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The Role of Drought in Outbreaks of Plant-eating Insects

Drought's physiological effects on plants can predict its influence on insect populations

William J. Mattson and Robert A. Haack

Substantial evidence indicates that drought stress promotes outbreaks of plant-eating (phytophagous) fungi and insects. Observations and experiments show that colonization success and prevalence of such fungi as root and stalk rots, stem cankers, and sometimes wilts and foliar diseases are much higher on water-stressed plants than on normal plants (Schoeneweiss 1986). The evidence associating insects and drought is more circumstantial, consisting largely of observations that outbreaks around the world of such insects as bark beetles and leaf feeders (see Table 1) are typically preceded by unusually warm, dry weather. There is also a consistent, positive correlation between insect outbreaks and dry, nutrient-poor sites (Mattson and Haack 1987).

To explain these phenomena, the following hypotheses have been proposed both separately and in combination. Drought increases pathogen and insect survival and growth through elevated plant nutrient levels, especially nitrogen (Rhoades 1983, White 1984); lowered plant defenses (Rhoades 1983, 1985); and a more suitable physical environment (Begon 1983, Rhoades 1983). We present

We present here a more holistic conceptual model to explain how drought may provoke insect outbreaks

here a more holistic conceptual model to better explain how drought may provoke insect outbreaks. Unlike arguments by Schoeneweiss (1986) that plant susceptibility and suitability to pathogens increase continuously with stress, our hypotheses assume that insect responses to drought effects are nonlinear; that is, the suitability of conditions for insect colonization and reproduction first

increases to an optimum, and thereafter decreases. Thus, severe and prolonged drought can become debilitating to phytophagous insects, just as it is to plants.

Drought stress affects plant traits

Gene expression and genomic change. Drought affects virtually every plant process; the magnitude of the effect depends on the drought's severity and duration as well as the plant's developmental stage (Kramer 1983). Drought stress includes aspects of water, temperature, and nutrient stress. At the molecular level, drought can have a significant impact on gene expression and genomic change (McClintock 1984, Walbot and Cullis 1985). For example, water stress

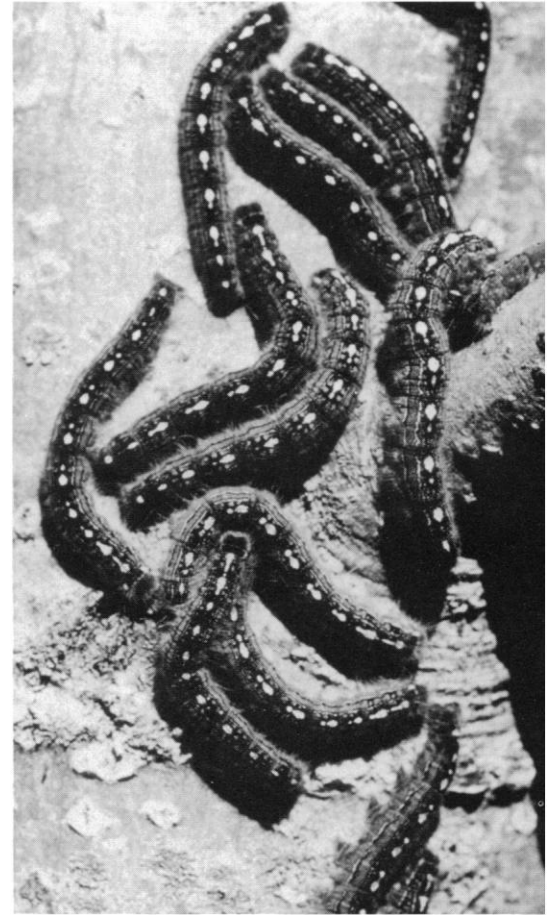
Table 1. Selected genera of forest and range insects that historically have reached outbreak proportions following drought. Source: Mattson and Haack (1987).

