

DEFOLIATION AND SECONDARY-ACTION ORGANISM ATTACK: WITH EMPHASIS ON *ARMILLARIA MELLEA*

by Philip M. Wargo

Abstract. Defoliation-induced changes in trees predispose them to attack by secondary-action organisms which can kill the tree. Both physical and chemical changes occur in defoliated trees that enhance the growth and metabolism of secondary-action organisms. Specific interactions of *Armillaria mellea* and chemical changes in roots of defoliated trees are described. Control strategies are discussed.

Damage and mortality after defoliation is a dieback and decline disease (Houston 1973, 1974). Diseases of this type are characterized by a progressive condition that begins when trees are altered initially by stress and ends when trees are killed by *secondary-action organisms*. Changes in a tree's physiological condition or processes predispose it to attack from these secondary-action organisms to which the tree is normally resistant.

In the absence or scarcity of these secondary-action organisms, or where the strain or variety of the organism is not pathogenic to the stressed host species, most trees recover from the effects of defoliation. Defect and mortality are mainly the result of attacks by these organisms. Therefore, the secondary nature of these organisms in dieback and decline after defoliation refers to their sequence in time, not to their importance in disease development. Defoliation (or any stress) and attack by secondary-action organisms then are inseparable; they occur in sequence and both are necessary to complete the disease cycle.

Thus, trees die back, decline, and die in response to stress from defoliation and attack by secondary-action organisms — sometimes slowly over several years and sometimes rapidly, depending on the severity and frequency of the defoliation, the growing conditions at the time of defoliation, and the abundance and aggressiveness of the secondary-action organisms (Wargo 1978).

The Secondary-action Organisms

Secondary-action organisms are opportunists. They are present in the normal tree environment in an innocuous condition but are usually in a position to take advantage of any changes in tree condition or form that favor their growth.

Armillaria mellea (Vahl ex Fr.) Kummer (*Armillaria mellea* (Vahl ex Fr.) Karst.) is perhaps the "opportunist par excellence" (Wargo 1980a). This fungus not only is present in most forest tree sites but also has colonized the surface of most trees' roots with rhizomorphs, the root-like structures from which the fungus derives its common name — shoestring root rot (Fig. 1). In response to stress-induced changes in the roots, the fungus penetrates into the tissues of the cambial zone between the bark and wood and begins growing (Fig. 2). It rapidly colonizes and kills these tissues, spreads from the roots to the root collar, and girdles and kills the tree (Fig. 3).

Another fungus that "takes advantage" of defoliation-induced changes in trees is *Steganosporium ovatum* (Pers. ex Merat) Hughes. This twig and branch fungus commonly invades lower, shade-killed branches on maple and oak. However, when trees are defoliated, the fungus can colonize weakened branches and subsequently the main stems on small trees (Fig. 4). It thus becomes a pathogen, killing branches and hastening tree death (Hibben 1964; Wargo and Houston 1974).

Another common secondary-action organism is *Agrilus bilineatus* (Web.), the two-lined chestnut borer. This insect is associated primarily with oak trees but does attack other species. The adult beetle, attracted to trees weakened by defoliation, lays its eggs on the bark. The larvae hatch and bore into the bark and begin feeding on the outerwood and inner bark tissues. The insect

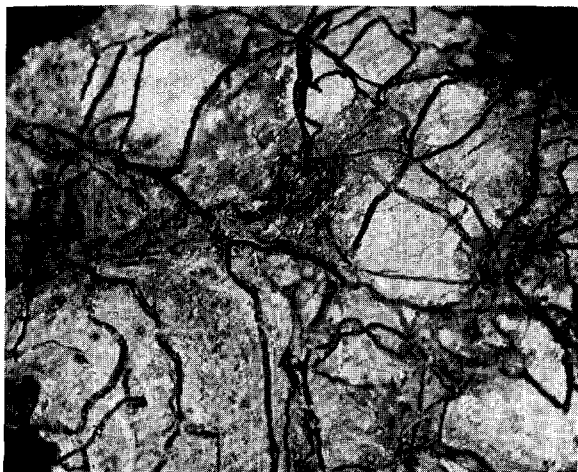


Figure 1. Shoestring-like rhizomorphs of *Armillaria mellea* on the surface of a white oak root.



