POTENTIAL CAUSES OF THE PEAR THRIPS OUTBREAK IN SUGAR MAPLE

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Introduction

No one knows what caused the 1988 outbreak of pear thrips, *Taeniothrips inconsequens* (Uzel), in sugar maple, *Acer saccharum* Marsh., in the northeastern United States. As an entomologist and ecologist who knows even less about this insect than most of the authors of this volume, I cannot presume to understand the causes of this event any better than anyone else does. This essay will of necessity be highly speculative.

Nonetheless, I will outline the kinds of things that must have happened to generate such an outbreak by this insect. There are really two issues involved in this particular case. This pest is called the "pear thrips" because it feeds primarily on plants in the Rosaceae, mainly in orchards (Parker et al. 1988). So the first question we might ask is "How has this insect come to feed on plants in quite unrelated families?" The second question that arises is the same one asked about every pest, namely, "Why are there so many of them?" After all, a pest is a species that is too abundant in a place where it is unwanted.

I will begin by reviewing current ideas about how insect species may add new host species to their diets. Then I will examine some common general hypotheses concerning causes of pest outbreaks and attempt to relate them to the pear thrips situation.

Colonization of Sugar Maple

The literature suggests that maple may be a relatively new host for the pear thrips (Cameron et al. 1916, Simons 1985, Stannard 1968). It is very difficult to be certain about such an assertion. Information in the pest management literature suggests that pear thrips feeds heavily on 15 or more forest tree species, but quantitative data are lacking (Lewis 1973, Simons 1985). We will have to assume for the moment that the favored and probably the original hosts for this insect were orchard trees in the Rosaceae (Borror et al. 1981). That makes it a bit surprising that beginning around 1979 pear thrips was observed doing quite well on maples in northeastern Pennsylvania (Simons 1985).

Pear thrips appears to have acquired the ability to complete its life cycle on sugar maple, which means the insect has acquired the ability to recognize, oviposit, feed, develop and reproduce successfully on the plant. The probability of combining all of the traits necessary for success at each step, as well as accumulating the correct combination of genes for this, should be quite low. Even if the female recognizes and oviposits on the plant, the offspring have to be able to recognize that plant to accept it and begin feeding. Feeding stages must have the right physiological traits, including biochemical adaptions for digestion, detoxification and development on that food. Solving the "chicken and egg" problem of how phytophagous insects integrate behavioral recognition with physiological adaptation when they colonize new hosts continues to elude theoreticians and field biologists (Futuyma 1983).

The taxonomic, evolutionary, and likely chemical distance between sugar maple (Aceraceae) and rosaceous hosts exacerbates this problem in the case of pear thrips. Although there are exceptions, we generally expect the chemical features of closely-related plants to be more similar than those of distantly-related species. When these features influence acceptability and suitability of the plant to an insect species (e.g., allelochemicals), we expect any insect species to switch among closely-related hosts more easily. This scenario seems unlikely for the possibly recent addition of sugar maple to the pear thrips' diet.

Maples and rosaceous trees do produce some of the same broad classes of allelochemicals. Both families produce a range of phenolic compounds, and members of each may produce alkaloids (Gibbs 1974, Barbosa & Krischik 1987). However, the alkaloidal structures differ substantially between the two families, and we know little about the phenolics of either. Members of the Aceraceae produce a fairly novel class of tannins ("acertannins") not found elsewhere (Bate-Smith 1977). Apples (genus *Malus*) produce a nearly unique set of monomeric phenolics (e.g., phlorizin) and other rosaceous trees produce species specific flavonoidal compounds (Robinson 1980). Rosaceous tree species, but not maples, commonly also produce cyanogenic glycosides (Robinson 1980, Gibbs 1974). These observations suggest that there may be substantial biochemical barriers to exploitation of maple by rosaceous-adapted thrips.

