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Uptake and effects of air pollutants on woody plants

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Key words. Forest decay; air pollution; woody plants; sulfur oxides; nitrogen oxides; ozone.

Introduction

Plant damage due to air pollution has aroused public concern for many years. It is therefore not surprising that numerous publications have sought to establish a better understanding of the injury development and its biochemical and physiological basis – and the literature flood is increasing daily.

Important reviews have been written by Ziegler[138] on the action of sulfur dioxide and by Heath[43] who compared the actions of sulfur dioxide, nitrogen dioxide or ozone on plant metabolism. The effects of oxidants on forest trees are listed by Smidt[119] and those of air pollutants on plant-pathogen interactions by Laurence[81].

SO_2, deriving from fuel combustion or from ore smelting, has been shown to be the most widespread air pollutant in the past. Therefore, it has often been used as a tracer for air pollution. The importance of photochemical oxidants as injury-causing compounds has been recognized in the USA already since the early 1950s and 1960s, whereas their role in Europe was presumed to be only minor for climatological reasons. Recently, however, it has been shown[1, 16, 108], that periods of ozone production during the summer may be sufficient to produce ozone damage even on woody species. Ozone injury to herbs was shown earlier (1973) in Europe[73].

This review aims at giving a short survey on the action of SO_3, NO_2 and O_3, singly or in combination, mainly on woody plants. These pollutants are thought to play a major role in the development of injury in plants.

Because much research has been done with important agricultural plants, we describe these as well. We do not intend, however, to offer a comprehensive survey of the most recent literature on this subject. Rather we will try to draw a clearer picture of the diversity of the different effects of air pollutants on plants. In this context readers are referred to the reviews by IERE[49] or Ormrod[105], which contain a lot of details not mentioned here.

Internal and external conditions

There are many internal and external conditions which may modify plant response to air pollutants. One of the important internal parameters we like to use is the physiological age of a leaf or of the whole plant for showing the modifying effect of the pollutants[7, 28]. It is well known that there is a seasonal change in the plant sensitivity to SO_2 with tissue age: young developing tissue in spring or old tissue in fall is less sensitive to SO_2 than fully mature and active tissue in summer[127]. Miller and Parmeter[94] showed, that older needles the first to be afflicted when pine seedlings were subjected to a prolonged fumigation with 250–350 ppb ozone. Guderian[39] pointed out that uptake of CO_2 and SO_2 is the same in young and old leaves, but whereas at low concentrations of SO_2 the older leaves are more affected, as SO_2 concentration increases younger leaves show signs of injury. Keller and Schwager[70] attributed this phenomenon, which they also observed in their fumigations, to the difference in the physiological activity of the needles. Costonis and Sinclair[21] reported that the effect of ozone on *Pinus strobus* varied with the season. A year later, they showed that the first 8 weeks of the growing season were most dangerous for *Pinus strobus*[118].

Wood and Davis[136] found that seedlings of 18 conifer species were rather resistant to ozone during the first month after bud break, whereas *Pinus virginiana* was most susceptible at a needle age of 4–10 weeks[22] or 3–5 weeks after needle elongation[25]. The highest susceptibility of *Pinus strobus* was at the needle age of 4–5 weeks[20] and at needle age of 6–8 weeks for seedlings of three other pine species[77]. Susceptible species were sensitive until the 13th week after budbreak. Dormant seedlings were found to be rather resistant[23, 25]. For 16 different deciduous species, it had been shown that foliage was more or less resistant to 250 ppb ozone during the 2 weeks after budbreak[135], and Karnosky[57] suggested that leaf age rather than leaf position was important in determining the sensitivity of *Populus tremuloides* to SO_2 or O_3.

Similarly, it had been observed that severe defoliation of *Ulmus americana* seedlings by SO_2 and O_3 fumigation occurred only in fully developed plants[19] and according to Noble and Jensen[98] the youngest, rapidly growing leaves of hybrid poplars in contrast to foliage of the later stages were not affected by fumigations with O_3 and SO_2.

