# What Keeps Trees Free From Attack by Insects & Diseases?

By Clive G. Jones

F.A. Baker/Bugwood & Univ. of Ga.

**Marssonina leaf spot on an infected aspen leaf.**

There is a tremendous diversity of insect herbivores and plant pathogens on trees, including a very large number of species that can adversely affect tree growth, survival and aesthetics. Given that every insect herbivore and plant pathogen species on every tree species is a unique combination, it can be pessimistically argued that managing problems will consist of specific local solutions that depend entirely upon the tree species and its condition, the local environment, and the particular insect or pathogen species. While I would never deny the critical importance of case-specific knowledge for managing these problems, in this series of three articles I argue that an understanding of general ecological relationships among trees and their consumers can do much to enhance management of insect and disease problems on trees.

The articles summarize our current understanding of relationships among trees, their insect herbivores and plant pathogens, and the environment, showing how this understanding may be of use in arboriculture. Patterns of insect and disease attack on trees have relatively orderly and predictable underlying ecological causes. These causes indicate that it may be possible to risk-rate trees and situations most likely to lead to problems, and suggest management strategies based on those causes that might help reduce the risk, frequency and severity of insect and disease problems. In the three articles I ask three questions:

- ♦ What keeps trees free from attack by insects and diseases?
- ♦ What causes insect and disease outbreaks on trees?
- ♦ Why do trees vary in suitability to insects and diseases?

The answer to each question in one article leads to the next question in the next article, and each answer has arboricultural implications.

## How much damage do trees receive?

One of the most interesting features of insect herbivores and plant pathogens on trees is that they are often conspicuous by their absence. Despite the fact that there are tens of thousands of these species feeding on trees worldwide, with many capable of very high rates of reproduction, trees are not routinely devastated by either. In fact, the overwhelming majority of insects and pathogens on trees are rare most of the time and cause relatively little damage.

We can draw this conclusion from estimates of how much new tree material produced by trees each year is actually eaten by insect herbivores and plant pathogens. Values for these estimates in different forest ecosystems – usually measured as the percentage of annual net primary production (ANPP) consumed – vary a lot from year to year and place to place, but on average only about 8 percent of ANPP is consumed each year by insect herbivores.

Although there are no directly comparable estimates for pathogens, these organisms are also reported to cause similarly low average levels of damage to trees. Estimates of combined consumption by both insect herbivores and plant pathogens have also been made by measuring how much tree material directly decomposes without being first eaten by either insect herbivores or plant pathogens. In temperate forests, about 90 percent ANPP (mostly litter) directly decomposes. This means that only about 10 percent ANPP is consumed by insect herbivores and plant pathogens. This amount is comparable to the direct estimate of 8 percent ANPP. So, on average, insect herbivores and plant pathogens on trees consume relatively small amounts and are often rare.

## What keeps trees green?

What keeps insects and pathogens generally rare and trees usually green? Are the trees responsible? Is it abiotic or biotic environmental factors, or is it some combination of all these factors? Based on findings accumulated from research in many systems over the years, three general factors emerge as being important.

First and foremost, plants – and trees are no exception – are generally poor quality food to both insect herbivores and plant pathogens, and low food quality is a major factor keeping both insect herbivores and plant pathogens rare.

Second, the natural enemies of insect herbivores – viruses, bacterial and fungal pathogens, small mammals, birds, ants, spiders, predatory beetles, insect parasitoids and the like – play a key role in keeping the densities of insect herbivores low and trees green. There is also good evidence that plants and natural enemies jointly conspire to help keep insect herbivores rare. The generally low food quality of plants keeps the growth and reproduction of insect herbivores low, which then makes it easier for natural enemies to further suppress their numbers. In contrast, although some plant pathogens do have a few natural enemies, these organisms appear to play a very minor role in determining the abundance of plant pathogens.

Lastly, the weather is an important constraint on population growth rates of both insect herbivores and plant pathogens because it often determines the degree to which conditions are favorable for growth, survival, development and reproduction.

## A focus on tree food quality

For the rest of this article I will focus on the role of tree food quality. There are a number of reasons for doing so. First, food quality consistently emerges as an important factor. Even in circumstances where natural enemies or the weather may be playing the most important role, the influence of food quality can often still be seen.