Order	Insect		Genera of woody hosts
	Family	Genus	
Coleoptera	Buprestidae	<i>Agrilus</i>	<i>Betula, Populus, Quercus</i>
	Cerambycidae	<i>Tetropium</i>	<i>Abies</i>
		<i>Corthylus</i>	<i>Acer</i>
	Scolytidae	<i>Dendroctonus</i>	<i>Picea, Pinus</i>
		<i>Ips</i>	<i>Picea, Pinus</i>
		<i>Scolytus</i>	<i>Abies, Carya</i>
<i>Aphis</i>		<i>Crataegus</i>	
Homoptera	Aphididae	<i>Cardiaspina</i>	<i>Eucalyptus</i>
	Psyllidae	<i>Neodiprion</i>	<i>Pinus</i>
Hymenoptera	Diprionidae	<i>Bupalus</i>	<i>Pinus</i>
Lepidoptera	Geometridae	<i>Lambdina</i>	<i>Abies, Picea</i>
		<i>Selidosema</i>	<i>Pinus</i>
		<i>Lymantria</i>	<i>Picea, several hardwoods</i>
	Lymantriidae	<i>Choristoneura</i>	<i>Abies, Picea, Pinus</i>
		Tortricidae	Several genera
	Orthoptera	Acrididae	

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The pine sawfly, *Diprion similis* (above), introduced from Europe, occurs throughout eastern North America. Young larvae feed gregariously, attacking primarily eastern white pine but also jack, Scotch, and red pines. Severe and repeated defoliations can result in tree death. The forest tent caterpillar (right), *Malacosoma disstria*, is found in most of the US and Canada. Larvae often feed gregariously on hardwoods such as quaking aspen, oaks, and water tupelo. Outbreaks occur sporadically over vast forested areas, causing reduced growth and some tree mortality. Outbreaks in Canada are often preceded by consecutive years of unusually cold winters and warm springs.



alone has been found to induce quantitative changes in patterns of protein synthesis in barley (Jacobsen et al. 1986) and both quantitative and qualitative changes in maize seedlings (Heikkila et al. 1984). High temperature or heat shock is known to upset normal patterns of protein synthesis in favor of novel heat shock proteins (Walbot and Cullis 1985). The full impact of these changes on a plant is largely unknown. Nevertheless, the wide distribution of these responses in prokaryotic and eukaryotic organisms suggests that they are an important and ancient developmental mechanism (Kurtz et al. 1986).

Plant growth and differentiation. One of the most sensitive and immediate plant responses to water stress at the cellular level is a reduction in the growth processes—cell division and enlargement (Kramer 1983). The net result is smaller plants and plant parts (e.g., leaves, buds, reproductive organs, and xylem growth rings). Photosynthesis itself is not as sensitive, declining only slowly until water stress becomes moderate to severe (Kramer 1983, Sharpe et al. 1985).

The process of differentiation (the

chemical changes that occur in maturing cells and the ensuing morphological changes) is not as sensitive to drought as are the growth processes. Differentiation may actually be enhanced during moderate stress, because with the decline in growth there are abundant photosynthates to fuel the maturation processes (Lorio 1986). The net result is thicker cell walls, more abundant fiber and conducting elements, and higher concentrations of such secondary products as terpenes, alkaloids, and waxes (Lorio 1986, Sharpe et al. 1985). However, severe stress eventually curtails the differentiation process when levels of photosynthates and other raw materials become limiting (Sharpe et al. 1985). Temperature stress can inhibit both plant growth and differentiation.

Spectral qualities, temperature, and acoustic emissions. The spectral and thermal qualities of plants change significantly with increasing drought stress. Leaf reflectance increases in both visible and infrared wavelengths (Drake 1976). For example, severe drought stress inhibits chlorophyll production and thus induces leaf yel-

lowing (Kramer 1983).

Even more importantly, drought-stressed plants are consistently warmer than well-watered plants. This effect is due to stomatal closure reducing the transpirational cooling. Although temperature differences are usually 2°–4° C, differences as great as 15° C have been recorded (Mattson and Haack 1987). In fact, the measurement of plant temperature has become an important and simple index of the degree of stress a plant is experiencing (Reicosky et al. 1985).

During the gradual dehydration of plants caused by prolonged water stress, there is a breaking, or cavitation, of the water columns in the conducting xylem tissue of leaves and stems (Pena and Grace 1986). The cavitations cause acoustic emissions that are believed to be vibrations coming from single cells. The frequencies of such vibrations may be in the audible range for large water-conducting cells (vessels) but are primarily ultrasonic (80–2000 kHz) for smaller cells such as fibers and tracheids (Sandford and Grace 1985). Cavitation apparently occurs first in

the largest conducting cells and then in smaller and smaller ones as stress intensifies (Tyree et al. 1984).

