Role of Stress in Predisposing Trees to Insect Colonization: Implications for Plant Health Care[1]

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Abstract

Plant health care is a program of preventive maintenance, based on the use of cultural, biological and chemical tactics, to enhance plant appearance, structure and vitality. Trees planted in the urban landscape are considered to be stressed and predisposed to successful colonization by many insects. This presumption that there is a simple index between vitality and stress, and that stressed trees are predisposed to colonization, may not always be true. The relationship between tree vitality and susceptibility to insect attack is highly complex. Tree susceptibility to insect colonization does not increase continuously with stress. Recent studies have indicated that mild stress may improve tree defenses and that a plant health care strategy aimed at maintaining rapid tree growth may not reduce susceptibility to insects. Extension specialists and researchers need to focus their efforts on understanding tree defense strategies and developing cultural recommendations aimed at improving defenses rather than growth.

Index words: integrated pest management (IPM), plant health care, tree defenses, vitality.

Significance to the Nursery Industry

Ornamental plant maintenance is becoming a significant part of the landscape-nursery industry, with an increasing number of companies performing maintenance as well as design/build and growing. While nursery production focuses on growth, achieving a salable plant in the shortest possible time, landscape maintenance focuses on maintaining established and generally mature plants The strategies for maintenance differ from those needed for growth. Plant health care provides a useful framework for managing plants in the ornamental landscape. An important part of plant health care is to develop a better foundation for plant health care strategies and tactics.

Introduction

Plant health care (PHC) is a management program that utilizes proactive strategies and tactics to improve the appearance, structure and vitality of landscape plants (1). While the phrase 'plant health care' is relatively recent, the strategies and tactics employed, pruning, cabling, and irrigation among others, have long been cultural practices used by the landscape maintenance profession. What is new, however, is the concept of combining and coordinating these cultural practices into a single program designed to manage the overall health of landscape plants. The plant health care philosophy is being adopted by the landscape maintenance industry as a long-term and cost-effective means of managing landscapes (50). Commercial plant health care programs are primarily focused upon the management of trees and shrubs, but the principles can be applied as well to other landscape plants such as turfgrasses. While plant health care is just becoming established, the idea of managing landscapes rather than individual plants is not new. Many landscape maintenance companies developed integrated pest management (IPM) landscape programs during the 1980s. These programs were primarily pest management services. They focused on monthly property visits to scout for pests and provide any necessary pesticide treatments. These programs had mixed success in attracting and maintaining clients (2). The philosophy of PHC expands from IPM in that the focus of the program is on the plant, not the pest. The plant and its ecological requirements become the center of management (33, 54). Plant health care, however, does not displace IPM, but instead incorporates it into PHC strategies and tactics.

The plant health care approach is expected to have greater client acceptance than has been experienced with IPM-based landscape maintenance services (1). Marketing studies have indicated that there is strong consumer interest in plant-focused maintenance programs (50).

Several national organizations including the USDA Forest Service and Cooperative Extension Service, the National Arborist Association, the National Landscape Association, and the International Society of Arboriculture are creating a wide array of educational materials and programs designed to promote the PHC approach to the landscape maintenance industry and the general public. This rapidly expanding management approach has many areas needing further development. The highest priority, however, is to better establish the underlying bases for the PHC approach. Without this, PHC becomes a collection of management strategies and tactics lacking a unifying framework.

Plant health and urban stresses. The primary goal of PHC is to maintain or improve plant health. Plant health is, in part, a composite of plant vigor and vitality. These terms, vigor and vitality, are often used interchangeably, but they are not synonymous. Vigor is a static property, the genotype's capability to survive injury, while vitality is dynamic, the plant's ability to grow and reproduce within the limits of its vigor (49). Plant health care practitioners cannot influence vigor

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beyond selecting superior genotypes for planting. Instead, practitioners focus on improving vitality through a variety of strategies that include nutrition and irrigation management among others. A frequently stated objective for the application of these strategies is to minimize or eliminate stresses (39). Stress is also a commonly used term in tree care, yet it lacks an exact biological definition. A general definition of stress is any environmental factor that decreases plant growth and reproduction (37). While a distinction is sometimes made between stressed and non-stressed trees, stress is a matter of degree rather than merely presence or absence (22). Stress can take the form of long-term, static, predisposing factors such as an unfavorable climate or soil type. It may also result from unpredictable short-term factors referred to as incitants (29). These incitants include such diverse factors as insect defoliation, drought and late or early season frost.

