Donald F. Schoeneweiss
Illinois Natural History Survey, Urbana

The Role of Environmental Stress in Diseases of Woody Plants

Fig. 1. A humidity cabinet inside a growth chamber provides equilibrium conditions for maintaining constant plant water potentials through an incubation period.

Anyone working with damage problems of plants in the field soon becomes aware of associations between environmental stresses and disease. Many early leaders in plant pathology—Sorauer, Ward, Jones, Gäumann, and others—recognized that environmental influence, which Sorauer called "predisposition," was important in the epidemiology of numerous diseases. The rapid development of modern fungicides, however, greatly simplified disease control, and for many years the importance of stress predisposition received little attention. Now that concern over environmental contamination has led to severe restrictions on the availability and use of pesticides, there is resurgent interest in utilizing all available means for disease control and minimizing dependence on chemical applications. This concept, commonly referred to as integrated pest management (IPM), is being incorporated into disease control programs. Because predisposing stresses may profoundly influence the incidence and severity of diseases, manipulation and management of environmental factors that stress plants are likely to become an important component of many IPM programs.

Observation Rather than Research

My own interest in environmental stresses and their relationships to woody plant diseases developed gradually over a period of years while I was working closely with growers and arborists concerned with disease problems of landscape plants. It became increasingly clear that some pathogenic diseases, particularly stem and crown cankers and diebacks, were most prevalent on plants subjected to environmental stress before symptom development. The questions most often asked were how and why did these plants become diseased, will they recover with treatment, and what should or could be done to prevent these types of infections?

Since I had had little personal experience with the effects of stress on plants and on plant diseases, I began in the mid-1960s to search the literature for useful information and to make inquiries of other pathologists working with diseases of woody ornamentals. It soon became apparent that little research on stress predisposition in woody plants had been published and that the available information was not derived from experimental evidence. The most comprehensive studies had been conducted by Bier and associates in Canada, who showed that water stress, estimated by relative bark turgidity, was a significant factor predisposing trees to attack by certain facultative parasites (2). With a few exceptions, other reports associating stress with disease were based on observations rather than valid scientific experiments.

From my own experience, plus observations reported by other workers, the two most common stresses predisposing woody plants to disease appeared to be drought (water stress) and freezing. In the nursery and landscape industries, plant damage associated with canker and dieback fungi often appeared after transplanting, although what specific stresses were involved in predisposing transplants was not clear. In addition, severely defoliated plants seemed to be more susceptible to attack by root rots as well as canker and dieback pathogens. Yet these associations had received little attention by researchers. Given the high level of interest among growers, horticulturists, and pathologists in the role of stresses in disease syndromes, why had so little experimental work been reported? Perhaps few researchers were willing to tackle the complex problems inherent in controlling and measuring environmental stresses under conditions compatible with disease research. In addition, grant support for research on woody plants was, and still is, meager and difficult to obtain.

Organisms that attack plants weakened or predisposed by stress are often nonaggressive pathogens, that is, they enter plants through wounds or natural openings but do not cause disease