Plant osmolytes, minerals, nitrogen, and carbohydrates. Most plants lower their osmotic potential during drought by accumulating such compounds (osmolytes) as inorganic ions, amino acids, sugars, sugar alcohols, and organic acids (Kramer 1983, Mattson and Haack 1987). Mineral nutrient uptake from soil is altered during drought because soil temperatures increase, soil water decreases, ion movement and root growth are reduced, and roots become more suberized, or corky (Kramer 1983). Several minerals (calcium, chlorine, potassium, magnesium, nitrogen, sodium) can accumulate to higher than normal levels in the above-ground tissues of drought-stressed plants (Mattson and Haack 1987).

Viets (1972) reported that a plant's depth of rooting influences its mineral content. During drought, for example, deep-rooted plants draw water mainly from deep soil where nutrients are scarce. As a result, the diluted tissue nutrients limit plant function before water does. On the other hand, in shallow-rooted plants, nutrients may become concentrated in plant tissue, and water becomes limiting long before nutrients do.

During drought, concentrations of such nitrogenous compounds as amino acids (especially proline), nitrate, and betaine often increase in plant tissues (Kramer 1983, Mattson and Haack 1987). Although soluble nitrogen generally increases during drought, the effects on total nitrogen are tissue and stress dependent. During mild to moderate water stress, for example, total nitrogen concentrations decline in roots and older above-ground tissues, but increase in younger above-ground tissues (Mattson and Haack 1987).

Likewise, as stress intensifies, concentrations of sugars and sugar alcohols (e.g., inositol) typically increase, while complex carbohydrates (e.g., starch) decrease (Kramer 1983). Total carbohydrate concentrations are often high in foliage of drought-stressed plants (Kramer 1983, Mattson and Haack 1987).

Plant allelochemicals and volatile

stress metabolites. Tissue concentrations of several classes of allelochemicals (secondary compounds that stimulate or inhibit other organisms) tend to increase during drought, including cyanogenic glycosides, glucosinolates and other sulfur compounds, terpenoids, and alkaloids (Gershenson 1984, Mattson and Haack 1987). However, the relationship between drought stress and foliar phenolic levels has not been clearly demonstrated (Gershenson 1984). Secondary metabolites may accumulate during mild to moderate drought because their synthesis is enhanced by the increased levels of available carbon and nitrogen (Lorio 1986, Sharpe et al. 1985). In stressed mint (*Mentha*) plants, for example, foliar terpenoid levels increase because the terpenoid-containing trichomes are more densely packed on smaller than normal leaves (Gershenson 1984). Likewise, in moderately stressed conifers, levels of low molecular weight terpenoids increase (Sharpe et al. 1985). Xerophytes allocate extremely large amounts of energy and carbon to allelochemical production (Hoffmann et al. 1984).

Plant allelochemical concentrations appear to exhibit a dome-shaped relationship to drought stress. Severe drought stress in conifers, for example, lowers oleoresin production (and also exudation pressure, flow rate, viscosity, and rate of crystallization) and induces compositional changes in the resin acid and monoterpene fractions (Hodges and Lorio 1975, Mattson et al. 1987). Similarly, severe drought in rubber (*Hevea*) trees reduces the production and flow rate of latex (Buttery and Boatman 1976).

Many environmental stresses commonly induce production of several volatile compounds (e.g., ethylene, ethanol, ethane, acetaldehyde) (Kimmerer and Kozlowski 1982). These compounds, along with abscisic acid, are often considered to be stress metabolites, but their effects at the level of the whole plant are poorly understood (Ayers 1984).

Implications for insects

We will consider six major mechanisms by which drought may affect aspects of insect behavior and physiology (Figure 1).

Drought provides a more favorable thermal environment for growth of phytophagous insects. Because insects have limited thermoregulatory capacity, the higher air and host plant temperatures associated with drought may enable them to grow and reproduce in a more nearly optimal temperature regime. Mattson and Scriber (1987) proposed that insects that feed on grasses and leaves of woody plants may have unusual enzyme and membrane systems with relatively high thermal optima. Small changes in temperature may evoke large responses by the insect (Begon 1983, Wagner et al. 1984). For example, Martin et al. (1980) reported that activity of the midgut proteases of *Tipula abdominalis* increased seven- to tenfold for each 10° C increment over the range of 4°–37° C. Growth rates of the whole insect typically increase in a sigmoidal fashion in relation to temperature (Wagner et al. 1984). Survival and fecundity usually exhibit an S- or a dome-shaped relation to temperature (Morris and Fulton 1970). Many studies have shown that merely providing insects with optimal temperature regimes, without changes in food quality, will permit them to grow faster and larger, suffer less mortality, and lay more eggs per unit of ingested food (Mattson and Haack 1987).