Figure 2. White patches of mycelium of *Armillaria mellea* on a root of red oak — bark removed.

forms meandering galleries as it feeds and grows (Fig. 5). These galleries disrupt the transport of food and water, causing the death of branches and eventually the main stem. In many situations the borer operates in conjunction with *A. mellea* and the combination is especially devastating to the tree (Wargo 1977).

These are the organisms that have been identified and characterized to some extent. They are by no means the only organisms associated with

defoliation-induced mortality. Our studies on dieback and declines have repeatedly shown that complexity is the keyword in describing these diseases. Multiple organisms are the rule rather than the exception.

The Changes

Many physical and physiological conditions and processes are altered by defoliation. When leaf tissue is removed, photosynthesis is altered; this, in turn, influences all carbohydrate metabolism and storage. Water relations are affected and this influences mineral uptake. Also altered are growth regulators, which have a variety of effects on growth and metabolism.

Physically, the tree is reduced in size (Wargo 1980c). Leaves on defoliated trees are fewer and smaller and are not as efficient food producers as are normal leaves. Branches die back or do not elongate normally; thus, height growth is reduced.



Figure 3. White mycelial fans of *Armillaria mellea* at the root collar of a beech tree — bark removed.



Figure 4. Wilted foliage on a small sugar maple sapling resulting from colonization by *Steganosporium ovatum* — black stipules are the fruiting bodies of the fungus.

Radial growth is also substantially less in defoliated trees, resulting in less tissue to conduct minerals and water. Roots also are affected. Rootlets die, fail to elongate, or fail to produce new branches, so the tree's capacity for water and mineral absorption is reduced.

Chemically, the tree is changed substantially by defoliation. There is much less starch stored in defoliated trees, especially in the roots (Wargo 1972; Wargo *et al.* 1972). Corresponding to this decrease in starch content is an increase in glucose and fructose (reducing sugars). Both the kinds and quantities of amino acids are changed by defoliation (Wargo 1972; Parker and Patton 1975). In addition, enzyme activities (Wargo 1975, 1976), phenolic compounds (Parker and Patton 1975), and growth regulators (Parker 1974) are altered to some extent by defoliation.



Figure 5. Meandering feeding galleries of *Agrilus bilineatus* on a branch of white oak — bark removed.

Although many changes do occur, some may be more important to secondary-action organisms than others. Physical changes may remove physical barriers, such as thick growth rings, or provide physical entrances (dead twigs or roots) that enable the organisms to gain entrance to the tree. Changes in the chemistry of the tree may stimulate metabolism and growth of the organism, remove a toxic or inhibitory chemical, or enable the organism to grow even in the presence of the toxic or inhibitor compound. Still other chemical changes may attract organisms to weakened trees.

Organism Requirements

Chemical. *Armillaria mellea* is a glucose-utilizing fungus (Garraway 1974). While it can grow on other sugars, its growth on glucose or on complex carbohydrates composed of glucose, such as maltose and starch, is spectacular compared with its growth on other sugars (Figs. 6-8). Thus, the increase in glucose in the roots of defoliated trees becomes very important in the relationship with this fungus (Wargo 1972). Glucose not only stimulates growth of *A. mellea* but also enables it to grow in the presence of inhibitory phenolic compounds (Wargo 1980b). Gallic acid, released when bark tannins are metabolized, can be inhibitory and sometimes even toxic to *A. mellea*. However, when more glucose is available the fungus can overcome the adverse effects of gallic acid (Fig. 9).

