What Causes Insect and Disease Outbreaks on Trees?

Part II

By Clive G. Jones

Introduction

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 argued pessimistically that managing problems on trees will necessarily always consist of specific local solutions that depend upon the tree species and it's condition, local environment and 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.

Sapwood stain caused by Dutch elm disease.

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 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.

Third instar larva of a spruce budworm in a swollen Douglas fir bud.

In the first article (See *TCI*, October 2001) I asked: What keeps trees free from attack by insects and diseases? I pointed out that, on average, insect herbivores and plant 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. Management strategies that maintain low tree food quality can help reduce the frequency and severity of insect and disease problems on trees.

Here I ask: What causes insect and disease outbreaks on trees? Does the answer to this question have anything to do with the answer to the first question, and what are the management implications of the answer?

Outbreaks

In the first article I pointed out that, on average, insect herbivores and plant pathogens annually consume less than 10 percent of newly produced tree tissues – Annual Net Primary Production. However, averages, while useful for revealing general tendencies, can also be misleading. For example, the gypsy moth consumes an average of about 10 percent leaf area a year by eating barely detectable amounts most years when moth populations are low and consuming up to 100 percent every 10 years or so during periodic outbreaks. Outbreaks certainly do occur on trees. In these situations insects or pathogens consume large amounts with detrimental effects on tree growth and survival, even to the extent of eliminating tree species from particular ecosystems. Some infamous insect examples in the United Kingdom include periodic eruptions of the winter moth on oak, aphids on lime and sycamore, and leaf miners on holly. In the United States and Canada, periodic outbreaks of the spruce budworm and gypsy moth on oak occur over millions of acres. Dutch elm disease has nearly eliminated American elm. Chestnut blight eliminated American chestnut as an overstory tree species in the United States in less than 50 years. In the first article in this series we saw that most of the time insect herbivores and plant pathogens are relatively rare, and trees usually stay green suffering relatively little damage. However, it is clear that not all insect herbivores and plant pathogens are rare all the time and not all trees stay completely green all of the time.

Outbreak characteristics

Outbreaks are highly variable phenomena. They vary in extent from individual trees to forests of millions of acres over entire regions. They vary in severity from minor to major in terms of tree defoliation or mortality – even for different outbreaks on the same tree species at different times or places. They vary in frequency of reoccurrence from single, unique events, to seemingly regular cycles that repeat every 10 to 50 years. Despite this highly variable phenomenology, outbreaks have some interesting properties that give insights into their causes.

Relatively few species of insects and pathogens are responsible for outbreaks, but they do not belong in unique taxa. There are outbreak species across a wide range of both insect and plant pathogen taxa, and many of the species that are closely related to outbreaking organisms do not outbreak. This indicates that the capacity to outbreak is not a particularly taxonomically unique or restricted feature.

Outbreaking insect and pathogen species invariably have high intrinsic rates of reproduction, although there are many species that have high intrinsic rates of reproduction that do not outbreak. This indicates that high reproductive potential is a necessary but not sufficient characteristic for being an outbreaking organism.

Many outbreaking insect and pathogen species are regular offenders, suggesting that these organisms can consistently respond given the right circumstances. Outbreaks usually involve a single species of tree; sometimes just a particular genotype of a tree, and occasionally, closely related tree species in the same genus. Outbreaks are often caused by a single species found only on that tree species. This indicates that these organisms are sufficiently well adapted to their host plant that they can take advantage of circumstance.

Outbreaks are often associated with extreme environmental conditions, such as drought, flooding, or hot or cold weather. Outbreaks tend to occur at particular sites within the overall geographic range of the plant, such as in stands of uniform age structure, on soils of particular nutrient or water content, or in places exposed to local air pollution. In the case of insect herbivores, but not plant pathogens, outbreaks have been observed to occur following a decline in the abundance of predators.

Although this is a diverse and by no means exhaustive list with no immediately obvious interconnections, it does indicate that outbreaks seem to require some sort of triggering or catalytic change.

What triggers outbreaks?