While incitants may be biological or physical, their common characteristics are that they are of short duration and result in severe injury to the tree. These predisposing and incitant stresses initiate host physiological changes which create a more favorable environment for contributing stresses such as bark beetles and other phloem boring insects (21). These contributing stresses serve to accelerate the decline of an already highly stressed tree and are often the primary focus of landscape managers and management centers when reacting to problems.

Instead, the focus in PHC is on identifying and modifying predisposing and incitant factors with an emphasis on prevention rather than reaction. A critical, but often overlooked, component of the plant health care approach is selecting trees and shrubs that have the genetic capacity to thrive in urban settings and are good ecological matches for the site (54). The identification of potential predisposing stresses should be an essential part of the landscape design process. Landscape managers, arborists and other plant health care practitioners are seldom included in the design process, but later assume the task of maintaining established plantings. Thus, plant health care practitioners are primarily concerned with alleviating short-term stresses such as drought, defoliation and others. While this may not be an ideal management situation, these short-term stresses do have a significant impact on plant defense systems (47). Understanding this relationship between short-term stresses and tree defenses is the key to the development of ecologically sound plant health care strategies. Although present in all environments, stress is a major issue in urban tree management (52). In urban environments, trees are often planted outside their natural ranges and on sites at the limits of their adaption. Two common stresses in the urban landscape are water and nutrient stress.

Water stress results from the lack of adequate soil moisture to meet the tree's physiological needs and is a common limitation on tree growth. Tree diameter growth is so sensitive to changes in growing season precipitation that growth increments are often used to construct historical precipitation patterns. While drought can be a short-term stress for any tree, the effect may be greater for urban trees due to their vulnerability to water deficit stress. The higher urban temperatures can increase transpiration demands even if adequate soil moisture is available (15).

Adequate soil moisture may be lacking due to a restricted root zone. Trees affected by water deficit stress are often considered more susceptible to pests, and this stress, as well as other environmental stresses, are regarded as primary factors regulating insect attraction (12, 42, 44). Borers are perhaps the most serious threat of all the organisms attracted to drought-stricken trees (30). Borers, particularly phloem and cambial zone feeders, are generally considered to be opportunistic or secondary organisms, colonizing trees already extremely stressed (34). They are considered key pests, common, ubiquitous organisms that threaten the health of important landscape species, and are a significant management challenge for plant health care practitioners (35). Many plant health care strategies are aimed at reducing host susceptibility to this group of organisms.

Nutrient stress related to a deficiency can also affect tree vitality. Nitrogen (N) is the most limiting nutrient for tree growth, and urban trees are often observed to suffer N deficiencies. In the typical ornamental landscape, this deficiency is often the result of a lack of organic matter being returned to the soil, the removal of the A horizon during building construction and other factors. Competition between root systems of turfgrasses and trees may also reduce N availability to the trees (32). This deficiency has led to the common recommendation to routinely add N fertilizers to the soils surrounding urban trees. Trees deficient in nutrients, particularly N, are often considered to be slower growing thus more susceptible to colonization by insects (9, 14).

The relationship between stress and defense. A common theme of PHC programs is to reduce the susceptibility of trees to insects, such as borers, by increasing vitality (50). The common belief that stressed trees are more susceptible to insect colonization has lead to the recommendation that cultural treatments, such as irrigation and fertilization, be used to maintain or improve tree vitality (36, 38, 44). The implication is that there exists a relationship between stress and vitality and that stress is the basic factor in predisposing trees to insect colonization (18). While this approach has provided PHC practitioners with some decision-making tools, it ignores the complexity of host physiological changes that occur in response to stresses and the influence these changes may have on the success of insect colonization.