Allelochemicals do not present the only barriers to host plant use. Many biological and physical factors interact to determine the likelihood that an insect species may "colonize," or develop the ability to complete development on, a new host plant species. Janzen (1968) suggested an "archipelago model" of adaptation to host plants, in which the degree of similarity between any two plant species in a variety of traits influencing insect success indicates the "ease" with which the two plants may be incorporated into the same insect's diet over ecological or evolutionary time. Factors of importance include refuge from physical factors, susceptibility to natural enemies, seasonal and spatial availability of suitable tissues, and physical traits of the plant (e.g., leaf surfaces). In this model, plant species are visualized as "islands," the distances among which are defined by similarities and differences in features influencing insect use. Similarity in one or more features may reduce barriers to colonization, but could be balanced by differences in others. Unfortunately, we cannot yet rank the importance of these various influences in any useful way (Bernays & Graham 1988, Smith et al. this proceedings).

Of course, the host's environment can also influence the likelihood that an insect will survive to oviposit again on the same host. Habitat parameters, both climatic and edaphic, may determine this

barrier independently of host plant traits as food. In the case of pear thrips, low overwintering success in soil or litter could reduce the likelihood of adapting to host species growing in marginal habitats. Use of either or both hosts would then depend on the presence of tolerable or favorable physical conditions (e.g., soils, litter depth and moisture, etc.) in stands of both hosts.

Herbivore susceptibility to natural enemies (parasites, predators and pathogens) often differs dramatically among hosts (Brower 1958). An insect species' ability to exploit a new plant species could be blocked by increased risks there, but it could also be facilitated by increased "risk-free space" (Brower 1958, Bernays & Graham 1988). In the case of maple and orchard trees, we have no information to help infer a conclusion about this effect, and the impact of enemies on pear thrips appears to be unknown, even in orchards. One could imagine that pear thrips might escape an enemy important in orchards by colonizing maple, but of course this would require overcoming other barriers to the use of maple.

The product of the probabilities of overcoming all of these barriers must be rather small. Obviously, the pear thrips has overcome what might be significant barriers to become successful on sugar maple. What factors may have facilitated this?

Frequent encounters with a new host species probably facilitate dietary expansion or switching (Futuyma 1983). Although originally far more abundant in the western United States than in the East, the pear thrips has no doubt been present in eastern orchards for some time. The large number of orchards within the distribution of sugar maple must have provided ample contact with maple and plenty of opportunities for colonization. Futuyma (1983) has pointed out that the more frequent such encounters become, the more likely it is that individuals possessing traits necessary for success on the new plant will remain there to reproduce. Indeed, repeated colonization attempts and failure on the new plant ought to comprise strong selection favoring any adaptations to the new host that may arise. The spread of pear thrips through orchards in contact with maple may have provided these

opportunities, especially if gravid females are often blown out of orchards into surrounding maple stands. Expanding orchards would have a similar effect.

Cultural procedures may also play a role (Scriber & Hainze 1987). One might speculate that the ability to deal with maple chemistry could evolve as a form of cross resistance arising from selection exerted by pesticide use in orchards. The inverse situation, in which cross resistance to pesticides is induced as a function of feeding on different apple cultivars, has been observed in other pest insects (Yu 1986). Although we don't know enough about the biochemical basis of plant exploitation by thrips to draw serious conclusions, it is possible that the expanded development of new cultivars, or changing pesticide use, may have selected for thrips genotypes capable of exploiting new host species.

Dramatic changes in forest composition also have occurred since apple orchards became common in the eastern United States. More than half of the observed forest pest outbreaks in the Northeast occurred after the major logging events and changes in forest structure that occurred from 1860 to 1900 (Nothnagle & Schultz 1987). We don't know that there is a functional relationship here. However, between 1860 and 1900 many trees were damaged during removal of other trees, and the forest structure changed. Among other things, forest succession was pushed back to earlier seres, of which sugar maple would be a minor component. The New England forests are now returning to the older, climax forest type as agricultural land use decreases. Perhaps the increasing dominance of sugar maple in recent years has increased contact with orchard insects like the pear thrips. Alternatively, the physical environment may also have been changed in such a way as to make various tree species susceptible to pests.

