Why Do Trees Vary in Suitability to Insects and Diseases?

By Clive G. Jones

This article is the third in a series of three examining ecological relationships among tree food quality to insects and pathogens, the environment and tree growth rates. The relationships have important implications for arboricultural management of insect and disease problems. The articles are based on a paper presented at "Trees 2000: Challenges for the future," a conference organized by the Tree Advice Trust and the Institute of Chartered Foresters, Keele, UK, that will appear in a book of the same name.

Introduction

There is a tremendous diversity of insects and 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 always consist of specific local solutions that depend upon the tree species and its condition and the local environment. While I would never deny the critical importance of case-specific knowledge for managing these problems, in this series of three articles (See *TCI* October and November 2001) I argue that an understanding of general ecological relationships among trees and their consumers can do much to enhance management.

The articles summarize our current understanding of relationships among trees, their insects and pathogens, and the environment, showing how this understanding may be of use in arboricultural management. 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 first article I asked: What keeps trees free from attack by insects and diseases? On average, insects and pathogens were relatively rare on plants, generally causing low amounts of damage. Although the natural enemies of insect herbivores (but not pathogens) and the weather do play an important role in keeping these organisms rare, the inherently low quality of tree tissues as food may well be the most important factor. Trees have low and very variable nitrogen content, a critical nutrient for insects and pathogens, and they contain a diversity of physical and chemical defenses that collectively make the extraction and processing of this limited and variable nitrogen difficult, dangerous and costly. By keeping tree tissues low in nitrogen and high in defenses, arborists may be able to reduce the frequency and severity of insect and pathogen problems on trees.


L.R. Barber - USDA/Bugwood & Univ. of Ga.

Webbing coneworm larva on loblolly pine cone.

In the second article I asked: What causes insect and disease outbreaks on trees? Outbreaks do periodically occur – despite poor food quality. Outbreaks are often caused by environmentally induced increases in food quality. Increases in tissue nitrogen content and/or decreases in defenses – hence increased food quality – can result when trees respond to an increase in the availability of environmental resources or stress and damage. By reducing the likelihood of environmentally induced increases in tree food quality, arborists may be able to reduce the frequency and severity of insect and pathogen outbreaks on trees.

In this final article I ask: Why do trees vary in suitability to insects and diseases? Does the answer to this question have anything to do with the answers to the first and second questions, and what are the management implications of the answer?

Variation in damage and predicting tree food quality

So far we have seen that low food quality is a major factor keeping insects and pathogens rare on trees most of the time, and that increases in food quality play a key role in causing outbreaks on trees. We have focused on explanations that can be applied to trees in general. But of course, the fact that most trees are green most of the time does not mean that all trees have the same amount of low-level damage, nor does it mean that outbreaks result in uniform amounts of damage to all trees. In reality, there is considerable variation in the amount of damage from tree to tree within and between species. During outbreaks, some trees are untouched, some are lightly damaged, while others are heavily attacked. These patterns occur both within and between sites for trees of the same and different species. Is this variation in consumer abundance from tree to tree and species to species idiosyncratic and unpredictable, or are there orderly patterns to this variation?

We have also seen that food quality can be expressed in terms of the relationship between tissue nitrogen and defenses, where high food quality generally equates to high concentrations of tissue nitrogen and/or low concentrations of defenses that make the extraction and processing of this nitrogen difficult, dangerous and costly. If food quality plays such a key role, and if we know in general terms what constitutes poor food vs. good food, then is it possible to predict whether or not a tree species or individual is likely to be good or poor food? Can we predict whether or not a particular tree species or individual in a given environment is likely or unlikely to increase in food quality in response to altered environmental resources, abiotic stress or damage?

The short answer is that tree growth rate within and between species is a primary determinant of tree food quality to insect herbivores. This may well be the case for plant pathogens, but as yet, we have less evidence that this is so. There are four ways in which the growth rate of trees is related to food quality.

