ACIDIC PRECIPITATION AND FOREST VEGETATION

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Most plants can take up nutrients from the atmosphere as well as from the soil solution. This capacity is especially important in natural ecosystems such as forests and bogs where nutrients from other sources are scarce and where fertilization is not a normal management procedure. Trees develop very large canopies of leaves and branches that extend high into the air. Thus, trees offer a very large surface for deposition and potential assimilation of substances dispersed in the atmosphere.

Air-borne substances that influence plants include: sea spray from oceans and large lakes, dust resulting from wind erosion of soil as well as from volcanic and cosmic sources; gases such as carbon dioxide, ammonia, sulfur dioxide, hydrogen sulfide, methane, etc. released from decomposing organic matter and volcanoes; biogenic particles such as spores, hyphal fragments, and pollen; particulate matter, aerosols, and gases produced by wild fires and controlled burning of agricultural, forest and urban wastes as well as from industrial, agricultural, residential and commercial heating, and transportation operations. Combustion of fossil fuels is the largest anthropogenic source of air-born substances. Some of these substances include beneficial nutrient elements; others are injurious to plants. Many of these substances originate from natural sources; others are pollutants produced by man.

Many of these atmospheric trace constituents are at least partially soluble in water and can thus be absorbed or assimilated by plants when precipitation is intercepted by vegetation. In a typical forest, an average raindrop washes over three tiers of foliage before it reaches the soil. Since some of the substances dissolved in precipitation are beneficial while others are injurious to plant tissues, the net effect of atmospheric trace constituents can be beneficial or injurious depending on the chemical composition of the precipitation, the species of plant on which it is deposited, and the physiological condition and maturity of the plant.

Rain and snow change in chemical composition within as well as between precipitation events (rain or snow storms). Thus a given plant may be subject to beneficial atmospheric influences at one time and to negative influences at another time in its development. Since trees persist for many years or even decades in the same environment, they are subject to very long-term changes in the chemistry of the atmosphere and precipitation.

The effects of acidic precipitation on plants is only one facet of the much larger subject of atmosphere-plant-soil interactions. Acidity in precipitation should be understood as a reflection not only of the amounts of substances yielding hydrogen ions (such as sulfuric, nitric, hydrochloric and organic acids) but also as a reflection of the total ionic balance between all the other cations and anions dissolved in precipitation. For all of the above reasons, the effects of a given "acidic rain" or a prevailing condition of "acidic rains" are very complex, variable in time, and involve significant interactions which are only partially understood. Thus, these effects are not easily resolved into simple generalizations.

Our hope in this brief introduction is to set the stage for the experimental contributions that follow in this section of the Proceedings. We will set forth a few general concepts as well as some theoretical postulations about the effects of acidic precipitation on vegetation. We hope that these ideas will have some value at least as a stimulus for debate and for experimentation that will increase our present meager understanding of acidic precipitation and its effects on vegetation.

POTENTIAL EFFECTS ON VEGETATION

A partial list of potential effects of acidic precipitation on vegetation is given in Table 1. The effects are classified as either direct or indirect although most direct effects will have many indirect consequences as well. Indirect effects mediated through the soil are excluded from Table 1 since they are discussed in the preceeding section of these Proceedings. A decreased rate of growth would be the expected consequence of most of the effects postulated in Table 1.

IMPLICATIONS FROM EXISTING KNOWLEDGE

As indicated in Figure 1, susceptibility to damage by sulfur dioxide varied with the time of day. Guderian (1970) found in red clover a close parallel between degree of injury, apparent photosynthesis, and amount of sulfur accumulated during the day. Since sulfur

Table 1. Potential Effects of Acidic Precipitation on Vegetation

Direct Effects

1. Damage to protective surface structures such as cuticle.

Damage to surface structures may occur due to accelerated erosion of the cuticular layer that protects most foliar organs. It also could result from direct injury to surface cells by high concentrations of sulfuric acid and other harmful substances that are concentrated by evaporation or adherence of soot particles on plant surfaces.

2. Interference with normal functioning of guard cells.

Malfunction of guard cells will lead to loss of control of stomata and thus altered rates of transpiration and gas-exchange processes and possibly increased susceptibility to penetration by epiphytic plant pathogens.