The fundamental difficulties of the present PHC approach are the beliefs that growth and vitality are synonymous and that the relationship between stress and pest susceptibility is a simple linear one. However, growth and vitality describe different conditions in relation to tree defense systems, and the relationship between stress and pest susceptibility is better described as nonlinear (30).

Trees produce a variety of secondary metabolites that provide protection against pathogens and insects and mites. These secondary plant compounds differ from primary compounds in that they are not considered essential for plant growth and development. In the past, secondary metabolites were described as by-products or plant waste products. However, now the importance of these metabolites is generally recognized (17). They are not waste products but appear to serve primarily for defense (41, 46). These metabolites can be carbon-based and serve as quantitative defenses or nitrogen-based which are more qualitative defenses (13, 41, 45). These metabolites, derived from carbohydrates, lipids and amino acids, require the tree to allocate energy for their construction and maintenance. Trees have limited energy resources to expend on physiological processes and cannot meet all demands simultaneously, but rather must allocate their energy resources (31, 57). Highest on the carbon allocation hierarchy are buds and new foliage, followed by roots, storage, diameter growth and defense (55). Some researchers have suggested that the low ranking of defense on the carbon allocation hierarchy implies that defense is only optimized when trees are vigorously growing. The production of these compounds has been considered to be secondary to the growth process, thus when stress occurs most available energy will be allocated to growth (11). When carbon allocation is viewed in light of plant development, however, a different picture emerges.

Plant development can be described in three phases: cell division, cell enlargement and cell differentiation (26). The first two phases are collectively referred to as growth, an irreversible change in plant size. Differentiation, the third phase, involves chemical and morphological changes that occur in maturing cells such as thickening cell walls and the production of secondary metabolites such as gums, resins, oils and other products (27). While growth processes takes precedence over other carbon demands in a low stress environment, this allocation may shift as stress increases (3). The growth-differentiation balance hypothesis (27) provides a framework for developing sound plant health care strategies that are designed to improve defenses. Environmental factors that slow growth more than photosynthesis can increase the allocation to the differentiation process that limits herbivory. The reverse may also be true. Environmental factors or cultural practices that increase growth may limit the allocation to the differentiation process and increase herbivory.

Internal water deficits are a common occurrence in trees. This deficit can occur from excessive water loss through transpiration or inadequate water absorption or a combination of both. Water deficits have a major effect on a tree's physiological processes and growth, but the initial response to water deficits is a reduction in the tree's growth process. Cell enlargement is inhibited before stomatal closure (19). Cell division is equally sensitive (24). Under moderate water stress, growth may be affected before the photosynthetic rate significantly declines. The products of photosynthesis accumulate in the carbon pool instead of being used for cell growth (20). The differentiation process is not as sensitive to water deficits and may even increase with mild water stress because of the availability of surplus carbon. There can be an increase in the formation of secondary metabolites with moderate water stress.

A tree's response to increasing degrees of stress, in terms of defense production, is not linear. As can be demonstrated with drought stress, a dome-shaped relationship occurs with the production of certain defenses increasing with mild stress and declining as stress becomes moderate to extreme (28, 30). Whether this relationship holds for other stresses is not well documented. However, trees have a limited range of responses to stress so the relationship described with moisture stress may apply to other short-term stresses as well (8). The relationship does appear to also hold true for nutrient stress. Growth is more sensitive to nitrogen limitations than photosynthesis (4). The rate of photosynthesis does not decrease in proportion to the reduction in nitrogen levels, similar to what is observed with moisture deficiencies. Carbon that cannot be used for growth, due to nitrogen limitations, is diverted to the production of defenses (16). High nitrogen fertilizing regimes can also alter allocation patterns. Trees fertilized with nitrogen may have reduced carbon storage as energy is required for the process of converting inorganic nitrogen to amino acids (6). Since the production of defensive compounds depends on reserves, fertilizing may have no effect or may increase, rather than decrease, a tree's vulnerability to insects. Fertilizing trees may have little effect on their response to borer colonization (40). A study of paper birch (*Betula papyrifera*) found that the tree responded to nitrogen fertilizer applications with a reduction in secondary metabolite production (5). This change in resistance with fertilization is not limited to borers. Fertilizing may reduce the resistance of balsam firs (*Abies balsamea*) to spruce budworm (*Choristoneura fumiferana*) (48) and loblolly pine (*Pinus taeda*) to Nantucket pine tip moths (*Rhyacionia frustrana*) (42).

