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Physiological Aspects of Air Pollution Stress in Forests

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Summary

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Air pollutants, such as ozone, sulfur dioxide, nitrogen compounds and others, affect health of forests in Europe and North America. Gaseous air pollutants enter plants mainly through stomata, although transcuticular transport can also be important for some pollutants. Toxic effects of pollutants depend on their effective dose that is proportional to pollutant ambient concentration and plant stomatal conductance. Mechanisms of air pollution toxicity are very complex and depend on various physiological and biochemical properties of plants. These mechanisms (including formation of free radicals) are still poorly understood. In addition, physiological responses of forest plants to air pollution stress can be modified by various biotic (e.g., insects, pathogens, mycorrhizae associations, genetic variation) and abiotic (e.g., increasing CO_2 concentrations, ultraviolet-B radiation, nitrogen deposition, nutrient deficiencies, drought) factors. An example of air pollution effects on forest trees may be responses of ponderosa pine seedlings to elevated concentrations of ozone in the Sierra Nevada. Various physiological changes caused by ozone (e.g., lowered net photosynthesis, altered carbon allocation, deterioration of photosynthetic pigments, etc.) have led to the reduced growth and biomass of the seedlings.

Introduction

Air pollutants affect forests worldwide (IUFRO 1993). These effects may be severe (e.g., in the Sudety Mountains in central Europe or the San Bernardino Mountains in southern California), or subtle (e.g., in Scandinavia, Germany, or the eastern United States). Various air pollutants have been identified as phytotoxic agents. Phytotoxicity of sulfur dioxide (SO_2) has been recognized for about a century

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(GODZIK & SIENKIEWICZ 1990), effects of ozone (O_3) for more than 30 years (MIILLER & al. 1963), acidic precipitation for almost 20 years (LIKENS & al. 1979), and effects of elevated levels of nitrogen compounds (nitrogen oxides [NO_x] and ammonia [NH_3]) in the last decade (NIHLGARD 1985). Importance of other pollutants such as peroxyacetyl nitrate (PAN) (TEMPLE & TAYLOR 1983), fluorides (MACLEAN 1981) or heavy metals (UNSWORTH & HARRISON 1985) has also been recognized.

Although physiological responses of forest trees to atmospheric pollution have been well documented (SMITH 1974, GUDERIAN 1985, WELLBURN 1988, MCLAUGHLIN 1994), the literature is dominated by seedling and sapling responses with only a few extrapolations to mature trees. Responses of trees to air pollutants may vary widely and these variations can be caused by many factors, such as differences in pollutant concentrations and distribution in time, the genetic origin, physiological activity, phenological stage, and nutritional status of plants as well as effects of various environmental factors.

Under field conditions detection of physiological changes in plants and identification of their causes is difficult. Therefore visible symptoms of injury are most commonly used for detecting air pollution damage. However, changes in physiology of plants may occur before visible, morphological damage takes place. If properly used, physiological changes can be used as early indicators of the deleterious effects of air pollution in forests.

Pollutant deposition to plants

Pollutants can be deposited to plants as gases, wet precipitation or particulate matter. Gaseous pollutants may be taken up by plants via stomata or cuticle. The effects of pollutants can be observed at various levels of biological organization (subcellular, cellular, plant organ, whole plant, plant population and community). The flux of pollutants from the atmosphere to plant cells follows the same pathway as carbon dioxide (CO_2). Each pollutant has a different diffusion constant for movement through air, solubility constant for movement across apoplastic water, and hydrophobic or hydrophilic properties that affect the rate of transfer across cell walls and membranes (Fig. 1) (BYTNEROWICZ & GRULKE 1992).

Concentrations of pollutants and the degree of stomatal opening determine the internal pollution dose and subsequent plant response (WELLBURN 1988). For instance, when O_3 toxicity is considered, the production of O_3 and stomatal conductance of plants undergo diurnal cycles driven mainly by sunlight. In or near the O_3 source areas these two processes co-occur, and under such conditions the maximum efficiency of O_3 uptake can be expected. However, most of the forest sites, particularly in the coastal and interior region of California or the Iberian Peninsula, are removed from the ozone source areas (MILLER & al. 1986, MILLAN & al. 1992). At these sites the highest ozone concentrations occur in the afternoon or evening hours when stomatal conductance of plants is low. Under such circumstances peak concentrations of O_3 could cause relatively low injury to plants (KRUPA & al. 1995) because the cumulative internal flux of ozone in plants might be minimal (RUNECKLES 1992).

Some air pollutants, e.g., nitric oxide (NO), nitrogen dioxide (NO_2) or gaseous nitric acid (HNO_3), can enter plants through the cuticle (LENDZIAN & KERSTIENS 1988, KRYWULT & al., 1994). This phenomenon was shown by a substantial increase of ^{15}N and induction of nitrate reductase activity in foliage of ponderosa pine and California black oak seedlings exposed in darkness to $H^{15}NO_3$ vapor (KRYWULT & al. 1994, 1995).