3. Poisoning of plant cells after diffusion of acidic substances through stomata or cuticle.

This could lead to development of deep necrotic or senescent spots on foliar organs including leaves, flowers, twigs, and branches.

4. Disturbance of normal metabolism or growth processes without necrosis of plant cells.

Such disturbances may lead to decreased photosynthetic efficiency, altered intermediary metabolism, as well as abnormal development or premature senescence of leaves or other organs.

5. Alteration of leaf- and root-exudation processes.

Such alterations may lead to changes in populations of phyllosphere and rhizosphere microflora and microfauna, including nitrogen-fixing organisms.

6. Interference with reproduction processes.

Such interference may be achieved by decreasing the viability of pollen, interference with fertilization, decreased fruit or seed production, decreased germinability of seeds, etc.

7. Synergistic interaction with other environmental stress factors.

Such reinforcing interactions may occur with gaseous sulfur dioxide, ozone, fluoride, soot particles, and other air pollutants as well as drought, flooding, etc.

Table 1.--Continued

Indirect Effects

1. Accelerated leaching of substances from foliar organs.

Damage to cuticle and surface cells may lead to accelerated leaching of mineral elements and organic substances from leaves, twigs, branches, and stems.

2. Increased susceptibility to drought and other environmental stress factors.

Erosion of cuticle, interference with normal functioning of guard cells, and direct injury to surface cells may lead to increased evapotranspiration from foliar organs and vulnerability to drought, air pollutants, and other environmental stress factors.

3. Alteration of symbiotic associations.

Changes in leaf- and root-exudation processes and accelerated leaching of organic and inorganic substances from plants may affect the formation, development, balance, and function of symbiotic associations such as mycorrhizae, nitrogen-fixing organisms, lichens, etc.

4. Alteration of host-parasite interactions.

Resistance and/or susceptibility to biotic pathogens and parasites may be altered by predisposing plants to increased susceptibility, altering host capacity to tolerate disease, altering pathogen virulence, etc. The effects of acidic precipitation may vary with: the nature of the pathogen involved (whether a fungus, bacterium, mycoplasma, virus, nematode, parasitic seed plant, or multiple-pathogen complex); the species, age, and physiological status of the host; and the stage in the disease cycle in which the acidic stress is applied -- for example, acidic rain might decrease the infective capacity of bacteria before infection and increase the susceptibility of the host to disease development after infection.

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dioxide is taken up through the stomata, injury occurs mainly during the part of the day when the stomata are open. Sulfur also may be taken up through the cuticle, but this is a much slower process.

The physiological condition and maturity of leaves also is important. Sometimes damage is concentrated along tips and margins of leaves, but this may be a simple consequence of the laws of physics -- edges and tips are more exposed to injurious molecules in the air than are the central parts of leaves.

