The Resource Allocation Trade-Off – *Part 2*

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**Learning objectives—
The arborist will be able to**

- understand the concept of tree carbon budgets and allocation patterns
- understand how nutrient availability affects the carbon allocation patterns of trees
- understand how trees acclimate to low-nutrient sites
- understand how carbon allocation patterns relate to pest resistance and stress tolerance

Fertilization and Tree Resistance to Insects

Fertilization commonly is considered to enhance the insect resistance of trees. However, there is little evidence to support this claim. To the contrary, the overwhelming majority of published studies strongly support the generalization that fertilization decreases the tree resistance to insects. Fertilization has been shown to decrease tree resistance to sucking arthropods, including aphids, adelgids, scales, psyllids, plant bugs, lace bugs and spider mites. Fertilization has also been shown to decrease tree resistance to chewing insects, including caterpillars, sawflies, leaf beetles, leafminers, and shoot and stem borers, as well as browsing mammals, including deer, moose and hares.

The general pattern that fertilization decreases tree resistance to insects has emerged in spite of great variation among studies in their experimental methodology, which includes the use of deciduous and evergreen species; mature and immature trees; and great variation in formulation, rate, and timing of fertilizer applications. Furthermore, similar patterns have been documented in forests across naturally occurring gradients in soil fertility. These findings suggest that fertilization influences insect resistance via general responses of trees to increased nutrient uptake, rather than through specific effects of particular formulations or timing of application.

Fertilization decreases insect resistance by increasing the nutritional quality of the plant for the insect and by decreasing concentrations of defensive chemicals known as secondary metabolites, or allelochemicals. The nutritional quality of plants plays a central role in their resistance to insects. As an essential component of protein, nitrogen generally limits the growth and reproduction of insects, as it does plants. The nitrogen content of insects ranges from seven to fourteen percent dry weight, while that of plants averages about two percent. Because of this discrepancy, the growth and reproduction of plant-feeding insects are almost always limited by the low nitrogen content of their hosts and almost always increase as the nitrogen content of the plant increases. Increased nitrogen content is virtually a universal response of plants to fertilization. Hence, fertilization almost always increases the nutritional quality of plants for insects.

To protect themselves from their natural enemies, plants produce toxic defensive compounds known as allelochemicals, or secondary metabolites. Thousands of such compounds have been isolated, including phenolic compounds such as tannins, terpenes (found in pine resins and many herbs), alkaloids (for example, nicotine and morphine), and cyanogenic compounds (cyanide-producing compounds) found in the foliage of cherries and other plants. The defensive role of these compounds against insects, pathogens, and mammals is well documented. Many studies have shown fertilization to decrease concentrations of allelochemicals in trees, and substantial evidence indicates that this decrease is the result of a trade-off between growth and defense. Slower-growing plants have been shown to have higher concentrations of defensive compounds and to be more resistant to insects.

Effect of Fertilization on Ability of Trees to Tolerate Defoliation

Fertilization of defoliated trees is frequently recommended based on the logic that defoliation will have less impact on fertilized than on unfertilized trees. Showing that fertilization lessens the impact of defoliation requires a direct comparison of fertilization effects on both defoliated and nondefoliated control trees. I am aware of only four such studies with woody plants: two with red oak seedlings, one with paper birch and sugar maple saplings, and one with containerized willow shrubs. None of these studies found fertilization to increase the ability of the plants to tolerate defoliation either during the year of defoliation or in the year after. Any positive effects of fertilization on the nutrient budget of the defoliated trees may have been counteracted by the fact that fertilization also can decrease stored carbohydrate reserves. The growth of defoliated trees may be limited more by their supply of carbon than their supply of nutrients. Studies with mature trees are lacking, but there are no data to support claims that fertilization can provide special benefit to defoliated trees (Figure 5).

Figure 5. Gypsy moth is the most important defoliator of deciduous trees in the eastern United States. Many studies have shown that fertilization increases the survival, growth and reproduction of chewing and sucking insects, including gypsy moth. There is no evidence that fertilization increases the ability of trees to tolerate defoliation.

Fertilization and Drought-Stress Tolerance

Fertilization also has been shown to decrease the drought-stress tolerance of trees. It is well documented that increased nutrient availability stimulates shoot growth proportionally more than root growth, which can increase the water demands of the tree to a greater degree than its ability to acquire water during drought. Hence, fertilized trees can be especially susceptible to drought stress. For example, in a forest planting of mature Monterey pine, drought caused more tree dieback and mortality in the fertilized than in the control plots because soil water was depleted more rapidly by the large canopies of the fertilized trees. In other studies, fertilization has been shown to decrease drought tolerance of red oak, chestnut oak, American elm, crabapple, and Norway spruce, as well as red, jack, lodgepole, and Scotch pines. Fertilization also may decrease drought-stress tolerance by decreasing concentrations of secondary metabolites, such as phenolic compounds and terpenes, which have been shown to protect leaves from drought-stress injury.

Trees and other plants have a remarkable ability to acclimate to their environment, largely because of great flexibility in the way they allocate their resources among growth, maintenance, reproduction and defense. Because plants operate on a tight carbon budget, they allocate their limited carbon in ways that increase the acquisition of the resources that most limit their growth in a particular environment.

Trees grow faster in fertile environments primarily by using a greater proportion of carbon to increase their total leaf area. However, because of trade-offs in the carbon budget, root growth is proportionally decreased, as are concentrations of defense and storage compounds. Under low-nutrient conditions, trees produce fewer and smaller leaves. Trees also increase their root:shoot ratios, which increases nutrient uptake. In this way, trees adjust the size of their canopies and their growth rates to the limited supply of nutrients, and they maintain high rates of photosynthesis and a strong energy budget even when they are growing slowly. Studies have shown that nutrient-“stressed” plants accumulate higher concentrations of defensive compounds and storage reserves and are more resistant to insects and tolerant of drought stress.

These responses make sense from an evolutionary standpoint. If a tree in a fertile environment does not grow rapidly, it soon will be suppressed by faster-growing competitors. In nutrient-limited sites, fast growth is not critical because its neighbors are not growing fast either, but higher levels of defensive compounds and greater root growth would increase insect resistance and stress tolerance in environments where the potential for regrowth of lost or damaged tissue is limited.

Clearly, fertilization can increase the growth rate and aesthetic quality of trees, especially on extremely nutrient-deficient soils characteristic of many urban sites. Furthermore, no controlled studies have addressed whether fertilized trees actually receive more insect damage in urban landscapes, although a large number of published studies suggest that potential. It is clear, however, that a large body of evidence refutes claims that benefits of fertilization include increased insect resistance and stress tolerance. There is a role for prescription fertilization in a Plant Health Care program, especially for high-maintenance landscapes. However, fertilization programs should be implemented with an understanding of potential consequences for pest resistance and stress tolerance.

Corresponding test questions for this article are available in the ISA compendium entitled “Tree Maintenance.” The compendium is a collection of *Arborist News* CEU articles with corresponding test questions worth a total of 9 CEU credits. ISA compendiums are available to purchase from the ISA online at www.isa-arbor.com or by phone at 888-472-8733.

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