You will recall from the first article that poor food quality, natural enemies, and the weather keep insect herbivores and plant pathogens rare. If so, then favorable changes in these factors seem reasonable candidates for initiating outbreaks. Findings accumulated from research in many specific systems over the years generally support this contention. As far as we can tell, increases in food quality, decreases in natural enemies and favorable weather are the most general, non-exclusive causes of outbreaks. Outbreaks can be initiated by increases in plant food quality that occur under a variety of abiotic environmental conditions, including the influence of the weather. I will return to these important effects shortly.

Second, for insect herbivores only, outbreaks can be caused by declines in their natural enemies, with the weather sometimes playing an important indirect role by decreasing natural enemy survival. Outbreaks of a number of insect species on trees have been shown to follow declines in natural enemies known to regulate herbivore populations at low density, i.e., prevent outbreaks. Examples include the pine looper, grey larch moth, black-headed budworm and winter moth in the United Kingdom, winter moth and spruce budworm in Canada, and gypsy moth in the United States and Eurasia. Our work on gypsy moth outbreaks in the United States is an example where a single natural enemy can determine whether or not outbreaks will occur.

Using a combination of long-term monitoring and experiments causing and preventing moth outbreaks, we have shown that in low density moth populations, white-footed mice are the key predators that prevent moth populations from increasing. Mice are generalist predators whose abundance is almost entirely determined by acorns and unaffected by moths, even though they feed voraciously on moth pupae. When there are bumper acorn crops, there are many mice that keep moths in check, but if acorn failure occurs, mouse populations crash and moth populations erupt. Unlike the gypsy moth example, the causes of declines in natural enemies are often not known, but there are situations where this appears to be caused by extreme weather conditions. For example, outbreaks of a psyllid, a sucking insect on *Eucalyptus blakeyi* in Australia, are associated with low temperatures that kill the parasitoids that attack the psyllid.

Lastly, weather can also be an important direct cause of outbreaks by creating conditions that enhance insect and pathogen growth rates, survivorship and reproduction. In particular, warmer, wetter conditions are often favorable for spore germination, growth and reproduction of pathogens, and higher temperatures are well known to cause increased growth and development rates of insect herbivores. Direct effects of the weather may also be strongest when the other factors are not particularly constraining, such as when plant food quality is high and/or when natural enemies are least abundant.

A focus on tree food quality

I will focus on outbreak initiation via increases in plant food quality that can occur under a variety of abiotic environmental conditions, including weather events. The reasons for doing this are very similar to those given for focusing on the role of food quality in keeping trees free from insects and diseases that appeared in the first article of the series.

First, increases in plant food quality often appear to be a major cause of outbreaks, and increases in food quality may be an important contributing factor – even when a decline in natural enemies or direct effects of the weather are playing the major role.

Second, increases in plant food quality associated with outbreak initiation may actually involve a relatively limited number of general mechanisms across a diversity of plant species, insect herbivores and plant pathogens. Not surprisingly, these general mechanisms appear to be closely related to the same three basic underlying causes of poor food quality in plants that were discussed in the first article: low nitrogen concentrations, variable nitrogen, and defensive mechanisms that make the extraction and processing of limited nitrogen difficult, dangerous, and costly. In contrast, although direct effects of the weather and natural enemy declines are often important causes of outbreaks, the particular weather conditions and the exact natural enemy species involved are largely idiosyncratic and case-specific across insect herbivores and plant pathogens. In fact, declines in the abundance of different natural enemies may be responsible for different outbreaks of the same insect.

Third, unlike natural enemies and the weather that are difficult or impossible to manipulate, there may be potential for preventing or moderating environmentally induced increases in plant food quality. An examination of the mechanisms responsible for increases in plant food quality ultimately reveals some important general traits and relationships that tree managers could influence to reduce the likelihood of outbreaks on trees.

Environment, outbreaks and tree food quality

Outbreaks are associated with a diversity of abiotic environmental conditions. Extreme environmental events – droughts, hot or cold weather – are perhaps the most well-known triggers of outbreaks. However, outbreaks also occur at more local sites. They have been reported when sites become flooded, in soil types of unusual nutrient composition, when plants have been heavily fertilized with nitrogen or phosphorus, and in places exposed to local air pollution. Outbreaks are probably most common in agricultural ecosystems, hence the need for pesticides and fungicides. Here the inputs of nitrogen, phosphorus and water are generally very high, and plant genotypes have been selected for high palatability to humans or livestock. Experimental outbreaks have

R.I. Anderson - USDA/Bugwood & Univ. of Ga.