Another important internal factor is the genetic make up of the plants. Even within a species there may be a wide variation in sensitivity[137]. There seems to be evidence that the resistance to air pollutants is genetically fixed[8, 46, 53, 58]. Further we can mention e.g. the differences of the stomatal conductance within five clones of *Populus tremuloides* during fumigation with 0.5 ppm SO_2 or less[73] or the differing CO_2 uptake of three *Picea abies* clones by 0.05 ppm SO_2 during 8 weeks[68].

In *Fraxinus americana* and *Fraxinus pennsylvanica* seedlings, the resistance to SO_2 and O_3 varied with their geographic origin. Seedlings of *F. americana* from coastal areas were more tolerant of O_3 than those from interior regions, and trees of southern provenance were generally more tolerant of both O_3 and SO_2 than those from northern areas[59].

Important external factors which modify plant response include:

- climatic parameters (temperature, light, humidity, windspeed, etc.),
- nutrition,
- fumigation conditions (conditions before, during and after fumigation, concentrations, length, fluctuations, etc.).

With regard to temperature, plants have been considered, for some time now, to be more resistant during dormancy, i.e. during the season of low temperature. Nevertheless, some plants and evergreens in particular are susceptible during this season as well, as shown by Huttunen[48] or Jones and Mansfield[54]. A winter fumigation with e.g. 0.225 ppm SO_2 or less may not only depress CO_2 uptake, increase peroxidase activity and late frost sensitivity[62, 67] or decrease stem wood formation in the subsequent growing season[69], but it may also diminish the number of flushing buds in beech[63].

Norby and Kozlowski found in seedlings of several woody species[100] and in *Pinus resinosa*[101], that post fumigation temperature greatly affected growth and SO_2 injury. Therefore they suggested caution in generalizing about the influence of temperature.

Both intensity and quality of light have been suggested to be important factors affecting resistance to pollutants. Davis and Wood[23] reported shaded *Pinus strobus* to be more susceptible than trees in full light. One year later they stated for seedlings of *Pinus virginiana*, that prefumigation-light protected, whereas darkness enhanced, injury[24].

For temperate regions with greatly varying day length and light quality, the report by Davies[27] may carry particular significance. She states that the tolerance of *Phleum* *pratense* to a SO_2 fumigation with 0.12 ppm depended on irradiance and day length. This may help to explain the obervations by Huttunen[48] that pine near the arctic circle is more susceptible to pollutants in winter (long nights) than in summer, although, of course, there are a lot of factors acting at the same time.

It has often been shown with herbs that relative humidity of the air affects plant sensitivity. This was also observed in trees. High humidity greatly increased sensitivity to ozone in pines[24, 118] or to SO_2 in *Fraxinus americana*[131] and *Betula papyrifera*[102].

Another important factor, in particular for trees reaching into higher air layers, may be wind velocity, which modifies the susceptibility of air pollutants to plants (see also chapter on stomata). Costonis and Sinclair[21] suggested that strong winds accelerated and intensified lesion development by air pollutants on needles of *Pinus strobus*. The findings of Ashenden et al.[4] with grass have to be considered here, too. They showed that a 4-week fumigation with 0.11 ppm SO_2 did not depress growth at a wind velocity of 0.16 m/s, whereas an effect was observed at 0.42 m/s.

There is wide agreement that plant resistance to an adverse environment is highest when the plant is growing under optimal conditions. Therefore there is a tendency to try to improve nutrition of trees on poor sites in highly polluted areas[121]. The complexity of factors acting at a site, however, usually makes it hard to obtain a clear-cut result of general applicability. Dässler[26] found repeated N fertilization successful for pine on poor sites. Ambiguous results with spruce, however, lead to the conclusion that a 'complete' fertilization, including K, was more beneficial for this species. For sandy soils in Poland a NPK fertilizer combined with lime was found most beneficial[104], especially when NPK fertilization was repeated[103]. According to Baule[5] Mg seems to be important over large areas. Particularly where corrosion of waxes and/or cuticula favors the leaching of K and Mg in addition to the injury of membranes[109] and appropriate fertilization may be indicated[139].