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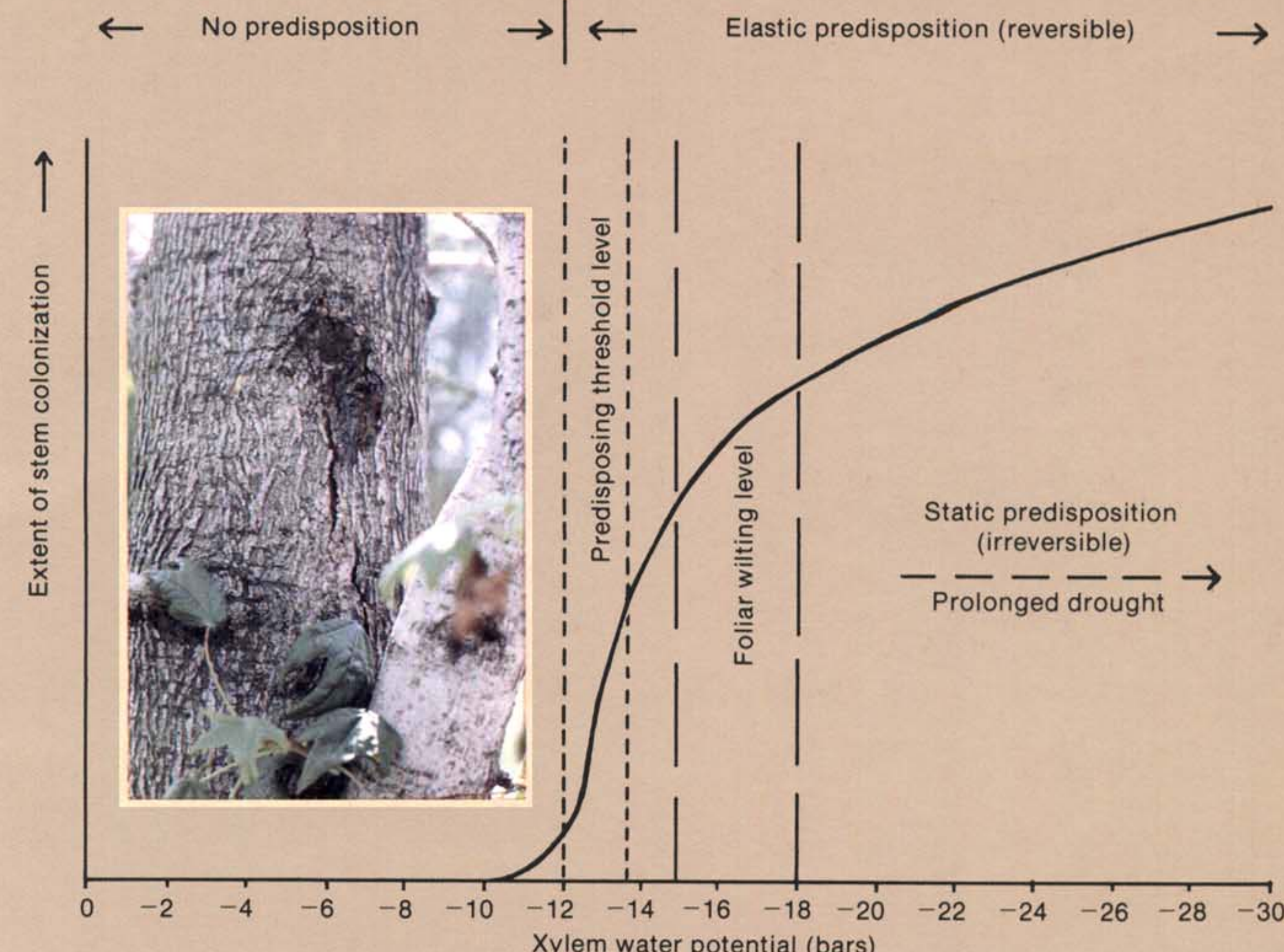

Fig. 2. Predisposing effects of water stress on colonization of woody stems by nonaggressive stem canker fungi. (Inset) Bleeding necrosis canker caused by *Botryosphaeria* on sweetgum stressed by several years of low precipitation.

damage as long as host vigor is high. Many of these organisms are common saprophytes of dead and dying plant tissue. Since they attack only weakened plants, they have often been referred to as "secondary" organisms and their possible role in plant damage has been disregarded. Yet it is rare indeed to find weakened or stressed plants that are not attacked by these organisms, particularly canker and dieback fungi. Are they primary pathogens, secondary organisms, or one of several factors that could be considered primary in the disease syndrome? Research data from controlled experiments were needed before these questions could be answered with any confidence.

A Controlled Environmental Stress Research Program

In contrast to the paucity of studies on stress predisposition to disease, very extensive studies had been conducted on the physiological and morphological effects of stresses in higher plants. It seemed logical that much of the information obtained and many of the techniques developed in these studies could be applied to disease research. To gain some insight into which stresses are effective predisposing factors and the level and/or duration of stress required for predisposition, a program of controlled stress research was initiated at the Illinois Natural History Survey in 1968.

Perhaps the most challenging problem was to create environmental stress conditions that could be controlled and measured yet have some relevance to stresses as they occur in the field. Since disease development in woody plants often requires days or weeks of incubation after inoculation, it was essential to work with whole plants rather than the excised stems used in previous studies on disease predisposition. This required chambers in which containerized woody plants could be subjected to controlled environmental stresses. Because funds were lacking, chambers were built by hand from wood and polyethylene (3). Although crude, these chambers proved to be satisfactory for many of the early studies.