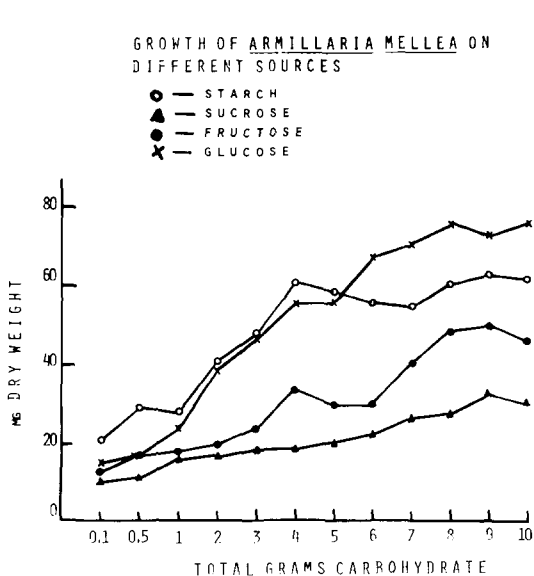


Figure 6. Growth of *Armillaria melleae* on artificial media containing various carbohydrate sources.

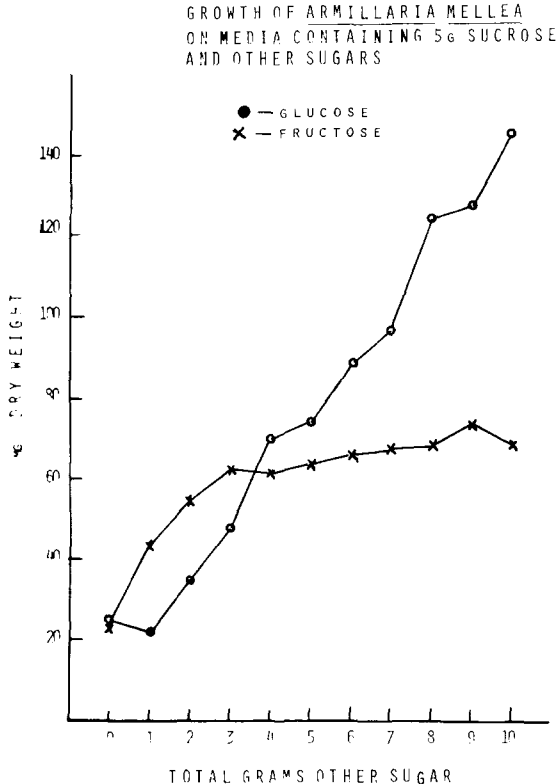


Figure 8. Growth of *Armillaria melleae* on artificial media containing sucrose and glucose or fructose.

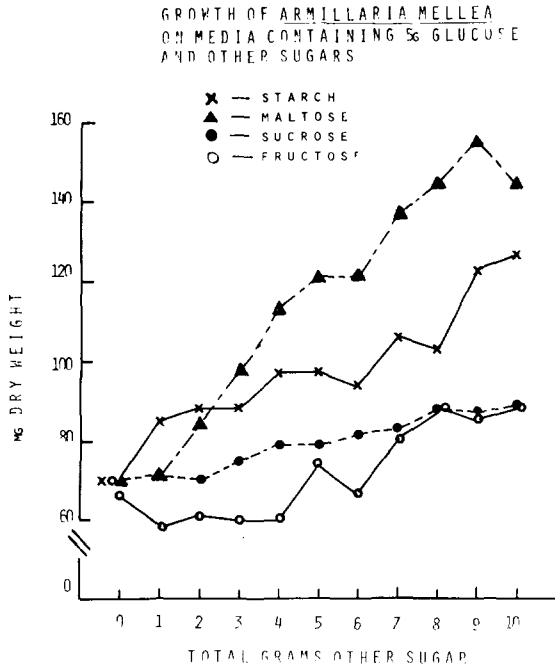


Figure 7. Growth of *Armillaria melleae* on artificial media containing glucose and other carbohydrate sources.

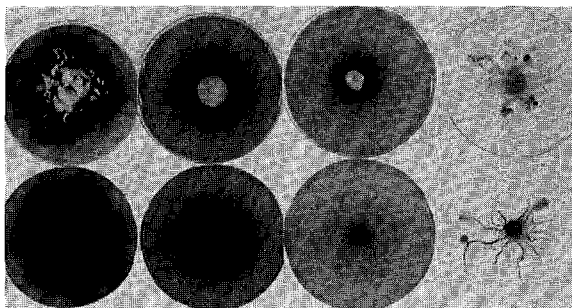


Figure 9. Growth of *Armillaria melleae* on artificial media containing, from left to right, gallic acid and high glucose (10 g/liter), medium glucose (5 g/liter), low glucose (1 g/liter), and medium glucose no gallic acid. Upper row shows upper surface, lower row shows lower surface.

