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Review article

Consequences of environmental stress on oak: predisposition to pathogens

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Summary — Stress alone, if severe and prolonged, can result in tree mortality. However, stress events usually are neither severe nor frequent enough to cause mortality directly. Mortality of stressed trees results usually from lethal attacks by opportunistic pathogenic organisms that successfully invade and colonize stress-weakened trees. Oak trees are predisposed to these organisms by defoliation, primarily from insects, but also by fungi and late spring frosts, and by drought. There is some evidence that injury from extreme winter temperature fluctuations also can act as a predisposing stress. Stress causes physical, physiological, and chemical changes that reduce energy available for trees to defend themselves, provide energy to pathogens for rapid growth, or make the tree more attractive to organisms that, through multiple attacks, overwhelm the ability of a tree to defend itself from attack. Fungal organisms, such as *Armillaria* spp in the root system, *Hypoxylon* spp on the bole, and a number of fungi that invade branch systems, and insect borers, such as *Agrilus* spp, take advantage of changes induced by stress and successfully attack and kill trees. These organisms may be secondary in the sequence of events, but are of primary importance in causing mortality.

decline / stress / secondary pathogen / *Quercus*

Résumé — Conséquences de contraintes de l'environnement sur le chêne : prédisposition aux pathogènes. *Un stress seul, s'il est suffisamment intense et prolongé, peut induire la mort d'un arbre. Cependant, dans la plupart des cas, les périodes de contraintes ne sont ni assez sévères, ni assez fréquentes pour causer directement une mortalité. Cette dernière résulte généralement d'attaques létales par des organismes pathogènes opportunistes, qui envahissent et colonisent avec succès des arbres affaiblis. Les chênes sont prédisposés à de telles attaques par des défoliations, dues primairement à des insectes, mais aussi à des champignons ou des gelées tardives, et par la sécheresse. Les contraintes provoquent des modifications physiques, physiologiques et chimiques qui réduisent la disponibilité en énergie pour assurer une défense efficace, mettent à la disposition des pathogènes des ressources permettant une croissance rapide, ou rendent l'arbre plus attractif pour des organismes qui, par le biais d'attaques multiples, submergent ses possibilités de défense. Des champignons comme les armillaires dans le système racinaire,* Hypoxylon *spp dans l'écorce, un certain nombre de champignons qui envahissent les branches, d'insectes mineurs comme* Agrilus *spp peuvent profiter de ces*

modifications induites par les contraintes et envahir, voire tuer, les arbres. Ces organismes sont sans doute secondaires dans la chronologie des événements, mais probablement de première importance comme cause de mortalité.

***dépérissement / stress / pathogènes secondaires* / Quercus**

INTRODUCTION

Decline diseases of trees are maladies related to the consequences of stress. Their incidence depends on the occurrence of adverse environmental factors, and their severity depends on the intensity, duration, and frequency of the stress event(s), and the successful attack of the stressed trees by opportunistic pathogenic organisms (Houston 1967, 1987b, 1992). Manion (1991) portrays the complexity of decline disease in his decline disease spiral, which illustrates the interactions of predisposing, inciting, and contributing factors in the progressive deterioration and death of trees. These diseases are progressive and trees may decline in health for several years before they die. Because many of the stress factors often are regional in occurrence, declines can occur suddenly over broad geographic areas (Houston, 1967). Sometimes declines are not evident until several years after the stress event. For example, birch decline which began in the mid 1930s was possibly triggered in part by freeze damage to shallow roots in 1932 (Hepting, 1971). Mortality in beech bark diseased stands occurs several years after the beech scale (the stressor) arrives in beech stands (Houston and O'Brien, 1983).

CONCEPTS

Model of stress-induced decline diseases

A general model for stress-induced decline diseases was proposed by Houston (1984, 1987b, 1992): *Step 1:* healthy trees + stress => altered tree (dieback begins); *Step 2:* altered tree + more stress => trees altered further, may lose ability to respond to favorable conditions (dieback continues); *Step 3:* altered tree + organisms of secondary action => trees invaded and (perhaps) killed (decline phase).