Water Stress

To obtain vigorous host plants with a high level of resistance to nonaggressive pathogens, tree and shrub seedlings were grown in containers until the root systems were well established. To subject plants to water stress, irrigation was withheld until plant water potentials, measured with a pressure chamber (10), reached desired levels. Turgid plants and plants in various stages of wilt were inoculated with stem canker fungi. Most of the water stress studies were conducted with trees and shrubs inoculated with isolates of *Botryosphaeria dothidea*, a common pathogen that forms stem cankers on a wide range of woody hosts predisposed by stress. Intact plants were then incubated in a humidity cabinet placed inside a walk-in growth chamber (Fig. 1) under constant temperature, high humidity, and little or no light. Under these equilibrium conditions, plant water potentials became stable within 48 hours and remained relatively constant throughout a 7- to 9-day incubation period (10). The predisposing effect of various levels of water stress was estimated by culturing inoculated stems to determine the extent of colonization by the pathogen.

In all cases, stems remained resistant to fungal attack, regardless of host species, until plant water potentials reached a

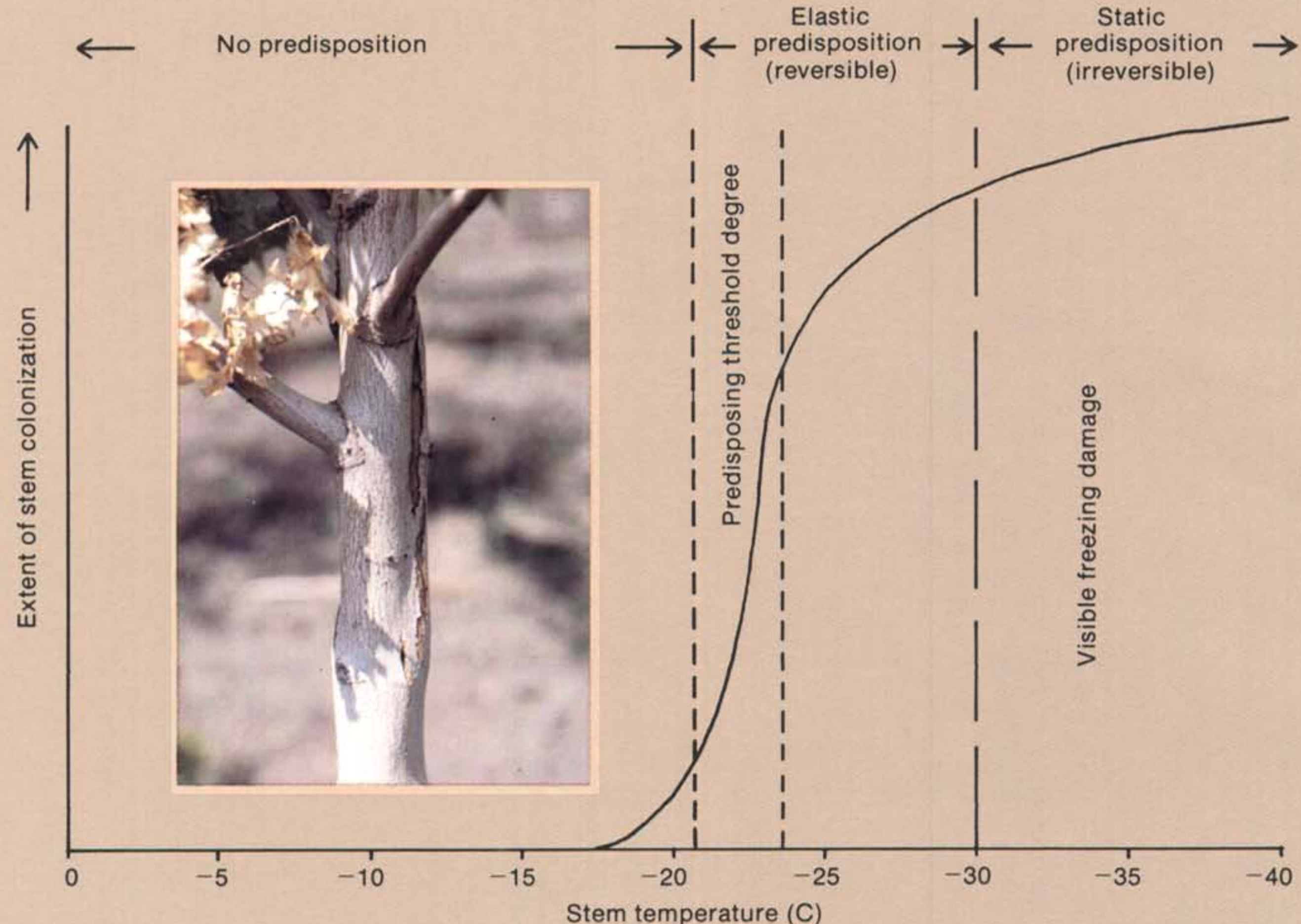

Fig. 3. Predisposing effects of freezing stress on colonization of woody stems by nonaggressive stem canker fungi. (Inset) *Cytospora* canker, with callusing and healing at margins, on red maple predisposed by freezing stress.

predisposing threshold level of −12 to −13 bars (Fig. 2). All stems with water potentials more negative than the threshold level were colonized by the pathogen, and the extent of colonization increased with decreasing water potential. Foliar wilt was not evident until plant water potentials fell to between −15 and −18 bars.

Data from additional studies on the duration of water stress required for predisposition indicated that woody stems were not predisposed unless plant water potentials remained at or below the threshold level for more than 3 days. Water stress predisposition in stems of woody hosts was reversible, and host tissues again became resistant to fungal attack 3–5 days after the stress was relieved (17).