One feature of the pear thrips that could facilitate host switching and the development of high population densities is its parthenogenic mode of reproduction. Bush (1974) proposed a model of host race formation by herbivores in which he pointed out that switching is facilitated if mating by adults is linked to the host. This link (e.g.,

mating on or near the oviposition site) ensures that male and female genotypes containing mutations permitting exploitation of a new host are combined in offspring feeding on the new host. This would increase the representation, and hence population size, of "preadapted" genotypes among offspring starting out life in a new environment (host), and should increase the likelihood that a new population capable of exploiting the new host becomes established.

Parthenogenesis in the pear thrips may provide an alternative means of increasing the genetic similarity among sibs produced by a single mother colonizing a new plant. Since that mother must recognize the new host to oviposit there, she places her genetically-similar offspring, which are likely to share most of her genes, together on the new host. If the mother's ability to recognize and oviposit on the new host (sugar maple) has a genetic basis, it is likely that most, if not all, of her offspring will carry the same trait. This would establish an entire population of "preadapted" thrips almost instantaneously, compared to outcrossing insect species in which many of the sibs may not carry the host-recognition genes of the maternal parent. Because parthenogenic species can establish larger populations of potentially adapted individuals when colonizing a new host, I suggest that adaptation barriers may be overcome by them more quickly than by sexually reproducing species. This may help explain what appears to be a sudden, explosive appearance of pear thrips on sugar maple.

It is impossible to determine the course of host-switching by an insect herbivore without knowing the details of plant traits and insect feeding, behavior, life history and habitat requirements. It is also important to put this information in a phylogenetic context, with comparative studies of related species. Research has not been extensive or intensive enough to provide a good basis for conclusions about pear thrips on sugar maple. However, given that the switch has occurred, what factors may influence the success of pear thrips on sugar maple trees and result in apparent "outbreak?"

Possible Outbreak Causes

There are almost as many hypotheses about the causes of pest outbreaks as there are investigators (Barbosa & Schultz 1987). I can focus here on only a few very popular ones. We need to beware of the use of the word "causes," because truly mechanistic studies are rare. The literature on pest outbreaks is instead dominated by correlative studies that generally serve to refine hypotheses rather than test or refute them.

For example, climate and weather variables are often identified as triggers, cues or actual causes of pest outbreaks in a particular forest system (Martinat 1987). The hypothesis that drought stress is a cause of pest outbreaks in forests is as old as outbreaks themselves (Mattson & Haack 1987). In the particular case of the pear thrips, there is some evidence that populations increase in orchards during drought years. There are, however, no studies of mechanisms that may be involved. We might speculate that superior overwintering success could be involved, or that reproduction improves. The possibility that stress may make hosts either nutritionally superior or more poorly defended chemically is popular at present (Mattson & Haack 1987). Interestingly, however, the plant physiology literature tells us that almost anything can happen to tissue quality under drought stresses, particularly in woody plants. That is, there are published examples of plant species that become better or worse nutritionally, and that increase or decrease putative defenses under presumably stressful conditions.

In the case of the pear thrips, there are virtually no studies on what characteristics of the host plant make it better or worse as food for the insect. Low rainfall in the years during or prior to the recent observation of thrips on Vermont maples may or may not have influenced tree quality. Depending on tree species, presumptive defense compounds may increase or decrease under drought stress (Gershenzon 1984). In some species protein or amino acid contents

may change, altering food quality. Any guesses about what host stress will do in sugar maple to make the plant better or worse for pear thrips comprise sheer speculation at this point.

Climatic events can also shift plant phenology, including leaf chemistry and nutritional value. Because species like sugar maple undergo dramatic seasonal changes in leaf traits (Schultz et al. 1982), there may be periods of time during which sugar maple leaves resemble leaves of other species chemically, perhaps including orchard species. For example, the distinctive acertannins in maples do not develop higher concentrations until mid- to late-summer; early in the season, the phenolic chemistry of maples tends to be dominated by monomeric phenolics that may be more similar to those of rosaceous trees (Schultz et al. 1982). If maple (or orchard tree) phenology were shifted by climatic events for one or two seasons, this could open a "window of opportunity" for colonization and growth success by thrips. This in turn would facilitate both colonization of maple and population growth and might produce an outbreak.