Drought-stressed plants are behaviorally more attractive or acceptable for insects. The leaf yellowing, higher temperatures, and greater infrared reflectance of drought-stressed plants may make them more attractive or acceptable to insects. The insects may detect thermal, acoustic, biochemical, and electromagnetic properties. Electromagnetic cues include those perceived with normal vision and with infrared receptors (Evans and Kuster 1980). Many insects are attracted to yellow hues (Prokopy and Owens 1983), and several others have heat and infrared receptors (Altner and Loftus 1985). For example, the buprestid beetle *Melanophila acuminata* has infrared receptors that apparently assist it in finding fire-scorched conifers, in which it oviposits (Evans and Kuster 1980). Although evidence exists that some insects use color and infrared perception in host finding, much research is still needed.

Acoustical cues may serve as short-range attractants or arrestants for some phytophagous insects. As plants dehydrate, cavitations of the water columns in xylem tissue produce acoustical, usually ultrasonic, emissions. Many branch- and trunk-infesting bark beetles and buprestids have well-developed acoustical senses (Barr 1969, Carlson and Knight 1969). Several insect species are capable of detecting ultrasonic sound, at least up to 100 kHz (Prosser 1973). Therefore, we can speculate that acoustical emissions influence the behavior of such insects as wood borers.

As they find and accept host plants, most insects appear to respond to blends of plant compounds (Miller and Strickler 1984). Because drought stress alters the biochemical composition of plants, qualitative and quantitative changes in these chemical blends could make stressed plants more attractive and acceptable to phytophages. In fact, the insect's chemoreceptors appear to be especially sensitive to such changes.

Phytophagous insects, for example, commonly have contact chemoreceptors that are sensitive to plant water, amino acids, sugars, salts, and allelochemicals (Städler 1984, Visser 1986). The amino acid and salt receptors are necessary to phytophages because their foods often contain only small amounts of these nutrients (Haack and Slansky 1987, Mattson and Scriber 1987). However, it is not clear why proline and inositol, which are not essential nutrients for insects, are feeding stimulants for so many species (Mattson and Haack 1987, Städler 1984). We hypothesize that because proline and inositol are common plant osmolytes that accumulate during drought, they may aid insects in detecting stressed plants.

Phytophagous insects appear to have the necessary sensory apparatuses to detect common plant osmolytes and moreover they exhibit positive feeding responses to most of these compounds (Mattson and Haack 1987, Städler 1984). As osmolytes increase during drought, they may