While devastating pathogens are rare, chestnut blight canker has almost eliminated the American chestnut tree in the United States.

been created by fertilizing with nitrogen or phosphorus, by withholding water, by over watering, by shading, and by fumigating with a variety of oxidants.

Why do we think that many of these outbreaks are caused by increased food quality? Increases in food quality can be definitively invoked to explain outbreaks caused by experimentally fertilizing plants with nitrogen or phosphorus, by withholding water or over watering, and by fumigating plants with a variety of oxidants before herbivores are added or pathogens are inoculated. Although direct climatic or natural enemy effects cannot be ruled out, outbreaks in agricultural ecosystems, or shading-induced outbreaks, food quality effects cannot be ruled out either. Many naturally occurring or experimentally created outbreaks are preceded by increases in *per capita* reproductive output of insect herbivores and plant pathogens. Increases in this parameter clearly indicate increased food quality – in contrast to increased survival that could be caused by declines in natural enemies, direct effects of weather or increases in food quality.

How do these conditions increase food quality? Drought, flooding, heat shock, freezing, air pollution exposure, shading, and nutrient fertilization are all well-known to have marked effects on plant growth, development, and physiology that result in profound changes in tissue biochemistry. Plant tissue biochemistry is often responsive to variation in the environmental availability of light, water and nutrient resources, and often sensitive to environmental perturbations that cause plant stress and/or damage, such as heat and cold shock, drought, frost, and oxidant injury. Compounds reported to increase in concentration in plant tissues in response to altered environmental resources, stress or damage include total nitrogen, total organic nitrogen, protein nitrogen, soluble amino acids, and sugars that can be readily metabolized as a source of energy by insect herbivores and plant pathogens. Components reported to decrease in concentration include carbon, fiber and lignin, simple phenolic compounds, tannins, alkaloids, and a variety of other defensive chemicals. Based on the general plant tissue characteristics that determine food quality that were discussed in the first article in the series, an increase in nitrogen and/or a decrease in defenses should lead to an overall increase in food quality to insect herbivores and plant pathogens.

Clearly, not all plants respond by uniformly increasing tissue nitrogen and decreasing defensive chemicals to the same degree. We can find examples where an increase in the same environmental resource, or stress or damage factor, caused increases in nitrogen and/or decreases in defenses in one plant species, but no change or even decreased nitrogen and increased defenses in other plant species. Consequently, we should not expect changes in the abiotic environment to uniformly increase food quality and uniformly cause outbreaks. We expect some situations to result in increased food quality, some to decrease food quality, and some to have no effect. Of those resulting in increased food quality, some smaller fraction will actually result in increased insect herbivore or plant pathogen abundance. We do know from studies that have measured both plant biochemical responses and insect herbivore or plant pathogen responses to altered environmental resources, plant stress or damage, either natural or experimental, that when there was an increase in consumer abundance it was usually accompanied by increases in one or more forms of tissue nitrogen and/or decreases in one or more chemical attributes that can be construed as defensive.

Two examples

Two contrasting examples of the role of food quality in outbreaks can help illustrate these complex relationships. A number of species of bark beetles undergo periodic outbreaks on conifers in the United States. These outbreaks are often associated with severe drought events. A primary defense of conifers against beetle attack is to exude copious resin containing toxins into the puncture wounds made by the beetles as they attempt to invade the tree. The resin traps the beetles and seals the wounds, and the toxins can kill the beetles as well as serve as antifungal agents against associated fungi that the beetles use to help overwhelm the tree defenses. Since the resin and toxins are primarily made of carbon, their production depends on rates of photosynthesis, which in turn depends on the availability of water. Furthermore, high rates of resin exudation into the wounds require high turgor pressure, also water-dependent. Drought stress reduces photosynthesis and turgor pressure, reducing resin and toxin production and resin exudation rates, allowing beetles to successfully attack the tree. The decrease in resins and toxin concentrations improve food quality to beetles and fungi, increasing beetle reproduction, hence outbreaks.