On larger plants grown under field conditions, predisposition caused by short-term droughts is also an elastic or reversible effect, as cankers caused by nonaggressive pathogens often heal after irrigation is resumed. Prolonged droughts, however, or several consecutive years of below-normal precipitation may result in static or irreversible predisposition (Fig. 2). Several tree diseases associated with nonaggressive pathogens caused extensive mortality during the dust bowl years of the 1930s, and other reports appear in the literature of decline and death of trees following prolonged droughts (14).

Freezing Stress

Canker and dieback pathogens also attack woody plants injured or stressed by freezing temperatures (4,5,8,13,16). In the Midwest, freezing stress often occurs when extended periods of mild weather in the fall or winter are followed by a rapid and extensive drop in temperature to near zero when a cold front moves in. The following spring, outbreaks of stem canker and dieback appear.

To study the predisposing effects of freezing, containerized tree and shrub seedlings were placed outdoors in the fall. After the plants entered dormancy and had been exposed to several light frosts but were not fully acclimated to low temperatures, they were inoculated with *B. dothidea* and subjected to controlled freezing. The plants were placed in a heated cabinet inside a walk-in freezer, and the heater thermostat was turned down (3). After the plants were frozen to various temperatures and thawed slowly overnight, they were observed for canker development for several weeks, then cultured to determine the extent of stem colonization by the pathogen. Again, a threshold level or degree of stress appeared to be required for predisposition (Fig. 3).

Subsequent tests with plants inoculated with other canker fungi and frozen in a programmed walk-in freezer produced similar results and confirmed the hypothesis that when temperatures fall below a critical or threshold level, freezing stress predisposes dormant but not fully acclimated woody plant stems. When fully acclimated plants were brought in and frozen in midwinter, very hardy species were not predisposed, even at temperatures as low as −30 C. However, less hardy species, such as *Euonymus alatus*, were predisposed at temperatures near −20 C, although the extent of stem colonization was less than in plants frozen in the fall.

In numerous controlled freezing studies conducted over a 10-year period, threshold temperatures required for predisposition were mostly between −20 and −30 C, regardless of the host species or pathogen. Stems became predisposed when temperatures reached the threshold level, and extending the exposure time at these temperatures did not increase the rate or extent of colonization (17). Uninoculated plants that were frozen to as low as −30 C showed no signs of