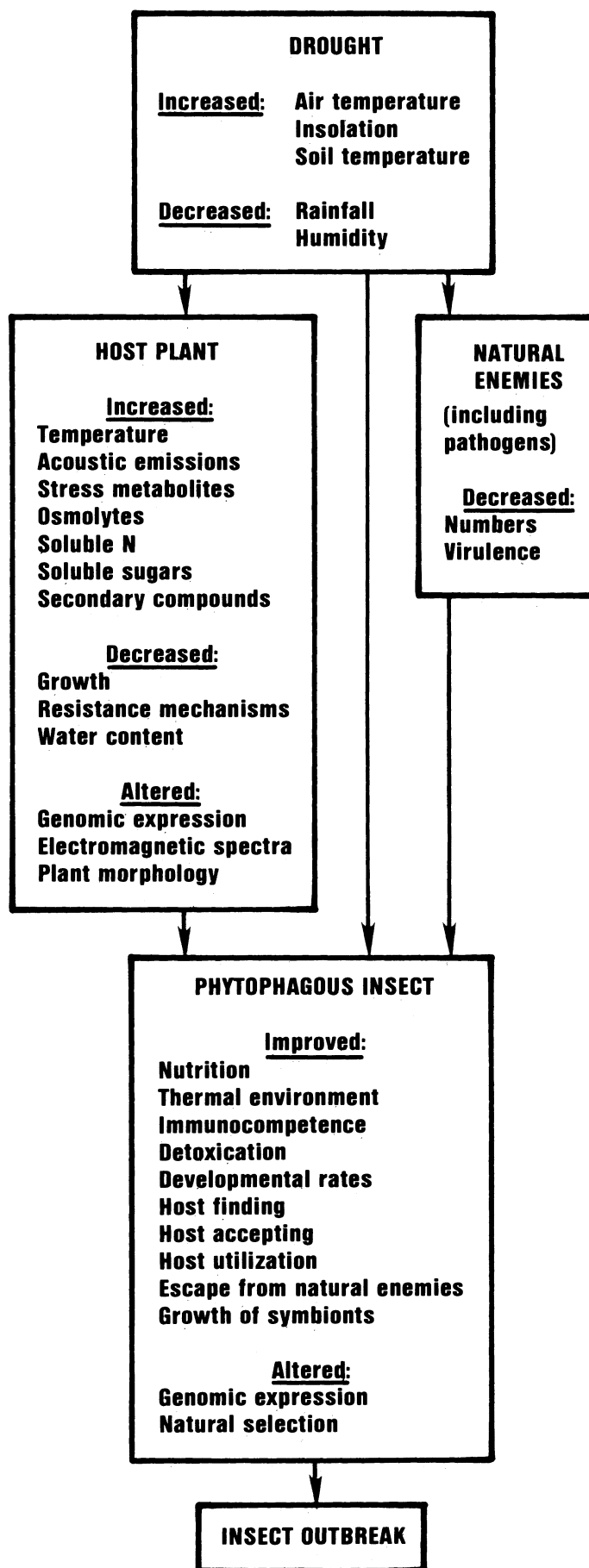


Figure 1. Hypothetical representation of how drought influences host plants, phytophagous insects, and their natural enemies to provoke insect outbreaks.

simultaneously stimulate greater host acceptance and feeding by insects. This hypothesis assumes that levels of these stimulatory compounds in unstressed plants are below the insect's optimal response level.

In the spruce budworm *Choristoneura fumiferana*, for example, the larva's peak feeding response occurs between 0.01 and 0.05 M sucrose (Albert et al. 1982), whereas sucrose levels range between 0.004 and 0.011 M in unstressed balsam fir (*Abies balsamea*) foliage (Mattson and Haack 1987). Hence, drought stress would likely increase the level of this stimulant and thus promote greater feeding. The same is true for some other insects, such as the grasshopper *Locusta migratoria* and several lepidopterans, that have peak responses to relatively high sucrose levels (Mattson and Haack 1987). In addition, the varying levels of osmolytes probably interact synergistically to further promote host acceptance and feeding (Visser 1986).

The increased levels of foliar allelochemicals in moderately stressed plants would seemingly be detrimental to insects. However, these increases may not be substantial enough to exceed the tolerance or detoxication capacities of specialized insects. Moreover, such increases may actually benefit the specialists that utilize allelochemicals as host finding and accepting cues (Mattson and Haack 1987, Visser 1986).

Increased production of ethylene, ethane, acetaldehyde, and ethanol following stress (Kimmerer and Kozlowski 1982) may likewise stimulate greater host finding and accepting. Ethanol serves as an attractant for many bark- and wood-inhabiting scolytid and cerambycid beetles (Dunn et al. 1986, Haack and Slansky 1987), but little information is available on the attraction of the other three compounds.

On the other hand, severe drought stress can reduce terpene emissions from conifer needles due to stomatal closure (Cates and Alexander 1982, Chararas 1979). Not all terpenes are equally reduced, and the concentrations of some, such as alpha-pinene, may increase (Cates and Alexander 1982), resulting in their increased dominance in the stressed plant's gaseous atmosphere. This increase may

explain in part why alpha-pinene is such a common attractant and arrestant for bark beetles that attack living but stressed conifers.

Chararas (1979) suggested that drought stress lowers the relative concentrations of most terpenes from a repellent to an attractant level for many bark beetles. Such trees may not only be more attractive to bark beetles, but they may be less toxic as well. For example, alpha-pinene, which increases in concentration with stress, is one of the least toxic monoterpenes, whereas myrcene and limonene, which decrease in amount, are among the most toxic monoterpenes to bark beetles (Cates and Alexander 1982, Mattson and Haack 1987).