Tree growth rate and food quality

Inherent growth rate and food quality

The first relationship involving growth rate relates an intrinsic measure of tree growth potential called the inherent growth rate to the baseline food quality of trees and the abundance of insects and pathogens. Tree species and genotypes can be characterized in terms of their inherent growth rate – a measure of the maximum growth rate that a tree species attains when unlimited resources of light, water and nutrients are made available. Inherent growth rate can be measured by growing saplings in common gardens and can be compared across species. Tree species show a wide range of values for inherent growth rates, but here I will just contrast extremes of an inherently fast-growing vs. an inherently slow-growing species and how this relates to food quality for insects and pathogens.

Inherently fast-growing species show marked, rapid increases in growth in response to the addition of light, water or nutrients. They are very responsive to changes in the availability of environmental resources, and very responsive to environmental stress and damage. In contrast, inherently slow-growing species are largely unresponsive to changes in the availability of environmental resources or environmental stress and damage. The marked differences in the maximum growth rates and the degree of environmental responsiveness between these two plant categories reflect a fundamental trade-off. Plants can either grow rapidly or they can protect themselves heavily, but they cannot do both simultaneously.

The trade-off between growth and defense can be used to understand relationships between inherent growth rate, the baseline food quality of different tree species (i.e., the degree to which food quality is better than the lowest quality), and patterns of insect herbivore and plant pathogen abundance (Table 1). Inherently fast-growing species have made a commitment to rapid growth. This "live fast, die young" strategy is well suited to resource-rich, stress-free environments where competition for light and space is intense. Rapid growth in resource-rich habitats allows these species to out-compete slower-growing neighbors, become mature, reproduce, and then die after their inherently slower-growing, longer-lived competitors eventually catch up and overtop them. However, rapid growth is a resource-demanding process requiring high nitrogen in leaves for high rates of photosynthesis and high rates of new leaf production. Most carbon from photosynthesis goes into growth. As a consequence, inherent fast growers store few resources, have low root-to-shoot ratios, and have short-lived tissues. Since these species do not have the resources to both grow fast and invest heavily in defense, their leaves and woody tissues are low in fiber, lignin, tannin and other defensive chemicals, and the tissues are relatively high in nitrogen. So inherent fast growers are generally high food quality to consumers (given that most plants are barely adequate food). Good examples of inherently fast-growing tree species include willows and poplars.

In contrast, inherently slow-growing species have made a commitment to longevity. This "live slow, die old" strategy is well suited to resource-poor and stressful environments where competition for resources is weak. Because growth demands for resources are low relative to the rate with which they are acquired via root uptake and photosynthesis, these species store large amounts of resources, and have high root-to-shoot ratios. Because growth is slow, tissues have to persist for a long time and require protection. Consequently these species invest heavily in defense. Their leaves and woody tissues are high in fiber, lignin, tannin and other defensive chemicals, and the tissues are relatively low in nitrogen. So inherent slow growers are generally of the lowest food quality to consumers. Good examples of inherent slow growers include some oak species, and the Kauri of New Zealand and *Aurucaria* species of Chile that have leaf longevities of 10 to 20 years.

Some of the very first research showing the relationships among tree-inherent growth rates, leaf longevity and food quality to insects found that as leaf longevity increases, tannins and fiber increase. In other words, food quality declines as growth rate declines and leaf longevity increases. As growth rate increases, defenses decline. This relationship has been confirmed from numerous studies.

Compared to inherent slow growers, inherent fast growers are also more likely to support higher densities of insects, have more rapidly growing populations of these organisms, and experience higher amounts of tree damage. The same type of relationship might be expected to hold for pathogens, however, to my knowledge, the relationship has not been investigated.

Inherent growth rate, environment and food quality

The second relationship involving growth rate relates environmental variation to changes in food quality and the likelihood of insect and pathogen outbreaks on tree species with different inherent growth rates (Table 1). Again I will contrast extremes of an inherently fast-growing vs. an inherently slow-growing species. The trade-off between growth and defense can also be used to understand the relationship between inherent growth rate, phenotypic plasticity, and the degree to which food quality is likely to change in response to changes in the availability of resources, or the presence of stress or damage. As pointed out above, the "live fast, die young" strategy requires that growth, development, and physiology be very responsive to changes in the availability of environmental resources, and very responsive to stress and damage. Consequently the tissue biochemistry of inherent fast growers is also very responsive. As a result, the food quality of these species has a high likelihood of changing in response to variation in resources, stress and damage. This does not mean that all changes in conditions lead to increased food quality. Some conditions – those increasing tissue nitrogen or decreasing defenses (e.g., fertilization) – will increase food quality, whereas other conditions will decrease food quality. The particular outcome will depend upon the type of environmental change and the way that the tree species responds to these changes. Variation in environmental resource availability, stress, and damage will generally result in variation in food quality for inherently fast-growing tree species.