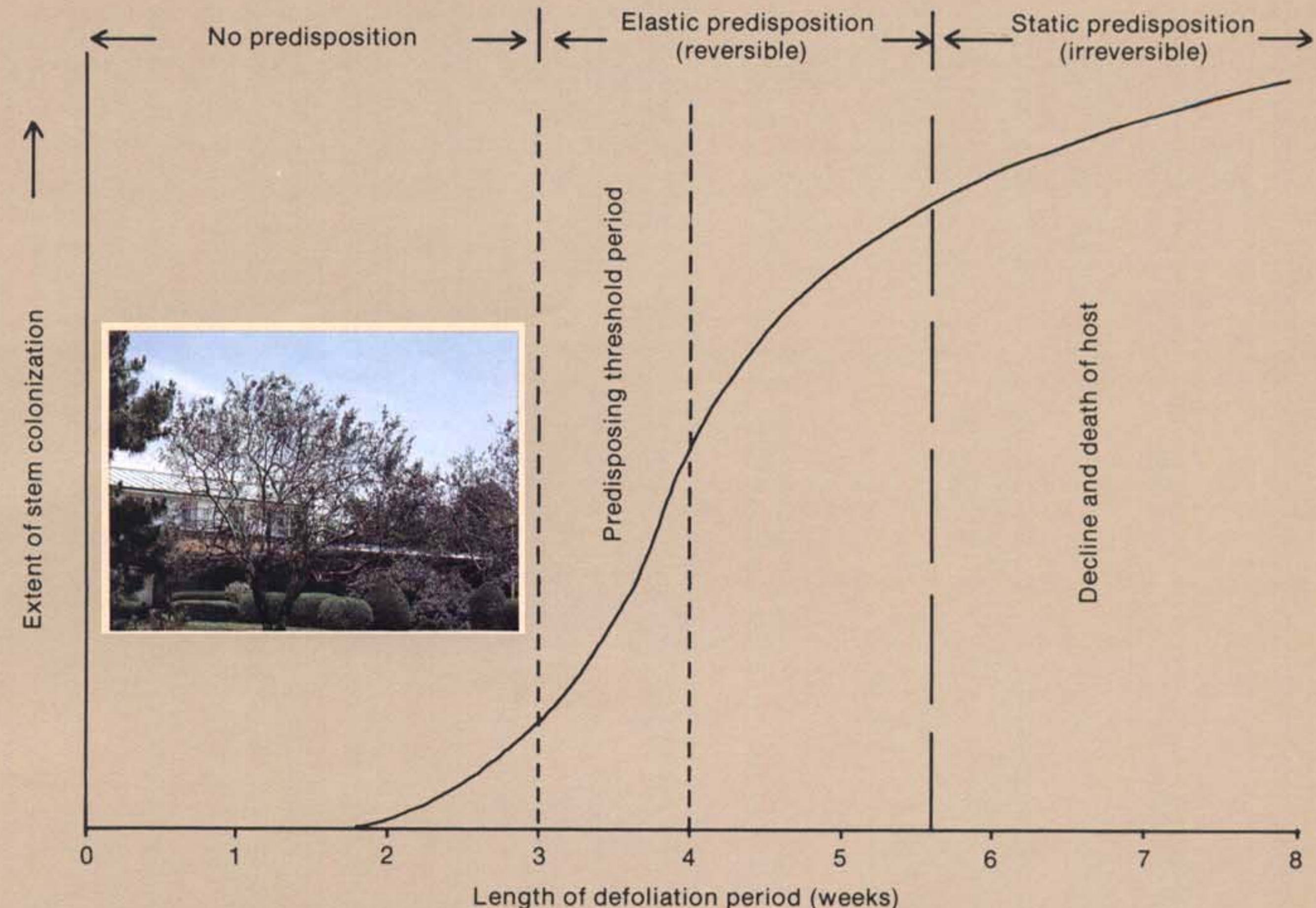

Fig. 4. Predisposing effects of defoliation stress on colonization of woody stems by nonaggressive stem canker fungi. (Inset) Apple scab defoliation of flowering crab.

freezing injury and grew normally after bud break. Apparently, either the predisposing threshold level of freezing was independent of physical freezing injury or the level of injury was too low to be detected visually or by most plant hardiness assays.

The predisposing effects of freezing near the threshold level were reversible, and stem cankers healed when growth resumed. By inoculating stems at various time periods after thawing, Wene (17) found that woody stems remained predisposed for a period of about 9 days, after which they were again resistant to fungal attack. Under field conditions, cankers that appear on plants stressed by freezing often callus at the margins during the growing season (Fig. 3), indicating that predisposition is elastic or reversible. In a few cases, when visible freezing injury followed controlled freezing or freezing in the field, cankers continued to expand until stems were girdled and killed. Thus, freezing predisposition may become static or irreversible if injury is severe.