In this model, the stress alone often can result in dieback and if intense, severe, and frequent enough, can cause death. Trees also can recover during the dieback phase with abatement of the stress(es). Dead branches are shed and new ones form to replace them. In the decline phase, pathogenic organisms attack trees whose defense systems have been impaired. Recovery at this stage is less likely to occur. The acceleration or abatement of the decline phase is affected by host vigor, pest aggressiveness, and the degree to which particular host tissues are invaded.

The organisms involved in the decline phase of these diseases usually are facultative parasites (saprogens) and secondary insects with the ability to invade weakened trees (Houston, 1984). These opportunistic organisms (Wargo, 1980a) often are ubiquitous inhabitants of natural ecosystems functioning as ecosystem roguers, killing weak defective trees and as scavengers, decomposing the dead trees.

Decline diseases occur only when trees that have survived normal competitive forces in the forest are subjected to, and altered by, extraordinary environmental perturbations (Houston, 1984). Trees succumbing to normal competitive factors provide secondary organisms continual sources of substrate, enabling them to maintain popula-

tions capable of colonizing and killing vigorous trees after they are stressed.

Stress factors

Stress factors that trigger decline diseases in forest trees can be both biotic and abiotic. Insect defoliation, moisture and temperature extremes, and attacks by sucking insects have been common initiators of tree decline episodes in the eastern United States throughout this century (Houston, 1987a). In oak forests, defoliation, drought, and frost damage have been the most frequent initiators of decline (Delatour, 1983; Houston, 1987a; Miller et al, 1989). Trees suffering from stress are changed both physically and physiologically, and these changes impair their ability to resist attacks by secondary organisms (Wargo, 1981a; Mattson and Haack, 1987).

Defoliation is caused primarily by insects (Staley, 1965; Nichols, 1968; Doane and McManus, 1981) but also by late spring frosts (Long, 1914; Beal, 1926; Balch, 1927; Miller et al, 1989; Hartman et al, 1991; Auclair et al, 1992) or by fungal leaf pathogens such as anthracnose (Wargo et al, 1983; McCracken, 1985) and powdery mildew fungi (Falck, 1923; Georgevitch, 1926; Day, 1927; Delatour, 1983). Drought has been implicated as a major stress factor in oaks forests in eastern and midwestern United States (Tainter et al, 1983, 1984; Houston, 1987a) and in Europe (Falck, 1918, 1924; Delatour, 1983; Becker, 1984; Hartmann et al, 1991). Frequently, outbreaks of defoliating insects accompany or occur shortly after drought episodes (Miller et al, 1989). Drought may enhance the attractiveness or acceptability of plants to insects, make plant tissues more suitable for insect growth, survival, and reproduction, or enhance the ability of insects to detoxify plant defensive chemicals and thus lead to outbreaks (Mattson and Haack, 1987).

More recent research has implicated winter injury from extreme temperature fluctuations as a factor in oak decline in Europe (Hartmann et al, 1991; Auclair et al, 1992; Auclair, 1993; Hartmann and Blank, 1993). Schoeneweiss and coworkers demonstrated that freezing temperatures can predispose stem tissue of European white birch, *Betula alba* L, to canker and dieback fungi (Crist and Schoeneweiss, 1975; Schoeneweiss, 1978, 1981a, b).