Drought-stressed plants are physiologically more suitable for insects. Drought-stressed plants may be more suitable for insect growth, survival, and reproduction because plant nutrients are either more concentrated or better balanced. This may be of particular importance to insects that feed on woody plants because amounts of nitrogen, sugar, and minerals are often less than optimal (Haack and Slansky 1987, Mattson and Scriber 1987, White 1984). Logically, increasing and/or improving the balance of these nutrients should favor insect performance (Haack and Slansky 1987, House 1974).

Several investigators have shown that feeding on drought-stressed plants led to improved growth, survival, or reproduction of various Homoptera, Lepidoptera, Orthoptera, and mites (Mattson and Haack 1987). In some cases, however, growth and survival of aphids and mites declined on severely stressed plants, probably reflecting supraoptimal temperatures, lowered turgor pressure, or increased cell-sap viscosity (Mattson and Haack 1987). The latter two factors are known to limit feeding by sap-sucking arthropods (Auclair 1963).

Some plants clearly become more susceptible to certain insects during severe drought owing strictly to a decline in ongoing defenses. For example, drought-induced reduction in oleoresin exudation pressure in conifers is closely linked to the colonization success of bark beetles and larvae of some needle-feeding Lepidoptera

(Mattson and Haack 1987). Drought may lower the inducible defense systems that some plants possess. For example, expression of the genes conferring resistance of wheat to stem and leaf rusts and to the Hessian fly *Mayetiola destructor* appear to be very temperature sensitive; resistance usually declines with increases in temperature, but for some traits the opposite may occur (Gousseau et al. 1985, Sosa 1979). Likewise, the rate of generalized wound healing in grand fir *Abies grandis* declines during drought (Puritch and Mullick 1975).

Drought enhances insect detoxication systems and immunocompetence. Because levels of many insect-resistance allelochemicals increase during drought, it would seem that stress may actually fortify rather than weaken plant defenses against some classes of consuming insects. How then can outbreaks of these consumers be explained? It may be that drought somehow enhances the herbivore's detoxication systems more than the plant's defenses. One possibility is that the increased temperatures associated with drought increase the insect's ability to detoxicate some plant allelochemicals. For example, Hinks (1985) reported that increasing temperatures reduce susceptibility of the grasshopper *Melanoplus sanguinipes* to pyrethroid insecticides. Similar relationships have been reported for other insects exposed to pyrethroids, DDT, and some carbamates (Hinks 1985, Mattson and Haack 1987).

The altered chemical composition of drought-stressed plants could also enhance an insect's ability to detoxicate compounds. Many studies indicate that pesticide efficacy varies with the plant cultivar or species consumed by insects prior to pesticide exposure (Mattson and Haack 1987). Decreased pesticide sensitivity as a result of dietary experience has been explained in two ways. First, the insect's diet may contain inducers, such as some nontoxic allelochemicals, that stimulate production of the insect's detoxicating enzymes (Terriere 1984); for example, the southern armyworm *Spodoptera eridania* was twice as tolerant to nicotine when its diet contained the inducer alpha-pinene (Brattsten 1979). Second, nutrient

concentrations may be more nearly optimal in those plants where insects show reduced pesticide sensitivity. Nutrient imbalances can lower the production and sensitivity of detoxication mechanisms, such as the mixed-function oxidase system (Campbell and Hayes 1974, Nutrition Reviews 1985). Wahl and Ulm (1983) reported that honeybees were more sensitive to various pesticides when their diet contained pollen that was unusually low in protein and vitamins. Although poorly understood, nutrition may also influence pesticide penetration and target site sensitivity (Campbell and Hayes 1974).

We hypothesize that both elevated temperatures and improved nutritional properties of drought-stressed plants can enhance the insect's detoxication system, at least with respect to some toxicants. The nutritional aspect of this scenario may be similar to the mechanism that permits the fungus *Armillaria mellea* to colonize roots of stressed trees. According to Wargo (1981), *A. mellea* succeeds in stressed trees because the increased concentrations of sugars and amino acids increase its ability to oxidize the normally inhibitory phenols and even to utilize the phenolics as a carbon source.