Climate could also have impacts on pest insects independent of the host (Mattson & Haack 1987, Martinat 1987). However, such host-independent effects ought to occur in orchards as well as in maple stands. There is no evidence that pear thrips populations are increasing in orchards concurrent with the present sugar maple infestation, although the heavy use of pesticides in orchards could obscure effects of natural enemies or other factors.

Once thrips is feeding successfully on maple, its populations could escape regulation by various factors important in orchards. In this case, we would say it has entered what some evolutionary ecologists call a new "adaptive zone" (Ehrlich & Raven 1965), or at least a way of life in which the insect experiences few barriers to population growth. Natural enemies and pesticides comprise common barriers in the orchard setting, and these may be absent on maple. Ordinarily, in natural systems it is not clear that the failure of natural enemies leads to pest outbreak, even if the pest population appears to be regulated by enemies at low density (Southwood & Comins 1976).

However, if pear thrips escapes an effective regulatory agent while living on maple (and if maple is suitable food), then its populations may achieve higher densities than are usually seen in orchards. Considering the degree to which insect populations in orchards are usually suppressed by pesticides, colonization of maple could produce an "outbreak" merely by eliminating that factor. If sugar maple were truly superior food, then rapidly growing pear thrips populations could even escape the regulatory impact of an enemy that followed it there. Information about the influence of food quality on thrips reproduction and about natural enemies is far too inadequate to propose more specific hypotheses.

In this light, it is important to consider the possibility that the pear thrips populations we observe in sugar maple stands do not comprise an "outbreak", i.e., they do not represent "unusually" high densities. Present thrips densities on maple may represent the overall carrying capacity of maple for this insect. We may continue to observe unabated high densities for the foreseeable future, now that the insect has managed to colonize this species.

Recent theory suggests that insects whose intrinsic rate of natural increase and certain other attributes conforms to certain theoretical criteria may be destined to exhibit irruptive population dynamics. It is difficult to demonstrate statistically that any pest outbreak is periodic, i.e., that it has a demonstrable cycle of "*N*" years. Hence, mechanisms that yield outbreak need not produce regular periods in outbreak cycles. May (1985) has suggested that pest species represent an adaptive type, or a particular way of life in which high reproductive rates and other traits combine to yield outbreak dynamics in chaotic fashion. In either case, density-dependent regulatory factors are usually operating, at least during the crash of epidemics. Anderson & May (1980) point out that use of artificial controls (e.g., pesticides) in such cases may be self defeating, in part because density-dependent regulation (e.g., via disease) is thwarted.

In attempting to control pear thrips on the sugar maple, we need to keep in mind the possibility that the commonly applied pesticides may fail on the new host plant. In particular, biological pesticides may fail because of the chemistry of the host (Schultz & Keating in press). Integrated pest management should account for the specific interactions among the plant, insect, and insect's enemies.

It is abundantly clear that no control program can succeed until we understand what the pear thrips eats, what food quality factors are important to its success, what role natural enemies play, and the importance of physical factors. Our information on all of this is woefully inadequate; we barely understand the basic biology of this insect. We must be prepared to assemble a major research effort (with significant support), and to spend significant time studying the basics of this system if we hope to design effective and environmentally sound control efforts.

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Discussion Period

Question: We're used to thinking of host plant chemistry attributing to outbreaks, are you suggesting that under some circumstances the host plant actually welcomes some new pests, and that the attributes of the host plant somehow contribute to the accumulation of pests?

Schultz: I think that almost all sugar maple trees very likely pass through windows of opportunity for colonization, ecologically and perhaps in terms of age. Apparently certain aged trees are more susceptible to this insect than others. My guess would be that this insect wouldn't be able to cross over as easily if maple didn't pass through a phase either each year or during its life time that made it much more like a pear than it is otherwise. I suspect there has been selection pressures on this insect for the ability to deal with the tree. It probably has a window of opportunity, though it appears to be doing well on both sides of the window as well. In 1909 Moulton hypothesized that the reason pear thrips were so successful on pears is that it has clustered flowers. Maples also have clustered flowers. In fact, there must be 150 species of trees in northeastern North America that have clustered flowers. Therefore the flower type alone must not be the characteristic that distinguishes maples from other potential thrips hosts.

