedlings grown in mixed mycorrhizal soils. There are several obvious pitfalls to these methods. First, you would be introducing an unknown mixture of mycorrhizae, some of which might associate with your crop, others which would not. At the same time, you might also introduce pathogens which could associate with your crop. The only way to avoid these problems is to grow the desired symbiont in pure culture and then introduce that inoculum into the growth medium or soil. Of course, the logistics of mass-producing inoculum of slow-growing ectomycorrhizal fungi is a problem to be reckoned with. And, if vesicular-arbuscular endomycorrhizae are needed, the problem is greater, or at least different, since these fungi cannot be routinely cultured. Spores of these fungi can be produced, however, in so-called "pot culture", wherein the inoculum is built up on a host and the soil containing the spores, free of pathogens, is transferred to the growth medium or nursery soil. Once produced, allowances must be made for shipment and storage of the inoculum.

Assuming we could introduce appropriate mycorrhizal inoculum into the growth medium or nursery soil, we must give consideration to promoting the development of mycorrhizae. We may have to change our whole way of thinking relative to frequency of watering; rates and frequencies of fertilizer applications; rates, kinds, and frequencies of fungicide applications; growth temperatures; light; soil mixes; etc., etc., etc. To make these adjustments, however, would not necessarily be uncomfortable since several could mean substantial financial savings during production, and increased profit at market since you would be selling a healthier plant, more able to adapt to its ultimate planting site.

The challenge before us, then, as Bowen has stated, is to "Select a fungus with as many high performance characteristics as possible, e.g., nutrient uptake, disease resistance, growth factor production, ease of introduction, and persistence". If we can learn how to handle our selected organism and stay in phase with exist-

ing practices used in culture of ornamental plants, we stand a good chance of harnessing mother nature's mycorrhizae in commercial enterprises.

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MODERATOR FURUTA: Our next speaker received his B.S. from the University of Illinois in 1955, then came to California to work with the Monrovia Nursery in Azusa. He is research director and has been there for 18 years and, among other things, he has found time to come back to the University of California at Riverside and get an M.S. degree in 1971. Most of you know Conrad Skimina, who will discuss "Re-cycling Water — Problems and Benefits."