The chemical changes induced in drought-stressed plants may influence interactions between phytophages and organisms pathogenic to them. The changes may either directly affect the pathogens or may enhance the insect's immune system. High gut levels of allelochemicals that accumulate in stressed plants can inhibit growth of ingested pathogens (Barbosa and Saunders 1985, Mattson and Haack 1987). In addition, improved nutrition could increase the insect's capacity to suppress pathogenic microorganisms (e.g., protozoans, fungi, bacteria, and viruses), nematodes, and parasitoids. Moreover, there may be significant synergistic interactions between the insect's immune and detoxication systems. For example, Wahl and Ulm (1983) reported that honeybees infected with *Nosema* were more sensitive to pesticides. Similarly, Brattsten (1987) demonstrated that sublethal virus infections markedly increased sensitivity of tobacco budworm *Heliothis virescens*

to insecticides. Hence, a stronger immune system might indirectly allow more potent detoxication or vice versa.

The immune system of insects is less complex than that of vertebrates (Dunn 1986, Götz and Bowman 1985). However, most research on the effects of nutrition and stress on immunocompetence has been done with vertebrates. The vertebrate studies indicate that nutrient deficiencies and imbalances can reduce general immunocompetence. For example, Porter et al. (1984) demonstrated that undernourished mice were more sensitive to virus; this is also generally true for insects (Biever and Wilkinson 1978, Mattson and Haack 1987). Chandra (1985) reported that protein and energy malnutrition and vitamin and mineral deficiencies can affect many components of the immune system. Furthermore, because competence of the vertebrate immune system depends on its anatomical and biochemical links to the nervous system (Garfield 1986, Mattson and Haack 1987), it is possible that certain plant traits may favor or disfavor insect immunocompetence via the central nervous system.

Drought favors mutualistic microorganisms but not natural enemies of phytophagous insects. Drought may influence phytophagous insects indirectly by optimizing conditions for their exo- and endo-symbionts. Because many microbes have thermal optima of 25°–30° C (Brock et al. 1984), the high temperatures associated with drought could stimulate microbial growth. Likewise, some of the chemical changes in drought-stressed plants could enhance microbial growth; for example, levels of glucose and fructose often increase in the inner bark and sapwood of drought-stressed trees (Hodges and Lorio 1969, Mattson and Haack 1987). Because these sugars are the most readily used sources of carbon by the blue stain fungus *Ceratocystis minor* (Barras and Hodges 1969), an external symbiont of the bark beetle *Dendroctonus frontalis*, fungal growth is likely to be accelerated when introduced by the beetle into drought-stressed pines (*Pinus*). Rapid growth and tissue penetration by blue stain fungi would decrease the likeli-

hood of resin exudation by conifer hosts and thus favor colonization by bark beetles. Future research must address the influence of changing environments on insect-symbiont interactions.

During drought, high temperatures may allow phytophagous insects to escape the control of their natural enemies. For example, Wilson (1974) reported that optimal temperatures for the microsporidian parasite *Nosema fumiferanae* of the spruce budworm were below 23° C, but optimal temperatures for the budworm are near 27° C (Haack et al. unpublished data, Regniere 1982). A similar divergence in optimal temperatures exists between the Banks grass mite *Oligonychus pratensis* and its predators (Toole et al. 1984). Glare et al. (1986) and Strong et al. (1984) give more examples.

In addition, the low humidity and high sunlight levels associated with drought may lower amounts and virulence of pathogens. For example, drought may restrict fungal diseases because spores require high humidity for germination and penetration of the insect's integument (Ferron 1985). Similarly, bacterial and viral diseases may be reduced during drought because many are inactivated by the higher ultraviolet radiation levels (Ali and Sikorowski 1986, Brock et al. 1984, Mattson and Haack 1987). Hence, the normal guild of natural enemies could be rendered less effective during drought, and thereby fail to regulate an incipient outbreak.

Drought may induce genetic changes in insects. The elevated temperatures and solar radiation associated with drought may not only affect the rate and efficiency of enzymatic reactions within an insect, but they along with various plant biochemical changes may induce random as well as programmed genetic changes in insect populations. For example, at the population level, these environmental changes may suddenly favor some uncommon allozyme variants and through classical natural selection cause them to rapidly increase in abundance (Haukioja and Hakala 1975). At the individual level, the markedly different physical and/or metabolic conditions of drought

stress may change gene expression to induce alternate isozymes (Hochachka and Somero 1984, Schott and Brusven 1980).