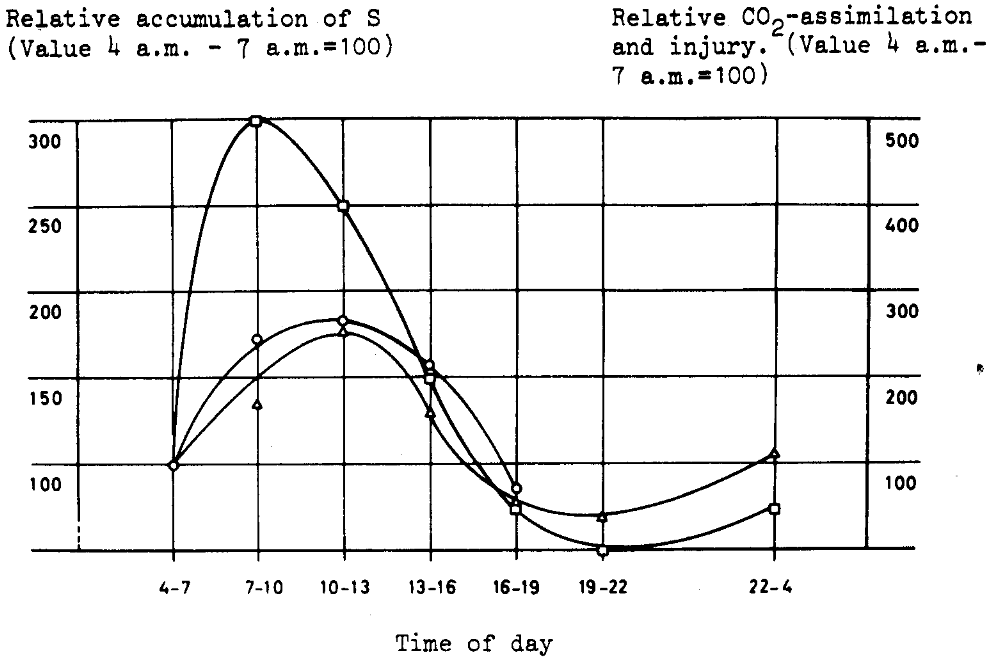

Figure 1. Accumulation of sulfur and degree of injury in red clover during different times of day, compared with apparent photosynthesis. ▢ degree of injury, o apparent photosynthesis, Δ sulfur accumulation. (Reproduced from Guderian, 1970).

Lichens, which do not have a protective covering of cuticle with stomata, are very sensitive to sulfur dioxide. For the same reason they also may be highly susceptible to the effects of acid rain. Schönbeck et al. (1970) found a very good inverse corelationship between the amount of sulfur dioxide in the air and the amount of living tissue remaining after exposure (Figure 2). Sometimes it is useful to use lichens as very sensitive indicators for air pollution because of the great difficulties of measuring air concentrations of sulfur dioxide in a physiologically meaningful way. Near sources of emission, the concentration of sulfur dioxide during any given 5-minute time interval may differ 2-5 fold from that during the next 5-minute interval (Figure 3). For this reason, a need exists for some type of biological assay, such as can be made by exposing lichens to air pollution over convenient periods of time.

Photosynthesis is very sensitive to air pollution. A strong reducing compound such as sulfur dioxide may affect both the chlorophyll itself and various steps in the photosynthetic process.

It is well known that plants differ greatly in their susceptibility to sulfur dioxide and other poisonous substances (Linzon, 1972). Genetically controlled variation in resistance or susceptibility to the effects of acid rain may likewise be expected both within and among

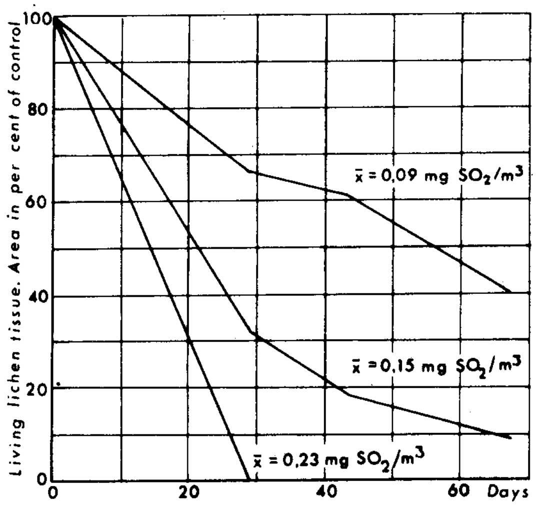

Figure 2. Influence of sulfur dioxide on transplants of a foliose lichen (*Parmelia physodes*) placed in the vicinity of an iron-ore smelter. Sulfur dioxide concentrations were measured according to the method of Stratmann. (Reproduced from Schönbeck et al., 1970).

