

Chemical Indicators of Stress in Trees: Their Ecological Significance and Implication for Forestry in Eastern Oregon and Washington

Abstract

Acute and chronic stresses in forest ecosystems can reduce growth or vigor of trees, and cause changes in their physiology or chemical contents. Ethanol, acetaldehyde, ethylene, and ethane are volatile compounds often produced in stressed, dying, or recently dead trees. Ethanol accumulation is ecologically important because it attracts insects that attack and damage trees, or spread disease. In addition, there are other chemicals conferring resistance to insects and disease, but they decrease in concentration under stress. Monitoring these compounds can assist in timing the lifting of nursery seedlings, detecting harmful effects from air pollution, confirming the presence of root disease, or identifying trees at risk to insect attack. Chemical indicators of stress have potential to be used in monitoring forest health across various scales, but not enough is yet known about options and techniques.

Introduction

Forest ecosystems are dynamic entities where constant change can be expected, but only partially predicted. Major disturbances are agents of change and represent acute forms of stress resulting from events of high intensity but low frequency (fires, drought, flooding, insects, disease, etc.), and often cause extensive mortality. The consequences of these disturbances; however, are not always detrimental to ecosystem functions or processes. In other instances these same events (drought, insects, disease) can occur more frequently, but at low intensity in which case they represent chronic stress (Wargo and Harrington 1991). Acute and chronic stresses are often linked, with the occurrence of one leading to the other. Fire suppression and selective logging during the past century have dramatically changed stand age structure and species composition creating chronic stress conditions that have subsequently encouraged disease, insect outbreaks, and invasion by non-native species.

Human population growth and climate change are two potential stress factors expected to greatly impact forest ecosystems on a global scale in the near and distant future (Ayres 1993, Pederson 1998). As these events unfold, resource managers will be challenged to provide sustainable ecosystem management. The integrity, productivity, and biodiversity of forest ecosystems are to be maintained in conjunction with social, economic, and cultural values (Bourgeois 1998). As demands

on forest ecosystems increase, the intensity and complexity of forest management practices will increase, and so could the frequency and intensity of stress. Acute and chronic stressors will always be present in forest ecosystems, but a more thorough understanding is needed to insure these ecosystems remain resilient and sustainable. This requires new knowledge and innovative ideas for predicting, detecting, monitoring, and mitigating stress.

Stressors and Their Interactions

Trees naturally experience various biotic or abiotic stressors during their life without serious consequences. Biotic stressors include inter- and intra-specific competition, animals (insects, mammals, etc.), pathogens, and direct or indirect anthropogenic causes—pollutants being an indirect factor. Abiotic stressors include extremes of solar radiation, or temperature, drought, flooding, nutrient deficiencies, fire, and others (Larcher 1995). There is considerable temporal variation in the type of stress, their duration and intensities. In arid eastern Oregon and Washington, climatic or other environmental extremes are relatively common (Hessburg et al. 1994), and periodically one or more stressors can reach levels that restrict the ability of trees, or entire forests to develop and function normally, or to survive. Trees are usually adapted to their environment and have evolved mechanisms to avoid, resist, or tolerate stress. Age-related and genetic variability

in these mechanisms, within and among trees, can strongly influence their response to stressors (Steiner 1974, Redfern 1978, Alfaro et al. 1996).

Physiological responses to stress have metabolic costs that can reduce growth and vigor, weakening trees so they become more susceptible to other stressors. For example, drought can predispose stands or entire forests to outbreaks of insect defoliators or bark beetles (Mattson and Haack 1987, Cobb et al. 1997), and trees suffering from water stress are more susceptible to infection by root disease organisms such as *Armillaria* spp. (Wargo and Harrington 1991). Trees scorched by fire are more vulnerable to bark beetle attack, and risk of attack typically increases with severity of burn damage (Furniss 1965, Geiszler et al. 1984, Rasmussen et al. 1996, Scott et al. 1996). Trees infected by pathogens are at greater risk to attack by bark beetle than healthy trees (Cobb et al. 1974; Lane and Goheen 1979; Goheen and Cobb 1980; Gara et al. 1984, 1985; Littke and Gara 1986; Witcosky et al. 1987; Goheen and Hansen 1993). Also, nursery seedling stock subjected to excessive stress prior to planting is more likely to fail than unstressed stock (Hawkins and Binder 1990, Templeton and Colombo 1995).