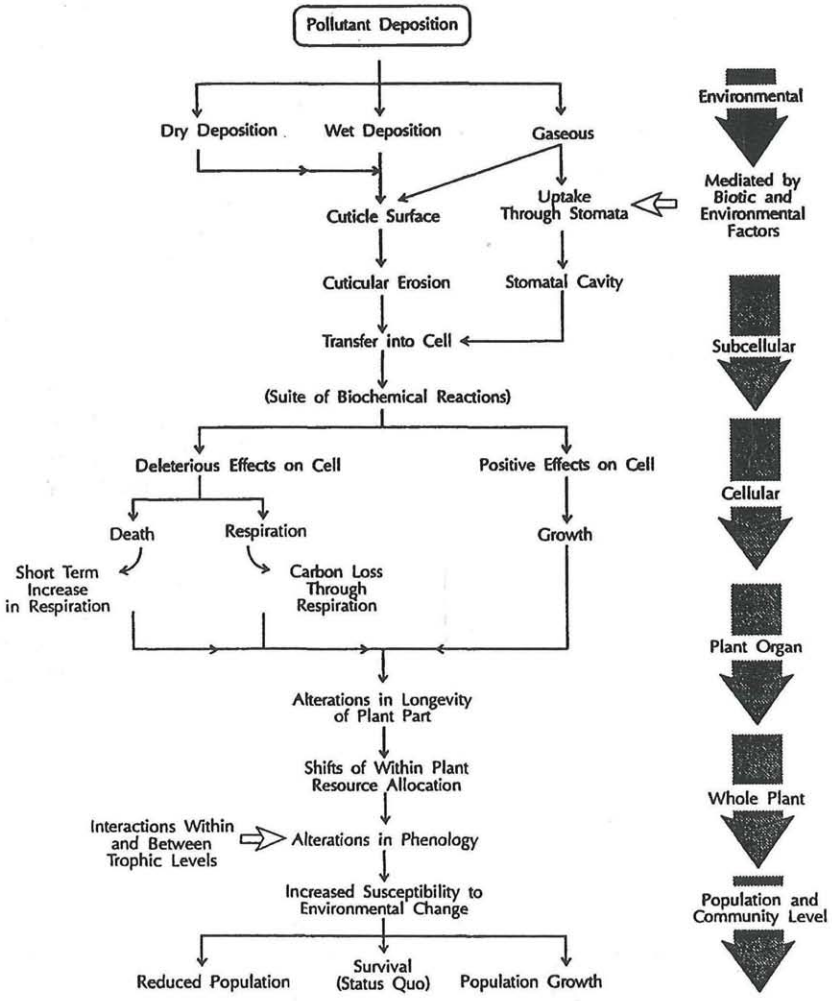

Fig. 1. Model of deposition of gaseous air pollutants and their effects on plants at different levels of biological organization. Note that at each level effects may not be deleterious nor detectable. Compensatory responses at one level may prevent effects at higher levels (after BYTNEROWICZ & GRULKE 1992).

Mechanisms of air pollution toxicity

Once pollutants enter the plant cell a suite of primary and secondary metabolic reactions as well as defense reactions start taking place (BYTNEROWICZ & GRULKE 1992). Although many review papers on metabolic changes caused by air pollutants have been published (WELLBURN 1988, KRUPA & MANNING 1988, ZIEGLER 1973, RENNENBERG & al. 1990) our knowledge of the mechanisms of air pollution phytotoxicity is still incomplete and continues to develop.

Toxic effects of O_3 and PAN have been explained by the formation of highly phytotoxic free radicals in plant cells that may damage most of the cell components (HEATH 1988, KRUPA & MANNING 1988, HEWITT 1990, RUNECKLES & CHEVONNE 1992). To some extent the phytotoxic effects of SO_2 can also be explained by free radical toxicity (WELLBURN 1988). However, phytotoxicity of SO_2 mainly results from accumulation of the immediate SO_2 metabolite, sulfite (ZIEGLER 1973, MILLER & XERIKOS 1979). Secondary sulfur metabolites such as sulfoxides (R-SO-R') and sulfones (R-SO_2-R') are also considered highly phytotoxic (GIETKO 1976). The chloroplast is considered to be a primary site of SO_2 toxicity (WELLBURN 1988).

Effects of biotic and abiotic factors

Biotic factors (such as insects, various pathogens, mycorrhizae associations, genetic variation) can influence physiological responses of trees to air pollutants (CHAPPELKA & CHEVONNE 1992). Chronic exposure to air pollutants may also predispose trees to bark beetle attacks, a situation commonly occurring in the O_3-stressed ponderosa pine trees in southern California (MILLER 1983).