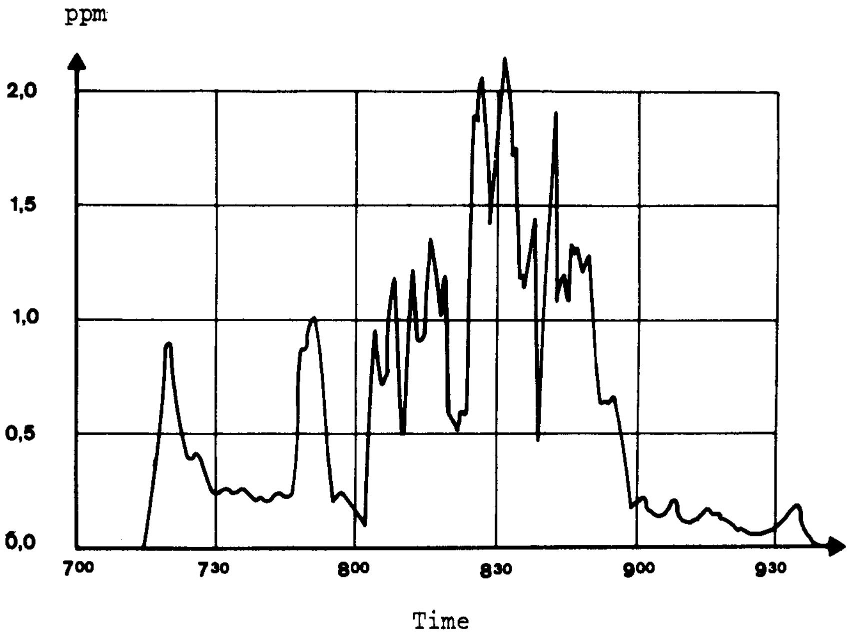

Figure 3. Variation in sulfur dioxide concentration at a station 600 m from cource of emission. (Reproduced from van Haut, 1961).

various species of forest trees. Figure 4 illustrates this variation in sensitivity to sulfur dioxide among various species and selections of woody plants. The concentrations of sulfur dioxide are shown on a logarithmic scale. The marks in the right-hand margin concern plants exposed for very long periods of time. The curved line is an empirical relationship developed by Thomas and Hill (1935) for the first visible

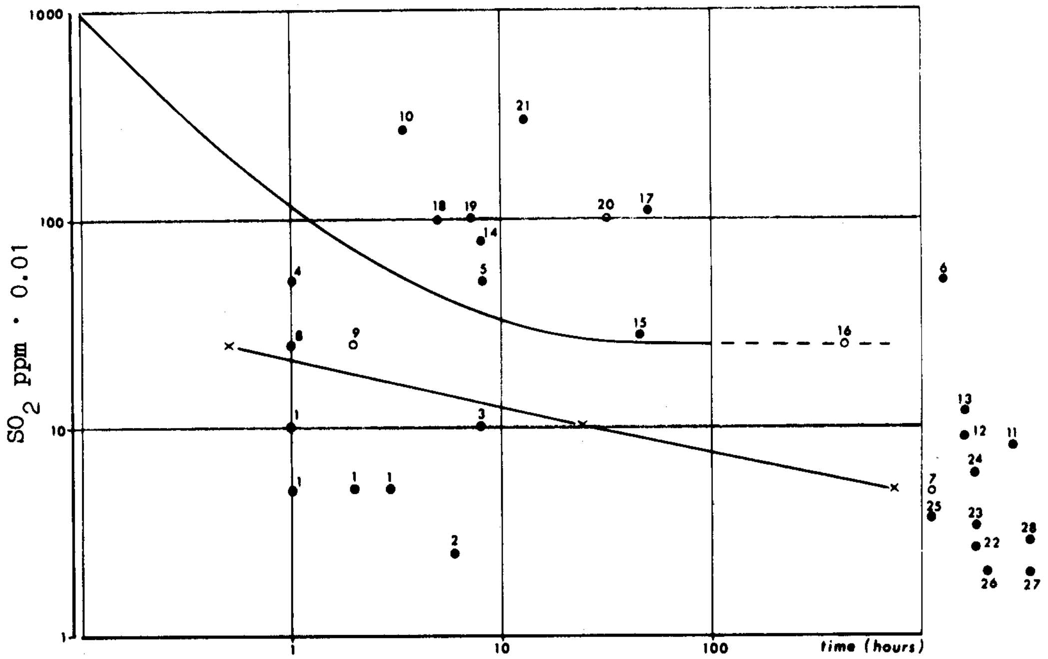

Figure 4. A compilation of values from the literature showing the effects of sulfur dioxide on various species of trees. The curved line represents Thomas and Hill's equation for first noticeable injury in alfalfa. The straight line represents the maximum air-quality standard for sulfur dioxide concentrations in Swedish cities, according to 1972 regulations. The concentration data given in the right-hand margin are for exposure times greater than one month. o noninjured plants, ● injured plants. For further explanation of the numbers in this figure, see the Key to Figure 4 printed below. (Reproduced from Tamm and Aronsson, 1972).