In contrast, inherently slow-growing species do not respond markedly to the addition of light, water or nutrients. The "live slow, die old" strategy requires growth, development, physiology, and tissue biochemistry to be relatively unresponsive to changes. Consequently, the tissue biochemistry of inherent slow growers is also unresponsive, and so the food quality of these species has a low probability of changing markedly in response to variation in environmental resources, stress and damage.

These basic differences between fast-growing species and slow growers have important implications for the likelihood of outbreaks of insects and pathogens for those outbreaks that are caused by increases in food quality. (These arguments clearly do not apply to outbreaks caused by natural enemy declines or direct effects of the weather.) We should expect to find a higher frequency of insect and pathogen outbreaks on inherently fast-growing species than inherently slow-growing tree species. While eminently plausible, , explicit tests of these relationships between outbreak frequency and inherent growth rate have yet to be made.

Realized growth rate, environment and food quality

The third and fourth relationships involving growth rate derive largely from the previous two relationships. They relate the realized growth rate of inherently fast-growing tree species to food quality and consumer abundance, and environmentally induced variation in food quality and consumer outbreak potential (Table 1). In essence, these are essentially extensions of the inherent growth rate concept applied to the actual growth rate of plants in a given environment – the realized growth rate. Since, as I have pointed out earlier, inherently slow-growing plant species have relatively invariant growth rates and food quality, these relationships really only apply to inherently fast-growing, phenotypically plastic species. Again, I will exemplify with the extremes, in this case an inherently very fast-growing species such as cottonwood or willow, growing across the broadest range of realized growth rates. So here the trade-off between growth and defense is being applied within a given species for trees growing under different environmental conditions, as opposed to comparisons

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between different species in the same or different environments.

As the availability of environmental resources increases, individuals of inherently fast-growing species usually respond by increasing their growth rates. The increase in growth rate creates a demand for carbon and nitrogen resources, requiring the commitment of high concentrations of nitrogen in leaves to support high rates of photosynthesis, new leaf production, and root growth for exploration of the soil. Most of the carbon from photosynthesis goes into growth and, as a consequence, rapidly growing plants often store relatively few resources. Since fast-growing individuals do not have the resources to both grow fast and invest heavily in defense, the concentration of fiber, lignin, tannin, and other defensive chemicals tends to decline as growth rate increases. At the same time, increased allocation of tissue nitrogen for photosynthesis often results in an increase in tissue nitrogen as growth rate increases. The end result is that food quality to insects and pathogens often, but not invariably, increases as growth rate increases. The caveat of "often, but not invariably" arises because under some circumstances the increase in plant biomass associated with increased growth can end up diluting the concentration of nitrogen in tissues unless nitrogen uptake rates from the soil keeps pace. Nevertheless, numerous studies have now shown a positive relationship between food quality to insects and the growth rate of inherent fast-growers in response to increased resources. Far fewer studies have been conducted with plant pathogens, but there are examples showing similar relationships.

Tree Characteristic	Inherent Growth Rate	
	Fast	Slow
Growth Strategy	Commitment to growth "Live fast, die young"	Commitment to longevity "Live slow, live long"
Environment Type	Resource-rich, stress-free	Resource-poor, stressful
Plant Competition	Strong	Weak
Nitrogen Demand	High	Low
Carbon Allocation	To growth	To storage
Stored Reserves	Low	High
Root/Shoot Ratio	Low	High
Leaf Longevity	Short-lived	Long-lived
Leaf Fibre	Low	High
Leaf Tannin	Low	High
Tissue Nitrogen	High	Low
Tissue Defense	Low	High
Food Quality	High	Low
Phenotypic Plasticity	High	Low
Sensitivity to Resource Availability	High	Low
Sensitivity to Stress & Damage	High	Low
Variation in food Quality	High	Low
Insect Herbivory	High	Low
Pathogen Attack	High*	Low*
Insect & Pathogen Outbreak Potential	High*	Low*
Examples	Willows, Poplars	Oaks, Kauri

Table 1. Comparative growth, physiological, biochemical and ecological characteristics of inherently fast-growing and inherently slow-growing tree species.