The importance of changes in the defensive characteristics of trees depends upon the feeding strategies of the insect. While borer success in colonizing fertilized trees depends upon the shifting of resources from defense to growth, sap sucking insects avoid many of these same defenses. Their increased success on nitrogen fertilized trees is more related to increased levels of amino acids in the phloem sap rather than in decreased levels of defensive compounds (45).

There can be significant competition for photosynthates between the growth process and the formation and maintenance of defense compounds. Short-term stresses can alter this competition in favor of defense. However, this is not the only influence on the allocation of carbon. Seasonal phenology can create a surplus of carbon beyond that needed for growth. There is a strong seasonal pattern to allocation of energy reserves in trees (7, 27). There are seasonal periods when trees are more susceptible to insect colonization because carbon demands for growth have reduced the production of defenses (28). The creation or extension of favorable conditions may result in growth processes receiving a priority over secondary metabolitism and other processes (3, 5).

These relationships require PHC practitioners to make a clear distinction between growth and vitality. While growth is an integral part of the definition of vitality, the essence of vitality is adaptation and survival, characteristics that depend upon storage and defense. Trees with slow growth may have an exhausted carbon pool and be inadequately defended. Equally possible, however, is that moderate stress may have resulted in slower growth, yet created a surplus of carbon that can be allocated to defense. There is also a third possibility. The slow growth may be inherent, part of the species' life history strategy. The cost of defense can be used to partition tree species into one of two general life history strategies (22, 25). The strategic trade off is to grow slow with more defenses or grow fast with few defenses. Plants, including trees, that inhibit resource-poor environments where growth is limited by water or nitrogen deficiency or other stresses often grow slow, but have strongly developed defenses (8, 10). Tree species categorized as grow fast/low defenses require resource-rich environments that can support rapid growth. Their survival depends upon outgrowing pest injury. Growth may act as a defense for fast-growing trees, but have less impact for trees that grow slowly. The current PHC strategy of creating highly favorable conditions to increase growth, thereby reducing insect susceptibility, may not yield the expected result. It may even have the opposite effect, particularly with tree species following the slow growth/high defenses strategy. Rapidly growing trees may become more vulnerable as changes in carbon allocation patterns limit their defense responses.

Implications for plant health care. Numerous techniques have been suggested for assessing vitality; stem wood production per unit leaf area (56) and cambial electrical resistance (51) are two of the most common. These techniques, while useful, are growth indicators and do not directly measure the underlying physiological changes that relate to the tree's ability to defend itself. A more suitable measure may be winter starch reserves (53). While measuring carbon storage, starch reserves may also be inadequate as the primary variable in determining defensive abilities relates more to fluxes of carbon for defense production rather than total carbon production.

The growth-differentiation balance hypothesis, with its emphasis on changes in allocation patterns, provides a more useful framework for developing PHC strategies. Research should focus on seasonal patterns of assimilation and carbon allocation and the changes in these patterns as the result of varying degrees and types of stresses. These data could be used to clarify the relationship between the growth-differentiation balance and the relative success of pest colonization. The ultimate use of this information will be to provide a base to better manage trees' ability to defend themselves, permitting PHC managers to evaluate tree vitality and develop strategies that focus on improving vitality rather than growth. Extension outreach efforts should also go beyond providing care prescription such fertilizing and be aimed at educating arborists and other tree care providers on tree defense strategies.

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