Transplanting Stress

The frequent appearance of stem cankers and diebacks on transplanted nursery and landscape plants suggests stress predisposition (6). During transplanting of trees and shrubs, root systems, whether bare or balled and burlapped, are pruned extensively, resulting in a loss of root food reserves and a reduction in absorptive root surface.

Whether transplanting predisposes plants by starvation or by water stress is not known. When containerized plants were root-pruned to simulate transplanting stress, then repotted, the stems remained resistant to attack by nonaggressive stem canker fungi as long as plant water potentials remained above −12 bars (11). If water potentials were allowed to fall below the predisposing threshold level for water stress, stem colonization occurred. Under the conditions of this experiment, water stress appeared to be a significant factor predisposing the transplants to disease.

Since other workers have shown that even well-irrigated trees may undergo severe physiologic shock after transplanting due to water stress, a reduction in plant water potentials to below the threshold level is likely the main cause of predisposition of transplants.

Defoliation Stress

A loss of foliage on woody plants, due to leaf drop resulting from water or heat stress or to defoliation by diseases or insects (Fig. 4), may predispose plants to attack by nonaggressive pathogens. Some years ago, forest seedling nurseries were experiencing extensive losses in cottonwood seedlings from blackstem, a stem canker problem thought to be caused by a *Cytospora* species. However, inoculation of cottonwood seedlings with *Cytospora* often failed to produce cankers. Because foliage of cottonwood seedlings was sparse and heavily infected with leaf rust in nurseries where blackstem was prevalent, we suspected that damaged plants were weakened or stressed. When potted cottonwood seedlings were inoculated with *Cytospora* and manually defoliated at weekly intervals, no cankers formed initially. After several weeks of continual defoliation, however, typical blackstem cankers appeared suddenly on all defoliated stems, while nondefoliated plants remained healthy.

Although the largest cankers were associated with *Cytospora* inoculations, many blackstem cankers were caused by infections by other fungi (7). Apparently, the black cankers were merely symptoms of infection on cottonwood stems and were not typical of any single pathogen. Subsequent studies with artificially induced defoliation stress, using other tree and shrub species inoculated with several nonaggressive canker fungi, confirmed that defoliation beyond a threshold period of 3–4 weeks predisposes woody stems to fungal attack (9). If plants were allowed to refoliate within a certain period, predisposition was reversible and canker formation ceased. Prolonged defoliation, however, resulted in irreversible predisposition, and plants continued to decline and die from girdling cankers (Fig. 4).

In recent years, extensive defoliation of oaks and maples by cankerworms in the Midwest has been followed by decline and death of trees due to cankers and boring insects (9). In the northeast, maples defoliated by the gypsy moth often succumb to attack by the root rot fungus *Armillaria mellea* (15). Thus, defoliation at a critical period or repeated defoliation over several years may stress plants beyond a threshold level and result in static predisposition to nonaggressive pathogens.

Differences in Stress Effects

Some significant differences have been noted in the predisposing effects of environmental stresses on woody plants. Although threshold levels must be exceeded in all the stresses we have investigated, a minimum period of days or weeks at predisposing levels is required with water or defoliation stress before plants are predisposed. In contrast, predisposition by freezing occurs whenever stem temperatures reach the threshold degree. In addition, patterns of colonization by canker fungi in stems of plants predisposed by freezing are nearly opposite to those resulting from drought or defoliation (Fig. 5). Bark and wood tissues near the cambium are extensively colonized in stems stressed by drought or defoliation. If the canker is expanding, the pathogen can often be isolated from bark and young wood beyond the canker margins, with much less colonization in older wood. This is in contrast to stems stressed by freezing, where the oldest wood tissues surrounding the pith are colonized, often for a considerable distance beyond the canker margins. In many cases, canker fungi cannot be recovered from bark or young wood at the canker margins. This effect of freezing on older wood is supported by the work of others on plant hardiness, who found that bark and cambium can withstand as much as 20 C more cold than the wood layers surrounding the pith.