Stress-Induced Volatile Compounds

Ethanol

Trees subjected to severe stress may produce volatile compounds, particularly ethanol, acetaldehyde, ethylene, and ethane (Kimmerer and Kozlowski 1982). Small quantities of ethanol are normally found in woody tissues of healthy trees (MacDonald and Kimmerer 1991, Gara et al. 1993, Kelsey and Joseph 1998, Kelsey et al. 1998). Much higher ethanol concentrations have been detected in trees or tissues stressed by pathogens, water deficits, hypoxia or anoxia, heat, flooding, freezing, girdling, crown removal, crushing injury, and pollutants such as SO₂ and NO₂ (Kimmerer and Kozlowski 1982, Kimmerer and MacDonald 1987, MacDonald et al. 1989, Sjödin et al. 1989, Gara et al. 1993, Templeton and Colombo 1995, Joseph and Kelsey 1997, Kelsey and Joseph 1998, Kelsey et al. 1998, Kelsey and Joseph 2001). Fire damage can also induce ethanol synthesis (authors unpublished data). Logs and stumps will produce ethanol as they age, but the quantities generated can vary greatly and are strongly in-

fluenced by species and surrounding environmental conditions (Kelsey 1994a, 1994b, 1996; Kelsey and Joseph 1997; von Sydow and Birgersson 1997; Kelsey and Joseph 1999a, 1999b). An elevated ethanol concentration is a general indicator of stress in trees, but not diagnostic for a particular cause.

When ethanol accumulates to high enough concentrations in trees and woody residues, it acts as a stress signal and primary attractant for various forest insects, particularly ambrosia beetles, "secondary" bark beetles, and weevils that attack and colonize logs, stumps, slash, and severely stressed, dying, or recently dead trees (Moeck 1970; Cade et al. 1970; Klimetzek et al. 1986; Chénier and Philogène 1989; Sjödin et al. 1989; Kelsey 1994a, 1994b; Kelsey and Joseph 2001). The attraction of these beetles and weevils to host terpenes, or their pheromones, can be enhanced or synergized by the simultaneous release of ethanol (Pitman et al. 1975, Tilles et al. 1986, Schroeder and Lindelöw 1989, Lindelöw et al. 1993, Ross and Daterman 1995). While most of these insects are typically non-aggressive and seldom damage larger, vigorously growing trees, they can cause a variety of problems for forest management, especially if population densities are allowed to increase above endemic levels. For example, ambrosia beetles prefer to attack aging logs containing higher ethanol concentrations than fresh logs or logs protected from rain (Kelsey 1994a, 1994b; Kelsey and Joseph 1999a). They create pin-sized gallery holes and introduce stain fungi that discolor the wood, and when abundant these beetles can quickly degrade logs and the value of finished lumber products (McLean 1985). Damage from ambrosia beetles can be minimized by quickly removing logs from the forest before ethanol accumulates.

When ethanol attracts secondary bark beetles and weevils to colonize trees infected with root disease their offspring can spread spores of the pathogen to adjacent healthy trees or stands (Witcosky et al. 1986a, 1986b; Nevill and Alexander 1992a, 1992b). Other bark beetles and weevils that reproduce in woody debris and stumps can severely damage or even kill regeneration seedlings, saplings, and occasionally, severely-stressed larger trees, especially when the insect populations increase to higher densities (Furniss and Carolin 1977, Nordlander 1987, Ciesla 1988, Wilson et al. 1996, Salom 1997). The behavior

of ambrosia beetles (Kelsey and Joseph 1999a) and some secondary bark beetles (Kelsey and Joseph 2001) can be manipulated by controlling the production of ethanol in their hosts. Ethanol synthesis and accumulation in woody residues and stressed trees are important processes in forest ecosystems with ecological consequences as described above. Understanding when and where ethanol synthesis occurs, the mechanisms causing it to occur, and how it can be controlled could be useful in monitoring and managing some insect and disease problems in forest ecosystems.