It is now well recognized that most terrestrial ecosystems are not affected by only one pollutant, that exposures are often chronic, and that effects in natural stands are largely the result of air pollution interacting with a suite of other environmental stresses (TAYLOR & al. 1994). Plants can be affected by various stresses either simultaneously or sequentially. Some of the most important stresses which may interact with air pollutants include: increasing concentrations of CO_2, elevated ultraviolet B (UV-B) radiation, high nitrogen deposition, nutrient deficiencies, drought, or temperature extremes. This applies, among others, to forests in the San Bernardino Mountains (southern California) where for decades elevated concentrations of O_3 and N deposition have interacted with changing climatic conditions (MILLER & RYAN 1977, FENN & BYTNEROWICZ 1993).

An increase in UV-B radiation has been observed throughout the troposphere, especially at high elevations (BLUMENTHALER & AMBACH 1990). There is great potential for various biological effects of increasing UV-B radiation and its interactions with elevated concentrations of CO_2 and O_3 (KRUPA & KICKERT 1993). At the mechanistic level, O_3 generally inhibits photosynthetic gas exchange, and although UV-B is also inhibitory in some species, others appear to be indifferent. Both factors affect metabolism: a common response may be increased secondary metabolism leading to accumulation of phenolic compounds, that in the case of UV-B, provide cells with some protection from radiation. Virtually no

information is available about the effects of simultaneous or sequential exposures to UV-B and O_3 on plants (RUNECKLES & KRUPA 1994). All these factors, and many others, will have to be considered in future attempts to evaluate air pollution effects on forests.

Effects of age and stage of plant development

Very young seedlings usually are more sensitive to air pollution than saplings or mature trees. Seedlings at the cotyledon stage of development often grow at threshold levels of available carbohydrates, hormones, and mineral nutrients and are especially susceptible to air pollution (KOZLOWSKI 1976). Despite the high sensitivity of young seedlings to air pollution, older trees in forests near the air pollution point sources are often more injured than young trees. This is probably because the crown canopy serves as a filter and the young trees are less exposed to the pollutant. Furthermore, the low stomatal conductance of the shaded, understory plants result in low rates of absorption of gaseous pollutants (KOZLOVSKI & al. 1991).

GRULKE & MILLER 1994 studied the effect of tree age on susceptibility of giant sequoias to elevated concentrations of O_3. The authors concluded that giant sequoia seedlings were sensitive to ozone until they were about 5 years old. Low stomatal conductance, high water use efficiency, and compact mesophyll cells all contributed to a natural ozone tolerance or defense, or both, in foliage of older trees.

Examples of physiological changes in trees caused by air pollution

In general, exposure to air pollutants changes the net carbon balance of a plant through effects on the light reactions or enzymatic functions, increased respiration from repair activities, or decreases in stomatal and mesophyll conductances (KOZLOWSKI & al. 1991). In addition, effects of low doses of pollutants may be stimulatory, but pollutant doses over a certain threshold become deleterious (BYTNEROWICZ & GRULKE 1992).

Changes in photosystems of plants caused by air pollution may be reflected by deterioration of photosynthetic pigments and reduced efficiency of photochemical reactions. In many studies decreases of chlorophylls and carotenoids have been associated with pollutant exposure. An example of such effects may be the change in the ratios of violaxanthin to antheraxanthin in Norway spruce foliage along the air pollution gradient in western Europe (WOLFENDEN & al. 1988). Chlorophyll fluorescence also proved to be a good indicator of O_3 effects on Scots pines in Finland (SAARINEN 1993).

Under the conditions of a well-defined O_3 stress (2 x ambient concentrations for two summers) ponderosa pine seedlings on the western slopes of the Sierra Nevada showed a wide range of responses: gradual increase of visible injury (chlorotic mottle) was accompanied by reduction of net photosynthesis, stomatal conductance, starch accumulations and pigment concentrations. Faster and

more pronounced reduction of net photosynthesis than stomatal conductance suggested that ozone injury to mesophyll, carboxylation, or excitation components of the CO_2 diffusion pathway were greater than injury to the stomata. As a result of all these changes plants reduced their growth and biomass production (TEMPLE & BYTNEROWICZ 1993).

Concluding remarks

Effects of air pollution on the physiology of forest vegetation are complex and still poorly understood. Because air pollutants interact with various biotic and abiotic factors, the responses of forest trees may widely differ. A better understanding of the physiological effects of air pollutants and of the observed changes in forest health may be accomplished by a closer cooperation of plant physiologists with biochemists, ecologists, atmospheric chemists, plant nutritionists, forest pathologists and other specialists.

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