Nitrogen requirements of the fungus have a similar role. The amino acids, asparagine and alanine, are good nitrogen sources for *A. mellea* and the fungus grows rapidly when these are added to its growth medium (Weinhold and Garraway 1966). Defoliation results in an increase in these particular amino acids (Parker and Patton 1979).

Even growth regulators can stimulate growth of *A. mellea* and may be involved in the predisposition of the tree to the fungus (Garraway 1974).

Other physiological changes that occur are related to the natural defense of the tree and not to the nutritional requirements of the organism. Enzymes present in the bark of trees are capable of dissolving the cell wall of certain fungi, including *A. mellea* and *Steganosporium ovatum*, and would be disruptive to the growth of these fungi (Wargo 1975, 1976). Defoliation alters the activity of these enzymes and may impair their functioning as part of the normal defense system.

Visualize a root covered with rhizomorphs of *A. mellea*. At many places along the rhizomorphs, hyphae of the fungus penetrate the outer bark tissues and "challenge" the root tissue. Enzymes in the bark continually dissolve the invading hyphal tips; gallic acid released from tannin in the bark also inhibits the fungus. The fungus cannot grow rapidly; the glucose level of the tissue is low, and nitrogen is present in a form not readily utilized by the fungus. The root resists attack by the fungus; but then defoliation, then changes, then successful invasion, then disease, then death.

Physical. Physical changes also can be important in satisfying certain requirements of organisms. Since *A. mellea* can exist as both a saprophyte (living on dead roots) and a parasite, the death of small feeder roots provides a place where the fungus can begin rapid growth and become established on the root system of the stressed tree. From here it can spread to living roots and eventually colonize the tree in response to the chemical changes.

Above ground, decay organisms can become established in the dead branches. Regrowth of branches around dead branches may result in further wounding because breakage of these weak-angled branches creates additional wounds and dead tissues for organisms to enter.

Reduced radial growth may be important for successful invasion of insects such as the two-lined chestnut borer (Cote 1976). The mechanism of borer resistance is unclear but it probably is related to water in the stem and the amount of new wood produced. Reduced radial growth also increases the amount of damage caused by borer feeding tunnels; thinner growth rings are more likely to be completely cut through by the feeding tunnels.

Control Strategies and Tactics

Because defoliation predisposes trees to attack by secondary-action organisms, the best control strategy is to prevent defoliation. This can be done with a number of pesticides, including chemicals and biologicals.

A second strategy is to maintain healthy trees to minimize the effects of any defoliation. Healthy trees can better tolerate defoliation and subsequent attacks by secondary-action organisms. This strategy requires that trees be maintained continuously, and includes the practices of matching tree requirements to particular site conditions, proper planting, and adequate watering and fertilizing. There is, of course, a greater risk of damage with this strategy since even the healthiest of trees can be affected if defoliation is repeated.

The third strategy is to treat the secondary-action organism. This is the least satisfactory strategy. Many times we are not aware of the secondary-action organism until the damage is done and the tree is doomed. Also, control measures are lacking for these organisms since in the past they were not considered important tree killers. Insecticides can be used to protect trees against borer attack and there are some expensive fumigation techniques to rid the soil of *A. mellea* (this must be done before the tree is planted). There are no proven techniques for ridding the tree of the borer or *A. mellea* once they have become established.

Probably the best strategy is a combination of the first two. In the absence of other stresses, healthy undefoliated trees will remain healthy.