Acetaldehyde

Acetaldehyde is another stress-induced volatile that may be a useful indicator of stress in trees. It is the biosynthetic precursor to ethanol (Harry and Kimmerer 1991), and can increase in concentration with ethanol in response to stress (Kimmerer and Kozlowski 1982). Acetaldehyde appears to be useful for the early detection of root disease in ponderosa pine (Kelsey et al. 1998). Trees stressed by root diseases can be difficult to manage, in part because infected trees are not easily identified (Wallis and Bloomberg 1981, Filip 1986, Thies and Nelson 1997). Crowns of diseased trees develop various visual symptoms, such as reduced terminal growth, discolored foliage, reduced needle numbers, or stress cones, but these symptoms do not appear and are not reliable indicators until infection reaches a moderate to advanced stage. In ponderosa pine, about one-third of the root system is damaged by disease before symptoms develop in the crown (Kelsey et al. 1998). Detecting root diseases earlier will allow more time to develop and implement ameliorative management options. Acetaldehyde measured in ponderosa pine sapwood sampled just above soil level was the best indicator among chemical and crown characteristics for identifying trees with root disease; unlike crown symptoms it was present in trees with lightly infected roots (Kelsey et al. 1998). In addition, acetaldehyde and methanol concentrations in diseased ponderosa pine may be helpful in estimating what proportions of their root systems are incapable of transporting water (Kelsey et al. 1998), although this requires further testing.

Ethylene and Ethane

Ethylene is a stress-induced volatile and also a plant hormone that occurs normally in tissues.

Without stress the quantities can vary depending on the tissue type and its stage of development (Taiz and Zeigler 1998). When stress does occur, ethylene concentrations are influenced by the type of stress and the plant species (Kimmerer and Kozlowski 1982). Ethylene produced by woody tissues from olive trees functions as a primary host attractant for the olive beetle (González and Campos 1996).

Ethane may also be detected in stressed plants, but it appears to be a better indicator of cell or tissue death than it is for stress (Kimmerer and Kozlowski 1982). Less is known about the ecological implications of ethylene and ethane in forest ecosystems than we know about ethanol.

Other Chemical Indicators of Stress

In contrast to stress-induced volatiles in trees, the concentrations of some "secondary" compounds that potentially confer resistance to insects and disease, decrease in response to stressors. For example, concentrations of nitrogen containing piperidine alkaloids in ponderosa pine foliage are positively related to site quality and foliar nitrogen content (Gerson and Kelsey 1998). Trees on the lowest quality and most stressed site, based on site and crown characteristics, produced no detectable alkaloids. Some of these stressed trees began to synthesize alkaloids when available soil nitrogen was increased by fertilization (Gerson and Kelsey 1999). Foliar alkaloids may have some value in evaluating the general physiological condition of ponderosa pine across a stand or watershed.

Another compound that decreases in concentration with stress is 4-allylanisole (4AA). Needles of ponderosa pine injured by smog contained 71% less 4AA than needles from healthy trees (Cobb et al. 1972). Also, when lodgepole pine were stressed by infections from Comandra blister rust or Armillaria root disease, their xylem resin contained 43% and 63% lower 4AA concentrations, respectively, than healthy trees (Nebeker et al. 1995). The response of bark beetles to primary host attractants or their pheromones can be inhibited by 4AA (Hayes and Strom 1994, Hayes et al. 1994, Werner 1995, Joseph et al. 2001), so lower concentrations in ponderosa pine stressed by air pollutants could partially explain their greater risk to attack by bark beetles than healthy trees (Stark et al. 1968).