PATHOGENS – SECONDARY ORGANISMS

Both insects and fungi function as stress-induced pathogens (opportunists) (Wargo 1980a, 1981a) on oak trees. The most commonly associated fungi are *Armillaria* species causing root disease (Intini, 1991; Luisi et al, 1991; Wargo and Harrington, 1991), *Hypoxylon* species causing bole cankers (Vannini 1987, 1991; Fenn et al, 1991), and a number of fungal species associated with branch and twig dieback, but whose role in the dieback-decline process is unclear (Balder, 1991, 1993; Delatour and Morelet, 1991; Hartmann et al, 1991; Przybyl, 1991; Bohar, 1993). Evidence also exists that another root fungus, *Collybia fusipes* (Bull ex Fr) Quel, plays an important role in oak decline in France and may be involved in other European countries (Delatour and Guillaumin, 1984, 1985). Most recently, the aggressive fine root pathogen, *Phytophthora cinnamomi* Rands, has been implicated in mortality of *Quercus suber* L and *Q ilex* L in the Mediterranean region of Europe (Brasier, 1993). In this disease syndrome, there is a relationship of drought, fungus attack, and tree decline and death. However, it is the fungus that apparently predisposes the tree to drought stress, rather than the reverse that is typical of stress-induced decline. Additional research is needed to clarify the relationship of oak mortality and *P cinnamomi* in

the Mediterranean region and to determine if it is involved in other regions of Europe.

Bark borers are the insects most frequently associated with mortality of stressed oaks. In the United States, *Agrilus bilineatus* Web, the two-lined chestnut borer, is a major factor in oak decline after defoliation and/or drought (Dunbar and Stephens, 1975, 1976; Cote and Allen, 1980; Haack and Benjamin, 1982; Haack, 1985; Haack and Blank, 1991). In Europe, *Agrilus biguttatus* Fabr is the dominant insect colonizer of stressed oaks (Jacquiot 1950, 1976; Hartmann and Blank, 1992, 1993). *Armillaria* spp are commonly found on trees with bark beetle attacks and in concert they are responsible for significant mortality (Wargo, 1977; Hartmann and Blank, 1993).

STRESS – PATHOGEN INTERACTIONS

Many physical and physiological conditions, physiological processes, and chemical relationships in trees are altered by stress (Wargo, 1981a; Mattson and Haack, 1987). Changes in photosynthesis occur and influence carbohydrate metabolism, allocation, and storage, and assimilation of other essential nutrients. Water relations can be affected thereby influencing mineral uptake. In addition, the kinds and quantities of growth-regulating compounds are altered and have a variety of effects on growth and metabolism.

Although many changes do occur, some are more important than others to secondary organisms (Wargo, 1984b). Physical changes may remove or open physical barriers such as thick bark, thick cuticle, wide growth rings, or intact bark tissues. For example, 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 galleries; thinner growth rings are more likely to be completely cut through by the feeding galleries.

Changes in tree chemistry may provide compounds that stimulate metabolism and growth of an organism, remove toxic or inhibitory chemicals, or enable organisms to grow even in the presence of toxic or inhibitory compounds (Wargo, 1972; Mattson and Haack, 1987). Still other chemical changes may attract organisms to stressed trees. The relationship of chemical changes induced by defoliation and drought and successful colonization by the *Armillaria* root disease fungus illustrates the complexity of these interactions.

Major changes in carbohydrates in tree roots are induced by drought and defoliation (Staley, 1965; Parker and Houston, 1971; Wargo, 1972; Wargo et al, 1972; Parker and Patton, 1975, Parker, 1979). Starch content is lowered substantially and in many trees is depleted. Survival of trees after defoliation is critically dependent on the starch reserves present at the time of defoliation (Wargo, 1981c). Corresponding to this decrease in starch is a decrease in sucrose levels in the bark and outerwood of the roots. By contrast, levels of glucose and fructose increase, especially in the cambial zone (inner bark-outerwood) tissues. Concentrations of reducing sugars can be four to five times higher than those in undefoliated trees at the same time of year, and four to five times higher than the seasonal high that occurs normally in the roots in the spring when carbohydrates are mobilized for growth (Wargo, 1971). The increase in glucose in the roots of defoliated trees is important to *Armillaria* because this fungus is a glucose fungus (Garraway, 1974). Although it can grow on many carbon sources, its growth on glucose or polymers of glucose, such as maltose and starch, can be one and a half to three times higher than

growth on other sources (Wargo, 1981a). The enhancement of growth of *Armillaria* on extracts from roots of defoliated trees can be attributed partially to higher levels of glucose (Wargo, 1972).