symptom of injury to alfalfa plants. The straight line illustrates the current standard for air concentrations of sulfur dioxide in urban areas of Sweden. The corresponding curve for the United States is somewhat steeper but otherwise not much different. The sensitive plants below the curve are almost all 5-needled pines. Although *Pinus strobus* generally is very sensitive to sulfur dioxide, there is also great genetic variation within this species, as indicated in the Figure. Figure 4 also shows that damage to *Pinus strobus* may be expected even if the current standards for clean air in urban areas in Sweden (and the United States) are strictly observed.

Acidic rain may cause direct injury to (or erosion of) the protective surface structures of plants such as the cuticle. Gaseous sulfur dioxide may not be corrosive enough to damage the cuticle at presently occurring ambient concentrations, but droplets of sulfuric acid in aerosols certainly may have this effect.

Key to Figure 4

Number	Species	Woody plants	Observer
1	Pinus strobus	4-5 week-old needles injured in sensitive clones	Costonis 1970
2	Pinus strobus	Injuries in sensitive clones	Stairs et al. 1970
3	Pinus strobus	Injuries in sensitive clones at fumigation 8 h/per day for 4-8 weeks	Dochinger et al. 1970
4, 5	Pinus strobus	Always injuries	Dochinger et al. 1970
6	Pinus strobus	Injuries	Berry 1964
7	Pinus strobus	No injuries	Jaeger & Banfield 1970
8	Pinus strobus	Injuries	Berry 1967
9	Pinus strobus resinosa banksiana	3, 5 and 7 week-old seedlings without injuries (27°C, 70% RH)	Berry 1971
10	Pinus silvestris	Reduction in photosynthesis. Complete recovery after 48 hours	Vogl & Börtitz 1965
11	Pinus silvestris	No stands in the Ruhr area	Knabe 1971
12, 13	Pinus silvestris	Injured trees die within two or three years	Podzorov 1969
14	Douglas fir	Slight injuries	Thomas 1951
15	Douglas fir	Slight injuries	Thomas 1951
16	Douglas fir	No injuries	Thomas 1951
17	Douglas fir	A few young trees die	Thomas 1951
18	Picea abies	Reduced photosynthesis in late summer, no other injuries	Börtitz 1964
19	Picea abies	Reduced photosynthesis in late summer, no other injuries at fumigation 7 h/per 24 hours during 240 hours	Börtitz 1964
20	Picea abies	No injury in hot weather (stomata closed)	Börtitz 1964
21	Picea abies	Needle necroses	Börtitz 1964
22, 23	Picea abies	Annual mean value, slight injuries	Knabe 1971
24	Picea abies	Annual mean value, severe injuries	Knabe 1971
25	Picea abies	Threshold value for injuries, long-term measurements	Materna 1971
26	Conifers, oak, beech	Thresholdvalue for injuries, mean value	Wentzel 1969
27, 28	Quercus robur Fagus silvatica Larix decidua Pinus silvestris Picea abies	Significant growth reduction at mean value for growing season	

Necrotic spots will develop where high concentrations of acids occur, especially when leaves are exposed to alternate cycles of wetting and drying. In this case, drops of acidic water evaporate leading to an increase in acid concentration and then to local necrotic spots. Similar high concentrations of acids may develop beneath soot particles adhering to plant surfaces.

As indicated in Table 1, if the cuticle and other protective structures are damaged, the plant may be harmed by other environmental and biotic stress factors. For example, loss of control of guard-cell function can lead to loss in control of gas-exchange reactions. Guard cells react, among other things, to changes in the pH of their cytoplasm. Once a plant loses control of its stomata, it will lose control of transpiration, and then may be injured by drought.

A very likely direct effect of air-borne acidic substances is a poisoning effect on metabolic processes within living cells. This requires transport to the cell surface and usually through cell membranes. In vascular plants it also requires diffusion through stomata or through the cuticle. Hence, stomatal frequency and all factors affecting stomata opening are important in determining susceptibility to metabolic poisoning.