Applications in Forestry

Currently, the most practical applications for chemical indicators of stress are in the nursery industry. Ethanol and acetaldehyde show promise in testing for frost injury/stress resistance and in determining the optimum period for lifting nursery seedlings (Hawkins and Binder 1990). Ethanol monitoring has been used operationally in the Province of Ontario, Canada, to identify seedlings potentially injured by handling stress between nurseries and planting sites (Colombo et al. 1995, Templeton and Colombo 1995). In the Ohio River Valley, elevated ethanol concentrations in leaves of various hardwoods is a good indicator that trees are being exposed to air pollution from NO₂ (MacDonald et al. 1989). Acetaldehyde may be useful in the early detection of root disease and estimating the proportion of nonfunctional root system in ponderosa pine (Kelsey et al. 1998). The presence of ethanol in phloem and sapwood of ponderosa pine or Douglas-fir stems near the soil is a strong indicator that their roots are infected with disease organisms (Kelsey and Joseph 1998, Kelsey et al. 1998). Trees that accumulate ethanol are at greater risk of being attacked by secondary bark beetles than trees containing low quantities of ethanol (Kelsey and Joseph 2001).

Our studies of ethanol have begun to answer some of the questions regarding bark beetle host-tree selection and possible mechanisms for insect-pathogen interactions. Initial results indicate that stress-induced volatiles could be used to detect trees with root disease, trees at risk to insect attack, or to monitor stress in high value trees found in campgrounds, parks, and urban forests. Chemical indicators of stress also have potential for monitoring the physiological conditions or "health" of forests, but additional research is required to develop suitable sampling protocols and procedures. The utility of chemical markers could span all geographic scales, from an individual tree up to stands spanning several eco-regions.

A simple, quick, and portable method to detect and crudely quantify ethanol in the field was adapted by the forest nursery industry in Ontario, Canada, from existing industrial technology (Co-

lombo et al. 1995). Use of this method in other forestry applications has not been examined. Portable breath alcohol analyzers may be useful in the field to detect ethanol in tree leaves, based on preliminary tests (MacDonald et al. 1989). For research purposes, gas chromatography is used to analyze a wide range of compounds. Headspace-gas chromatography is the method of choice for stress-induced volatiles because it is very sensitive and detects all compounds of interest simultaneously (Kimmerer and Kozlowski 1982). Also, it can be automated to process large numbers of samples in a relatively short time, and multiple headspace extractions allow accurate quantification (Kolb et al. 1984, Kelsey and Joseph 1998).

Summary and Future Research

The knowledge of chemical indicators associated with stress, such as ethanol and acetaldehyde, is advancing but still requires hypothesis-driven research in order to fully realize its significance and potential application. The need to understand, detect, monitor, predict, and mitigate stress in forest ecosystems is likely to increase in the future because of global climate change and increasing anthropogenic disturbances. Depending on a forest's geographic location, changes may occur in the most common types of stressors, including their frequency, intensity, duration, and predictability (Ayres 1993). In the future, resource managers will struggle to maintain sustainable forest ecosystems that are resistant and resilient to stress. A more thorough understanding of how trees and forests respond physiologically to stress, and associated ecological consequences is essential (Ayres 1993, Larsen 1995, Lorio et al. 1995). Expanding the knowledge about chemical indicators of stress has potential to provide new tools and procedures that can guide resource managers to achieve their goals.

Acknowledgements

The author thanks Liz Gerson, Dr. L. Liegel, and Dr. G. Joseph for their comments and suggestions to improve this manuscript.

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Note

This special issue of *Northwest Science* is a set of papers reviewing the state of knowledge about disturbance processes in eastern Oregon and Washington, related management practices, and effects on key management issues.