Literature Cited

- Cote, W.A. 1976. The biology of the two-lined chestnut borer and its impact on defoliated oaks. Ph.D. thesis. SUNY Coll. Environ. Sci. and For., Syracuse, 102 pp.
- Garraway, M.O. 1974. *Stimulation of Armillaria mellea growth by plant hormones in relation to the concentration and type of carbohydrate*. Eur. J. For. Pathol. 5:35-43.
- Hibben, C.R. 1964. *Identity and significance of certain organisms associated with sugar maple decline in New York woodlands*. Phytopathology 54:1389-1392.
- Houston, D.R. 1973. *Diebacks and declines: Diseases initiated by stress, including defoliation*. Proc. Int. Shade Tree Conf. 49:73-76.
- Houston, D.R. 1974. *Diagnosing and preventing diebacks and declines*. Morton Arbor. Quart. 10(4):55-59.
- Parker, J. 1974. Effects of defoliation, girdling, and severing of sugar maple trees on root starch and sugar levels. USDA For. Serv. Res. Pap. NE-306. 4 pp.
- Parker, J., and R.L. Patton. 1975. *Effects of drought and defoliation on some metabolites in roots of black oak seedlings*. Can. J. For. Res. 5:457-463.
- Wargo, P.M. 1972. *Defoliation-induced chemical changes in sugar maple roots stimulate growth of Armillaria mellea*. Phytopathology 62:1278-1283.
- Wargo, P.M. 1975. *Lysis of the cell wall of Armillaria mellea by enzymes from forest trees*. Physiol. Plant Pathol. 5:99-105.
- Wargo, P.M. 1976. Lysis of fungal pathogens by tree produced enzymes — a possible disease resistance mechanism in trees. Proc. 23rd Northeast. For. Tree Improv. Conf. pp. 19-23.
- Wargo, P.M. 1977. *Armillariella mellea and Agrilus bilineatus and mortality of defoliated oak trees*. For. Sci. 23:435-492.
- Wargo, P.M. 1978. *Insects have defoliated my tree — now what's going to happen?* J. Arboric. 4:169-175.
- Wargo, P.M. 1980a. *Armillaria mellea — opportunist par excellence*. In Proceedings of the Midwestern Chapter of the International Society of Arboriculture. (In press.)
- Wargo, P.M. 1980b. *Interaction of ethanol, glucose, phenolics and isolate of Armillaria mellea*. (Abstr.) Phytopathology 70:470.
- Wargo, P.M. 1980c. *Defoliation and tree growth*. In The Gypsy Moth. Research toward integrated pest management. U.S. Dep. Agric. Tech. Bull. 1584. (In press.)
- Wargo, P.M., J. Parker, and D.R. Houston. 1972. *Starch content in roots of defoliated sugar maple*. For. Sci. 18(3):203-204.
- Wargo, P.M., and D.R. Houston. 1974. *Infection of defoliated sugar maple trees by Armillaria mellea*. Phytopathology 64(6):817-822.
- Weinhold, A.R., and M.O. Garraway. 1966. *Nitrogen and carbon/nutrition of Armillaria mellea in relation to growth-promoting effects of ethanol*. Phytopathology 56:108-112.

U.S. Forest Services
NE Forest Expt. Station Lab
151 Sanford Ave.
Hamden, Connecticut

ABSTRACT

Whitcomb, C.E. 1980. **How shade and fertilizer levels affect woody plant growth**. Am. Nurseryman 151(11): 7, 56, 60, 62, 64.

Some reports have suggested various amounts of shading for growing nursery stock better. None of the literature mentioned root growth or possible effects of shading on root system development. Principles of basic physiology suggest that once light intensity is reduced below the point of light saturation for even a portion of the leaves, root system development is likely to slow down. The purpose of this study was to determine responses of several species of woody plants growing in containers to varying levels of shade and fertility. The plants fell into three groups based on the data obtained: those that require sun, those that require shade and those that prefer shade. All species tested looked better and were more tolerant of high light intensity when the fertility level was high. There was no benefit from shade levels above 30 percent with the species preferring shade (azalea, abelia, barbery, and holly). All species except Euonymus requiring full sun (juniper, Pyracantha, and elaeagnus) were decidedly restricted by any shade at low fertility levels. Shading generally reduced the root system before lessened top growth could be detected visually. Because shade structures are expensive to construct and maintain, and because root growth suffers most from excessive shading, woody nursery plants should be grown under the highest light intensity possible. This would provide the most roots to help plants become established in the landscape while reducing the potential for burn, which usually occurs when plants are moved from moderate or heavy shade to full sun.