Second, the important effects of food quality arise from a relatively limited number of general mechanisms that occur across a diversity of plant species with their even more diverse assemblages of insect herbivores and plant pathogens. In contrast, the effects of weather and natural enemies tend to be far more idiosyncratic. The particular natural enemy species or weather conditions responsible for keeping herbivore or pathogen species rare invariably differ from species to species, and can even differ for the same species from one time period to the next.

Third, unlike the weather and natural enemies, food quality is a factor that arborists may have the potential to influence directly. An examination of the mechanisms responsible for low plant food quality reveals some important general traits and relationships that can potentially be managed to reduce insect herbivore and plant pathogen damage on trees.

## Why trees are poor quality food

An interesting pattern emerges if you compare the performance – survival, growth or reproduction – of insect herbivores on synthetic diets and plant pathogens in culture media, with their performance on living plant tissues. In many cases, performance on plant tissues is often much lower than can be achieved on synthetic diets or culture media. So, although many insects and pathogens can have high rates of growth and reproduction when food quality is high, plants are generally such poor quality food that insect herbivores and plant pathogens spend most of their time eking out an existence. Why are plants such poor quality food? There are three general reasons:

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**Elm spanworm (ennomos subsignarius); male and female moths under an aster leaf.**

### 1. Low nitrogen content.

First and foremost, the nitrogen content of insect body tissues and fungal and bacterial cells is much higher than the nitrogen content of the plant tissues they eat. The nitrogen content of plants ranges from extremely low levels of less than 0.0003 percent dry weight in xylem fluid to about 5 percent in leaves and up to 8 percent in seeds. In contrast, the nitrogen content of animals, fungi and bacteria ranges from about 9 to 15 percent dry weight, and the nitrogen content of insect eggs and fungal spores and can be even higher. (See Figure 1.) Most leaf-feeding insects contain about five times more nitrogen in their body tissues than the leaves they eat, and for insects that feed on phloem or xylem sap, the difference is much greater.

Since the nitrogen in protein is critical for growth and reproduction, the much lower nitrogen content of what is eaten versus what the organism, its eggs or spores are made up of, is a fundamental constraint on growth and reproduction.

Evidence that insect herbivores and plant pathogens are limited by the low nitrogen content of the plants they consume is convincing. For example, there is often a strong positive correlation between the growth and reproduction of insect herbivores, mites and plant pathogens and the nitrogen content of the tissues of their host plants, including trees. A very large number of experimental studies fertilizing plants with nitrogen, again including trees, have shown that fertilization has a positive effect on insect and mite growth, survival, reproduction and/or density in a large majority of cases. Similar results have been found for plant pathogens, with positive effects of plant nitrogen fertilization on pathogen growth, survival or reproduction occurring in over 70 percent of about 50 studies.

### 2. Variable nitrogen.

The second reason also relates to nitrogen. It is not just the low average nitrogen content of plant tissue that is a problem for insect herbivores and plant pathogens. Tissue nitrogen content is highly variable in space and time. For example, a leaf can vary by well over 100 percent in nitrogen content across the growing season. Similarly large amounts of variation can be found between higher nitrogen sun leaves and lower nitrogen shade leaves of trees, and even bigger differences can be found between leaves of trees growing in nitrogen-rich compared to nitrogen-poor soils.

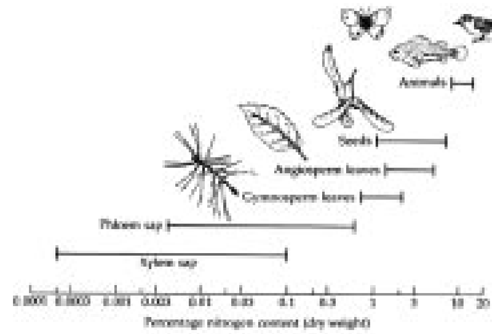
Variation in nitrogen content has many important consequences to insect herbivores. Leaf nitrogen varies substantially across the season, going from higher values in buds and expanding leaves to much lower levels in mature leaves, and then rising again in senescing leaves. Aphid reproduction is restricted to just the two periods when there is adequate nitrogen in growing and senescing leaves.

The non-uniform distribution of nitrogen means that mobile insects have to make a substantial energy investment just to find food. For example, caterpillars of some specialist tree leaf-feeding Lepidoptera may expend as much as 50 percent of their energy budget simply moving around the plant to find an adequate leaf amidst a sea of low nitrogen leaves. For plant pathogens, variable nitrogen means that there is a high likelihood that spores will fall on tissues where the nitrogen content may be too low to support any growth or reproduction.