Striking differences in stress effects on predisposition have also been noted in relation to the portion of the plant affected. Water or defoliation stress usually predisposes the entire plant, including the root system, to attack by nonaggressive pathogens. Freezing stress,

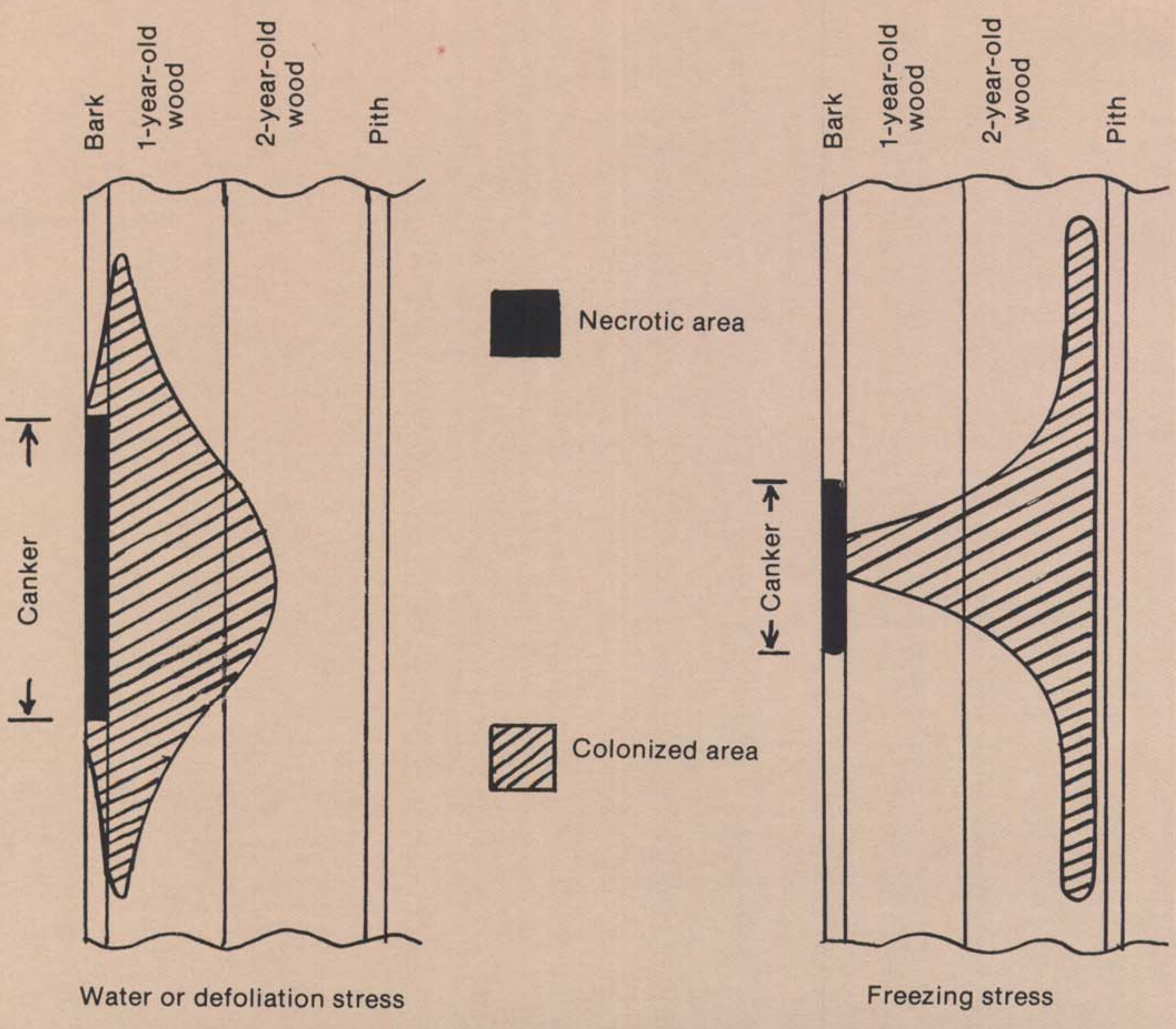

Fig. 5. Patterns of colonization in bark and wood of 2-yr-old woody stems predisposed by water, defoliation, or freezing stress.

however, predisposes only that portion subjected to temperatures below the threshold temperature. By insulating root systems and portions of stems, we were able to differentially freeze whole plants, simulating conditions that may occur when trees and shrubs are protected by mulch or snow cover. Canker fungi colonized only the bare stem portions exposed to predisposing temperatures and did not grow into insulated portions of intact stems (18).

How Can Stress-Related Disease Be Prevented?