Glucose not only stimulates rapid growth of *Armillaria* but also enables the fungus to grow in the presence of inhibitory phenols such as gallic acid (Wargo, 1980b). Gallic acid, released when bark tannins are hydrolyzed, can inhibit and sometimes kill isolates of *Armillaria*. However, when more glucose is available, the fungus not only overcomes the inhibition by gallic acid but also uses the oxidized phenol as an additional carbon source and grows even more vigorously than on glucose alone (Wargo 1980b, 1981b). This also occurs with other phenol compounds.

Stress by defoliation or drought also alters nitrogen metabolism and causes increases in amino nitrogen. Alanine, asparagine, leucine, and other amino acids increase in the bark and wood of roots of defoliated trees and seedlings (Wargo, 1972; Parker and Patton, 1975; Parker 1979). Asparagine and other amino acids increase in tree seedlings in response to drought (Parker, 1979). Alanine and asparagine are (individually) very satisfactory and leucine moderately satisfactory nitrogen sources for growth of *Armillaria* (Weinhold and Garraway, 1966). The fungus also responds to increases in total amino nitrogen, and defoliation and drought increase the overall level of amino nitrogen in the roots (Parker and Patton, 1975).

Available nitrogen may be critical to *Armillaria* for the oxidation of phenolics in root bark (Wargo, 1984a). When grown in culture without sufficient nitrogen, oxidation of phenols by this fungus is limited and so is its growth. Successful colonization of root tissues may depend on the fungus's ability to oxidize phenols and the tree's inability to restrict the oxidation reaction. In healthy trees, *Armillaria* is confined to wounded and necrotic tissues; contiguous healthy tissues are not affected, ie, 'browned', by fungal enzymes. In weakened trees, contiguous living tissues are 'browned' by the fungus and then colonized (Wargo and Montgomery, 1983). In healthy tissues, necrosis is prevented by a highly reductive chemical state. Perhaps in stressed tissues this ability to confine the oxidative processes is lost, and necrosis continues as the fungal oxidative enzymes are secreted. The increased glucose and nitrogen stimulates vigorous fungal growth and enzyme secretion while the inability of the tissue to restrict the oxidation processes allows the fungus to successfully colonize and kill the roots.

Other physiological changes that occur are related to the natural defense of the tree and not to the nutritional requirements of the organism. Enzymes (glucanase and chitinase) capable of dissolving the cell wall of *Armillaria* are present in the bark and wood tissues of trees and could be disruptive to the growth of this fungus (Wargo, 1975, 1976). Defoliation reduces the activity of these enzymes and may impair their functioning as part of the normal defense system (Wargo, 1975, 1976).

Roots of forest trees are probably continuously 'challenged' from epiphytic rhizomorphs of *Armillaria* which grow from colonized food bases to healthy living trees (Redfern and Filip, 1991). Lytic enzymes in healthy inner bark may continually dissolve the invading hyphal tips, while gallic acid, released from tannin in the bark, 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 stress occurs, then changes, then successful invasion, then disease, and then death.

These same processes and responses also may occur in the stem tissues thus allowing canker fungi to colonize and kill weakened main stem and branch tissues.

For example, *Steganosporium ovatum* (Pers ex Merat) Hughes, a twig and branch invading fungus on oak sp (*Quercus*) and sugar maple, *Acer saccaharum* Marsh (Wargo, 1981a), and *Nectria coccinea* var *faginata* Lohman, Watson, and Ayers, one of the *Nectria* spp associated with beech bark disease (Ehrlich, 1934; Houston, 1980), are susceptible to cell wall degradation by glucanase and chitinase (Wargo, 1976, and unpublished results), and penetration and establishment by these fungi could be inhibited by these enzymes. Such a resistance mechanism could also be responsible for restricting latent infections, such as those of *Hypoxylon atropunctatum* (Berk and Rav) Cke on oak (Fenn et al, 1991).