Outbreaks of a psyllid in Australia follow droughts as well as periods of unusually low temperatures that I mentioned earlier. In contrast to the low temperature outbreaks caused by declines in a natural enemy, drought-induced outbreaks result from increases in phloem nitrogen concentrations and increased psyllid reproduction.

In summary, while I do not want to dismiss the importance of declines in natural enemies or direct effects of the weather in initiating outbreaks, it is likely that many outbreaks on trees are caused by environmentally induced increases in food quality. Plant growth, developmental, physiological and biochemical responses to environmental resources, abiotic stress and damage cause changes in the chemical composition of plant tissues. These changes often, but not invariably, involve increases in plant tissue nitrogen content and/or decreases in defensive chemicals – those food components that are either most limiting to insect and pathogen growth, development and reproduction, or those that make the extraction and processing of limiting nitrogen difficult, dangerous and costly. Not surprisingly, these are the same characteristics that we saw in the first article make plants generally poor quality food and keep insect herbivores and plant pathogens rare most of the time.

Outbreaks, tree food quality and arboriculture

What are the implications for commercial tree care companies?

First, arborists should be alert to the environmental conditions that are often associated with outbreaks. There may be little that an arborist can do to directly alleviate environmental conditions such as drought, flooding, extreme cold or heat, or

Suggested Further Reading

Coleman, J.S., Jones, C.G. and Krischik, V.A. 1992. Phytocentric and exploiter perspectives of phytopathology. *Adv. Plant Pathol.* **8**: 149-195.

Graham, R. D. 1983. Effects of nutrient stress on susceptibility of plants to disease with particular reference to trace elements. *Adv. Bot . Res.* **10**: 221-276.

Hartley, S.E. and Jones, C.G. 1997. Plant chemistry and herbivory: or why the world is green. In: *Plant Ecology,* Second Edition, ed. M.J. Crawley. Blackwell Science, Oxford, 284-324.

Jones, C.G. and Coleman, J.S. 1991. Plant stress and insect herbivory: toward an integrated perspective. In: *Response of Plants to Multiple Stresses*, eds. H.A. Mooney, W.E. Winner and E.J. Pell. Academic Press, San Diego, 249-280.

Schoeneweiss, D.F. 1986. Water stress predisposition to disease — an overview. In: *Water, Fungi and Plants*, eds. P.G. Ayers and L. Brody. Cambridge University Press, Cambridge, UK, 157-174.

USDA / APHIS PPQArchives/Bugwood & Univ. of Ga.

Year-to-year damage from gypsy moths is minor, but during outbreaks they may consume up to 100 percent of a tree's foliage.

major air pollution events. However, the occurrence of such events can be a warning signal and a stimulus for increased insect and disease monitoring.

Second, site-based knowledge, such as which soils are the most nitrogen-rich, where fertilizer has been heavily used, or what locales are most prone to drought, flooding, or air pollution, may help identify places where outbreak potential may be higher.

Third, avoid damage and injury to trees, both above and below-ground. Although low levels of damage can sometimes increase tree resistance, moderate to severe injury can weaken plant defensive systems.

Fourth, for reasons that will be explained next month in the last article in the series, some types of tree species are less likely to undergo environmentally induced increases in food quality than others. Irrespective of the value of using particular tree genotypes that are stress-tolerant, arborists may also want to select these "environmentally insensitive" types of trees for planting because they can have a lower overall risk of insect and disease outbreaks.

Acknowledgments

I thank Fred Last, Bill Mathews, and Derek Patch for giving me the opportunity to integrate insights gathered over many years; Cynthia Mills for suggesting I write articles for this magazine; a very large number of scientists for their research in this area; and The Tree Advice Trust, The Institute of Chartered Foresters, and The Institute of Ecosystems Studies for financial support. This article is a contribution to the program of The Institute of Ecosystem Studies.

Clive Jones is a research scientist at the Institute of Ecosystem Studies in Millbrook, NY. An ecologist, he studies how trees defend themselves against attack by insects and pathogens, how the environment affects tree defense, and what causes insect outbreaks.

TCI