Host species vary in sensitivity to different stresses. Some species are easily predisposed by freezing yet are barely affected by water stress. Others are predisposed by water or freezing stress but remain resistant to prolonged defoliation. Knowing which stresses are important in predisposing a given host species is therefore essential if disease management is to include measures to prevent stress predisposition. Methods have been developed for subjecting woody plants to some of the most common stresses, and we are continuing to investigate the relative importance of individual stresses in the epidemiology of diseases we suspect result from stress predisposition. Hopefully, this information will be useful for effective disease management.

Results from research on predisposition in woody plants under controlled conditions have provided new insights into how environmental stresses influence disease. Pathogens that cause cankers, diebacks, and root rots on stressed plants are usually nonaggressive fungi or bacteria that are saprophytes in wounds or dead plant parts. Many of these organisms can be isolated from asymptomatic stem and root tissue of vigorous plants and are commonly thought of as nonpathogens or "secondary" organisms. When plants are subjected to predisposing stress, however, these organisms attack weakened host tissues, causing lesions and eventually girdling, dieback, or plant death. Without these organisms, plants recover with no apparent adverse effects as soon as stress is relieved. Are the organisms primary or secondary causes of damage? Considering the combined influence of predisposing stress and attack by nonaggressive pathogens as the primary cause of disease seems most logical, since one without the other will not result in damage.

If nonaggressive pathogens exist within host tissues as saprophytes or nonpathogens, application of protective fungicides and bactericides is not likely to prevent infection. When injected into the soil before inoculated plants were subjected to predisposing stress, the systemic fungicide benomyl protected

Donald F. Schoeneweiss

Dr. Schoeneweiss has been a research plant pathologist at the Illinois Natural History Survey in Urbana since he obtained a Ph.D. in botany and plant pathology from Ohio State University in 1958. He is also an adjunct professor of plant pathology at the University of Illinois. For more than 20 years, he has conducted research on diseases of nursery and landscape plants, with particular emphasis on environmental stresses as predisposing factors in disease.

rooted dogwood cuttings in containers against attack by *B. dothidea* (12). Such treatments may find use in container culture but are probably too costly to be practical for field-grown landscape material.

With each of the most common stresses predisposing woody plants under field conditions—drought, freezing, and defoliation—a threshold level must be exceeded before predisposition occurs, yet plants subjected to threshold levels may not show signs of stress. How then are we to manage plants to prevent stress-related disease damage? In the case of water stress, plants may become predisposed before they wilt. Therefore, a program of irrigation during dry periods or after transplanting, without waiting for plants to wilt, is essential to prevent disease. Woody species sensitive to freezing stress should be protected or placed in a sheltered site, and any practice that delays cold acclimation, such as excessive fall fertilization and watering, should be avoided. Diseases and insects that cause defoliation must be controlled early, and varieties and cultivars subject to foliar problems should be replaced with more resistant ones. Although all these measures are commonly recommended, their importance in control of stress-related diseases may be overlooked. Maintaining a high level of vigor and hardiness is still the most effective means of preventing disease predisposition by environmental stresses.

Many Unanswered Questions

Whole plants grown in containers can be predisposed by artificially induced stresses, but whether plants in the field respond in the same manner has not been adequately demonstrated. Climatic conditions are highly variable, and duplicating natural environmental stresses in the greenhouse or growth chamber is not feasible. In addition, stresses to woody plants vary from year to year. We know that individual stresses predispose plants, but the combined effects of cycled and varied stresses is not clear (1). For example, atmospheric pollutants such as sulfur dioxide increase transpiration and may contribute to water stress predisposition. If plants predisposed by freezing during the fall or winter are subjected to water stress during the growing season, is the extent of damage greater than with either stress alone? Do plants that drought-harden under mild water stress become less sensitive to the predisposing effects of additional drought stress? Why are vigorous plants resistant to attack by nonaggressive pathogens that gain entrance and are in intimate contact with host cells? Do stresses predispose plants by reducing or disrupting host defense responses and if so, what host processes are affected? These and many other questions remain unanswered.

At present, far more research effort is devoted to the influence of stress on diseases of agronomic crops than on diseases of woody plants. Recent studies on the effects of water stress on carbon fixation and nutrient transport suggest that nutrient depletion or imbalance may influence predisposition. These stress effects may be similar to defoliation stress or may contribute to the total effect of other environmental stresses on disease. Much work is needed on stress predisposition in woody plants, but the increasing worldwide interest in the influence of stresses on plant survival and production will undoubtedly stimulate further research.

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