### 3. Defended nitrogen.

The third and last reason plants are such poor quality food again relates to nitrogen, but in a more complex manner. Nitrogen in plant tissues is mixed with a tremendous diversity of other ingredients. Some of these ingredients are found in virtually all plants, while others are much more idiosyncratically distributed among plant species and genotypes. Nevertheless, these ingredients can all be thought of as collectively making it risky, difficult and costly to extract and process the nitrogen.

**Figure 1**




**Ranges of nitrogen content in plant and animal tissues, as percent dry weight shown on a logarithmic scale. The nitrogen content of fungi and bacteria are not shown, but range from ca. 9 percent to 15 percent. Reproduced with permission from Figure 2.6 in Strong. D.R., Lawton, J.H. and Southwood, T.R.E. 1984. "Insects on plants: community patterns and mechanisms," Blackwell Scientific, Oxford, UK.**

Nitrogen in leaf, stem and roots always co-occurs with large amounts of indigestible cellulose, fiber and lignin. In fact, trees and other woody plants generally have the lowest nitrogen content and the highest concentrations of fiber and lignin of all plants. Nitrogen in phloem or xylem is massively diluted by water and sugars and has to be concentrated. Most plant tissues, particularly those of trees, contain phenolic compounds such as tannins that form chemical complexes with nitrogen when cells are injured. These complexes may inhibit digestion and may have to be disassociated before digestion. In other plants, including some tropical trees, most of the nitrogen is in the form of compounds like alkaloids that are toxic and non-utilizable, and plants contain a tremendously diverse array of non-nitrogen defensive chemicals that must be overcome in order to take advantage of any nitrogen that is present.

Although insect herbivores and plant pathogens have evolved sophisticated adaptations for dealing with nitrogen limitation and the problems of finding and extracting nitrogen amidst the specific defenses of their host plant, most still remain fundamentally limited by poor food quality. So the leaf-feeding caterpillars that expend as much as 50 percent of their energy budget wandering around trying to find suitable the leaves may expend the remaining 50 percent on the cost of extracting and digesting the adequate plant nitrogen found in these few leaves.

In summary, a major reason why trees are usually relatively free from insect and disease attack is because they are poor quality food. Insect herbivores and plant pathogens face fundamental constraints on their survival, growth and reproduction because plant tissues have low and variable nitrogen concentrations, and because plants have a tremendous diversity of defensive mechanisms that make the extraction and processing of this limited nitrogen difficult, dangerous and costly. While I do not want to dismiss the importance of natural enemies or the weather as major influences, the intrinsically low quality of plants as food is very likely the most



consistently and generally important constraint limiting the abundance of insect herbivores and plant pathogens, keeping them rare and the world green.

## Tree food quality and arboriculture

What are the management implications of finding that trees are generally poor quality food for insect herbivores and plant pathogens?

First of all, as is the case in natural ecosystems most of the time, most trees will be relatively free from attack by insect herbivores and plant pathogens, and severe damage will be uncommon. While this does not preclude the need to take care of problems when they arise, it does mean that the need for active intervention will occur relatively infrequently.

Second, from the perspective of minimizing problems, arborists should try to avoid directly increasing the nitrogen content or decreasing the defenses of trees. Fertilizing trees with nitrogen, particularly with large or repeated doses, often increases tissue nitrogen in many tree species. At the same time, for reasons that will be explained in the third article, nitrogen fertilization also tends to simultaneously reduce tree defenses. So, although fertilization can increase tree growth rates, if it also results in increased insect or disease problems, there may be no net gain from fertilization.

Third, arborists should try to be aware of the existing local environmental conditions that could promote increases in tissue nitrogen or decreased defenses. These conditions will be discussed in more detail in the second article, but, for example, trees growing in particularly nitrogen-rich soils, growing in or next to lawns that are being heavily fertilized, or growing where agricultural fertilizer runoff is high may be more likely to experience insect and disease problems.

Fourth, for reasons that will be explained in the last article in the series, some types of tree species have lower nitrogen content and higher concentrations of defenses in their tissues than others. Irrespective of the value of using tree genotypes that are resistant to a specific insect or pathogen, arborists may also want to select these "low nitrogen/high defense" types of trees for planting because they can have a lower overall risk of insect and disease problems.

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## Suggested further reading.

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