IMPLICATIONS AND CONSEQUENCES

Diagnosing decline disease

Decline diseases, by their nature, are complex. They invoke interactions of host genetics and vigor, site factors, climate, stress, and pathogenic organisms, sometimes several acting in concert or sequence. Because these diseases are triggered by both biotic and abiotic stress, they occur sometimes quite suddenly over broad geographic areas. Even biotic stress factors such as defoliation may occur over considerable areas simultaneously; for example in 1981, more than 12 million acres (5 million ha) of forest in the northeastern United States were heavily defoliated by the gypsy moth, *Lymantria dispar* L. A major problem then is determining if the disease problem is actually a stress-induced decline. Diagnosing declines is the first step in the process.

Diagnosis of decline diseases is a three-step process: i) recognition of symptoms; ii) identification of agents of secondary action; and iii) association in time and place of the stress event(s) that triggered the problem (Houston, 1987b). Steps (i) and (ii) are relatively easy compared to step (iii). The triggering stress event may have abated entirely or decreased to inconspicuous levels by the time mortality is first observed, since decline and mortality often occur several years after the triggering event. For example, oak mortality associated with *Armillaria* spp and the two-lined chestnut borer usually occur 1 to 2 years after a major drought (Clinton et al, 1993) or up to 3 years after 2 to 3 successive years of severe defoliation (Wargo, 1981c). Indeed, the organisms that attack the trees also are important clues as to whether a disease syndrome is a decline disease.

Susceptibility to stress. Vulnerability to effects

Since decline diseases occur generally after the stress event, the occurrence of a decline problem indicates that the forest already has been affected. However, many forests are affected by stress but do not experience decline disease. Some forests are susceptible to stress events but are not vulnerable to their consequences, while others are less susceptible but are highly vulnerable. For example, stands that are most susceptible to gypsy moth defoliation may not be the most vulnerable to the effects of defoliation. Historically susceptible stands in the northeastern United States (where defoliation has occurred frequently in the past) often show low mortality after stress episodes (Houston, 1981). Such sites typically exist where frequent stress occurs from water shortages, storm damage, etc. Trees in such stands are probably tolerant of and less adversely affected by these stresses and, in turn, less adversely affected by defoliation than are their counterparts in less-stressed, mesic, fast-growing stands. However, these less-often defoliated stands (more resistant to defoliation) are more vulnerable when

defoliation does occur and mortality often is quite high in such stands (Houston and Valentine, 1977; Hicks, 1985). Knowing whether a forest is or is not susceptible to stress events and if it is also vulnerable are important factors in assessing risk and assigning a hazard rating to a particular forest (Houston and Valentine, 1977; Houston, 1979; Valentine and Houston, 1984).

Although stress is the primary issue in the predisposition of trees to opportunistic agents of dieback and decline diseases, it is not the only factor that must be considered in hazard-rating stands based on expected mortality (Hicks et al, 1987). Response of trees to stress depends on the integration of all environmental factors affecting them before, during, and after the stress event, and the influence of those same factors on the secondary pathogens responsible for the death of the trees. Thus, vulnerability of stands depends on species composition, stand age or ages, site conditions, and the aggressiveness and abundance of the available agents of mortality. Methods for assessing vulnerability of stands to gypsy moth defoliation have been developed but are not completely satisfactory (Herrick et al, 1989; Crow and Hicks, 1990; Hicks, 1990). Predicting the effects of secondary organisms is the weakest link in the 'model' because there is not adequate information on population dynamics and inoculum potential of these organisms (Crow and Hicks, 1990).

Role of secondary organisms

Secondary-action organisms are ubiquitous in most oak ecosystems and act as ecosystem roguers of weakened trees; it is difficult and perhaps unwise to attempt to eliminate them from the forest. As roguers, they play a unique role in ecosystem responses to stress. They kill weakened trees that become marginally productive members of the forest and in this process provide space on and light to the forest floor. Some, such as *Armillaria* species, also act as scavengers, decaying the dead tissue and releasing nutrients for rejuvenated growth of younger members of the present or replacement species.

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