*** Plausible hypotheses about patterns that have yet to be widely tested or generally confirmed.**

We should also expect that the higher the realized growth rate, the greater the probability that stress and damage will result in outbreaks – provided trees are not growing at their maximum growth rate (i.e., environmental resources are still limiting, which is usually the case). The somewhat complex rationale is as follows: It is clear that any environmental stress and damage that decreases food quality reduces the likelihood of an outbreak, irrespective of realized growth rate at the time of stress or damage. However, it seems reasonable to suppose that as the realized growth rate increases and food quality increases, any environmental stress or damage that results in yet further increases in food quality has a higher likelihood of raising food quality high enough to cause outbreaks. As far as I am aware, this possibility has not been evaluated.

In summary, the answer to the question

Suggested reading

Bryant, J.P., Chapin, F.S. III and Klein, D.R. 1983. Carbon-nutrient balance of boreal plants in relation to vertebrate herbivory. *Oikos* **40**: 357-368.

Coley, P.D. 1983. Herbivory and defensive characteristics of tree species in a lowland tropical forest. *Ecological Monogr.* **53**: 209-233.

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Herms, D.A. and Mattson, W.J. 1992. The dilemma of plants - to grow or defend. *Q. Rev. Biol.* **67**: 283-335.

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of what causes trees to vary in suitability to insects and diseases, is that tree growth rate – inherent and realized, within and between species – appears to be a primary determinant of food quality to insects and perhaps pathogens.

Tree growth rate and arboriculture

If tree growth rate largely determines food quality to insects and pathogens, and if food quality is a primary determinant of insect and pathogen abundance on trees, and if increases in food quality are a primary cause of insect and disease outbreaks, then it may be possible to use tree growth rate as an insect and disease management tool. A number of possibilities are worth considering.

Knowledge of inherent and realized growth rates might be used to risk-rate tree species, individual trees, sites and environmental conditions for potential insect and disease problems. For example, we might expect the highest risks to be found among inherent fast growers in resource-rich sites with environmental conditions that are most likely to promote rapid tree growth. Conversely, the lowest risks would be expected to occur among inherent slow growers, in the most resource-poor sites under a wide range of environmental conditions, including extremes.

It may be possible to reduce consumer damage and manage the risk of outbreaks by reducing growth rates. For example, could we reduce the risk by replacing inherent fast-growers with inherent slow-growers, or by shifting stand composition from dominance by inherent fast-growers to inherent slow-growers? Of course, any growth rate management plans would have to fit within overall tree management goals and existing pest management strategies. However, it may well be possible to make modifications to existing strategies for monitoring growth and tree condition, planting and replanting, pruning and thinning, managing plant succession, and managing soils, soil organic matter, nutrients and water.

An approach based on these general growth/food quality relationships is not going to be a precise, finely tuned tool. These types of ecological relationships, while sound, are nevertheless subject to many other sources of uncontrolled variation. Such an approach is best thought of as an adjunct to, not a substitute for, meeting the specific requirements of site, tree species, and the particular insect and disease problem. Nevertheless, the approach can take advantage of natural processes that are environmentally compatible, and some degree of augmentation of these processes might be accomplished at low or reasonable cost.

Let me end with posing some general questions that arborists may want to consider. Do current practices tend to promote high or low tree growth rates and the establishment of fast-growing or slow-growing species? What are the consequences of these current practices in regards to insect and disease problems? Would a growth rate management strategy be useful? How would it fit within existing management goals, strategies and practices? Could such a strategy be implemented? If so, where would it be most likely to work and what further information and research is needed?

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