I tend to focus on leaf feeding because that is my specialty. I think the suggestion that availability in spacial distribution of a resource like the flowers is interesting but there are other maples that have similar flower clusters and I'd be curious to know if the insect is successful on those. However, maples differ greatly in their secondary chemistry which may also influence host susceptibility. This must be integrated with other host information.

Question: Do you assume that there is genetic variability between the pear thrips on pears and those on maples?

Schultz: Certainly that is possible, but I have no idea. There are many potential sources of genetic variation. The statement that all of the genetic offspring of a female are identical to her is not strictly speaking true. Considering the number of generations of pear thrips in North America, I am sure we are now looking at other genotypes. I don't assume that the maple feeders are a different genotype but they probably are. If not, there is a tremendous congruency of characteristics between maple and pear.

What makes this question so interesting to me is I can't figure out how an insect that is a good Rosaceae feeder switches over to a different host so successfully. For other insects that feed on a wide variety of plants, when a new plant is introduced into the system, the insect may just include it in the host range and there is no fundamental difference in population structure. That could apply here.

David Jenson pointed out that leaf eating insects eat leaves and that is determined by the unique characteristics of the leaves and all the other ecological circumstances that may be available. Until we know what the requirements are for thrips success we can in no way indicate what plants should and should not be hosts. It is just astonishing to me that we have no idea how this insect makes its living. I assume that nitrogen is important to it, and secondary chemicals can influence it as well.

Comment: I want to mention a few points about the genetics of thrips. Thrips have what we call myotic parthenogenesis, whereby the polar body fuses with the opening so you actually get very little genetic variation. It is possible however that pear thrips males do occur in the United States. They might be so short-lived that they have not been found. I worked on a species of thrips in Colorado that only occurs for a very short time and in very localized populations each season.

In some species of thrips the males are not very important to female reproduction and there are other species in which the males are present and needed for reproduction.

Question: Are there any comprehensive genetic studies that really identify the system of inheritance in thrips?

Answer: No.

Question: Has anyone investigated the correlation between the outbreak of this pest and the stress on sugar maple trees caused by acid rain?

Schultz: I'm not aware of anyone doing such work associated with acid rain and the pear thrips outbreak. I haven't seen any evidence that there is a significant relationship between any major insect outbreak and acid rain, and quite frankly I wouldn't expect there to be much of one. I see the contribution of acid precipitation to the leaf as minor.

A possible factor contributing to this outbreak might be drought. A one-to-three year drought could have a profound effect on the physiological state of sugar maple trees and make them unusually susceptible to thrips. I do not know however why maple might be susceptible and beeches and birches are not. One report I found in the literature pointed out that pear thrips is particularly successful and prone to outbreaks in orchards during drought years, presumably as a result of higher winter survival.

The effect of tree phenology on thrips success and damage remains an important question. We watch the buds burst and the leaves get bigger, but many things are going on inside the leaf at different rates that we don't see. Chemicals are coming and going. In oak trees the composition of the molecules in the young leaves changes daily over the first 10 days of leaf expansion. If one of those compounds is essential to one of these insects, the synchrony of the insect and tree becomes critical. Because we do not yet know what is crucial to the survival of pear thrips, it is impossible to know what characteristics of maple phenology are important? One of the crude changes that occurs during leaf development is that the leaves get tougher day by day. I think the issue of phenology is critical. Maples may go through a stage in which they are not like other Rosaceae trees.

The question remains why pear thrips haven't been a pest problem for the past 20 years. I'm really curious about that. We've had apples, pears, and sugar maples in the Northeast for a long time and the insect has been in the Northeast since the turn of the century. So I don't know why all of a sudden it has managed to find sugar maples suitable. These facts suggest to me that a significant shift has occurred in the thrips ability to deal with this host. Perhaps the trees have changed since the thrips arrived, possibly due to some predisposing factor associated with this outbreak.