Cellular metabolism also may be affected by sulfur and nitrogen oxides without direct evidence of poisoning. Needles of conifers and leaves of deciduous trees often have a shorter functional life-span in polluted areas. In some cases this premature ageing has been accompanied by large accumulations of sulfate in the cells (Lihnell, 1969). Sulfate is much less poisonous than sulfite (Linzon, 1972); in fact, formation of sulfate is a detoxification process in plant cells although accumulation of sulfate still may imply a disturbed metabolism.

Acidic precipitation or acidic substances in the atmosphere may also affect plants by synergistic interactions with various other air pollutants such as ozone or fluoride. Soot particles adhering to plant surfaces may absorb gases from the air and thereby concentrate these substances. The concept of synergistic effects covers a wide range of possibilities. Figure 5 shows the close similarity of distribution patterns for sulfur and lead from atmospheric sources in Scandinavia. Perhaps the concentrations observed to date are not yet great enough to induce synergistic effects on a regional scale, but these and other poisonous substances with potential synergistic effects on living organisms often occur together.

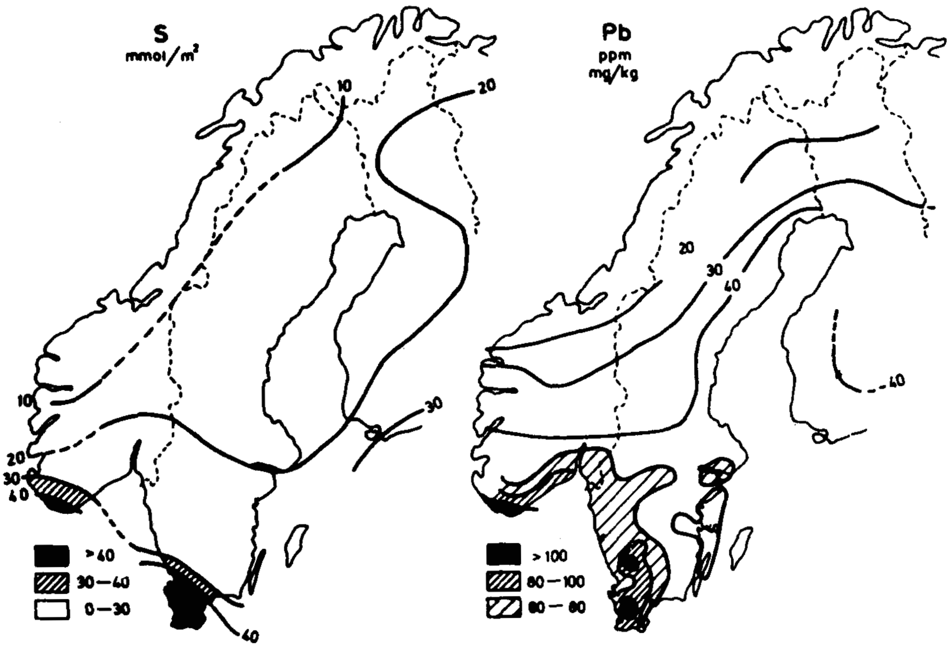

Figure 5. The calculated increase in annual supply of sulfur in precipitation (left) and the lead content of the moss *Hylocomium spendens* in different parts of Scandinavia (right). Note the similar distribution patterns of these two different pollutants. The figures refer to conditions in about 1970. The figures for sulfur are expressed as "excess sulfur" from Granat, 1972, Fig. 5 and for lead from Tyler, 1972. (Reproduced from Malmer, 1974).

In studying the direct and indirect effects of acidic precipitation on plants, it is important to distinguish between local effects and regional ones. The local effects usually are more conspicuous and thus more easily studied. But in some areas of Europe and North America, the regional concentrations of harmful substances in the air are approaching concentrations at which serious long-term effects may be suspected.

In conclusion, it is important to recognize that present knowledge of the effects of acidic precipitation on vegetation is wholly inadequate. Much research is needed to determine the importance of the various potential effects listed in Table 1. We hope that much more complete information about the biological and economic consequences of these effects will become available in the future.

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