Moreover, the thermal and dietary (biochemical) effects of drought can trigger genomic modifications, such as induction of heat-shock genes (Petersen and Mitchell 1985, Van der Ploeg et al. 1985), amplification of genes (Mouches et al. 1986, Rucker and Tinker 1986, Walbot and Cullis 1985), transposition of movable elements (McClintock 1984, Walbot and Cullis 1985), and other rearrangements such as polyploidy. (Bidwell et al. 1985). While the effects of extreme temperatures and toxins are generally well appreciated, the effects of nutrients per se can also significantly affect gene expression (Rucker and Tinker 1986). The issue of rapid genomic response to stress deserves attention, especially considering that certain grasshoppers and Lepidoptera are found in different forms (morphs) during outbreaks and latent phases of their population gradients (Baltensweiler 1984, Rhoades 1985). We propose that there could be high-temperature forms of insects that possess enzymes in higher concentrations and/or with higher catalytic efficiencies, allowing more efficient detoxication and nutrient utilization.

Variation among insect feeding guilds

The importance of the mechanisms by which drought may promote insect outbreaks is likely to vary among insects of different feeding guilds, such as external leaf feeders and inner-bark feeders. The relative importance of the individual mechanisms may depend upon the types of host defenses normally encountered; the nutritional quality of host tissues or fluids; the level of exposure to natural enemies; and the degree of enclosure or contact with host tissues (Haack and Slansky 1987, Mattson et al. 1987).

Most external leaf feeders, we believe, are regulated by a combination of delayed inducible plant defenses, natural enemies, and low nutrient levels. It is sufficient for plants to control these insects imprecisely, because most plants can compensate for and recover from the feeding damage

(Mattson et al. 1987). Drought provokes outbreaks of leaf feeders by providing thermal and nutritional conditions that favor their growth, detoxication, and immunocompetence. Moreover, these changes also favor the insects' escape from regulation by their natural enemies. Drought-induced genetic changes in the insects may also be involved in outbreak development.

Outbreaks of leaf feeders often last for several years and then rapidly decline. Intense, long-term defoliation can lead to severe reductions in quality and quantity of foliage (Baltensweiler 1984, Rhoades 1985, Tuomi et al. 1984). Such reductions, coupled with decreased phytophage "virulence" and the growing numbers of the insects' natural enemies, reduce populations of defoliating insects to more innocuous levels (Mattson and Haack 1987).

In contrast, inner-bark boring insects, such as bark beetles, appear to be primarily regulated by powerful host defenses, such as preformed oleoresin or latex systems and immediate inducible defenses (Mattson et al. 1987). Unlike the leaf feeders, inner-bark borers usually encounter nutrient-rich food and receive substantial protection from many natural enemies (Haack and Slansky 1987). The gregarious behavior of many of these insects makes them especially dangerous. If one insect becomes established, it rapidly attracts others through pheromonal communication. Plants require an iron-clad defense against such insects because their damage, the girdling of the conducting phloem and xylem, is devastating. Recovery even under ideal conditions is nearly impossible.

Compromised plant defenses, droughts, and such other factors as fire, lightning strikes, and natural plant senescence make normally protected plants highly susceptible to inner-bark feeders (Haack and Slansky 1987). Drought effects on insect growth, detoxication ability, immunocompetence, natural enemies, and genetic changes are probably secondary. Once weather conditions normalize, populations of these insects decline primarily, we believe, because of the plant's restored defenses. However, even these "recovered" plants may be overwhelmed by mass attacks

of insects whose populations were greatly enlarged during the stress period (Mullock and Christiansen 1986).

Drought and other stresses

A plant's repertoire of stress responses is rather limited. Therefore, we hypothesize that plant reactions to other kinds of stress are very similar to their reactions to drought; one should be able to detect similar reactions to a diverse array of perturbations. For example, just as drought stress increases levels of soluble sugars and nitrogen in plant foliage, inner bark, and sapwood (Mattson and Haack 1987), so do air pollutants such as sulfur dioxide (Kozlowski and Constantinidou 1986), salts (Braun and Flückiger 1984), nutrient deficiencies (Göring and Thien 1979, Huber 1984), and flooding (Kozlowski 1984). If plants have more or less universal responses to stress, then many phytophagous insects appear to be adapted to detecting and capitalizing on these situations. In support of this contention are reports of insect outbreaks on trees stressed by air pollutants (Baltensweiler 1985, Kozlowski and Constantinidou 1986), salt (Braun and Flückiger 1984), and nutrient deficiencies (Mattson and Haack 1987).

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