Plants response is influenced by yet other external factors, such as the conditions before, during and after fumigation, as Heck and Brandt[44] have pointed out. Fumigations may be carried out by either constant or variable concentrations of pollutants. A change of concentration may allow a detoxification and regeneration, particularly when periods with pure air are included. Such changes were used by Garsed et al.[38] in order to determine the effect of peaks. These authors fumigated pine seedlings (initially 3 years old) for 650 days with 100 $\mu g/m^3$ SO_2 or with either of two peak concentrations (300 or 750 $\mu g/m^3$) intermittently with intervals of pure air to yield the same average concentration of 100 $\mu g/m^3$. The effect on growth indicated that short but frequent peaks – regardless of which of the two concentrations was used – depressed growth to approximately the same extent as the constant continuous fumigation. At either concentration, long occasional peaks, however, were even more dangerous and depressed growth by an additional 10%.

Wentzel[129] also asserts that high peaks of pollution, with a relatively rare occurrence, are more injurious to the forest than low average values.

It is well known that pollution thresholds evaluated under laboratory conditions are usually too high compared with those estimated from field observations. There are at least three reasons which contribute to this fact:

1) In the field there are usually several pollutants which influence the plant at the same time. Therefore combined actions of two or more gases cannot be excluded.
2) Field plants in a natural habitat, especially forest trees, grow under suboptimal conditions, whereas laboratory plants are usually well supplied with nutrients and water, for example. This may prevent these plants from early fumigation damage.
3) Plants in the field are subjected to low, but long lasting pollutant concentrations. Thus damage may develop over a long period of time; a situation which is difficult to simulate in laboratory experiments. In addition, we may assume that plant reactions (e.g. detoxification) differ not only with different pollutants but with different levels of pollution and times of exposure.

Combined effects of several pollutants

When several pollutants act on plants, the effects may be additive, antagonistic (less than additive) or synergistic (more than additive), when compared with the action of single gases. The mechanisms of synergism or antagonism may be related to 1) direct reactivity between pollutants either in the air or in the plant leaves, 2) an effect of either gas on the stomata, 3) competition for reaction sites, 4) a change in the sensitivity of reaction sites, or 5) a combination of these[42].

Synergism usually occurs when injury from SO_2 or O_3 alone is slight or moderate. Antagonism is often detected when injury from either gas is severe. For example, when apple trees were treated with high concentrations (0.8 ppm) of SO_2 and O_3 the effect was less than additive[116]. There were interactive effects of SO_2 (0.1 ppm) and NO_2 (0.1 ppm) in *Tilia cordata, Betula pendula, Pinus nigra* and *Betula pubescens*, resulting in greater than additive responses. Those plants, which were significantly affected in terms of dry weight also showed significant decreases in stem height and diameter[130]. Similar things were reported from grasses[3]. A possible explanation for this finding was suggested recently. According to Wellburn et al.[128] the presence of SO_2 inhibits the increase of nitrite reductase activity in grasses, which takes place during fumigation with NO_2 alone. This increased activity is believed to be a detoxification mechanism for NO_2 in the plant, which prevents the formation of free radicals within the cells and subsequent membrane damage analogous to the action of SO_2 or O_3. In combination with SO_2, this detoxification of NO_2 is not possible anymore.

50 ppb O_3 sometimes reduced growth in *Platanus occidentalis* seedlings and the effect was more pronounced in combination with 140 ppb SO_2[78]. In another study, *Pinus taeda* and *Platanus occidentalis* exhibited significant growth depressions, *Fraxinus americana* and *Liriodendron tulipifera* significant growth stimulation when exposed to 50 ppb O_3. Antagonistic interactions were observed in 100 ppb O_3 and 100 ppb NO_2[80]. Adding 0.1 ppm NO_2 to a mixture of 0.05 ppm O_3 and 0.14 ppm SO_2 lead to inconsistent effects in seedlings of *Pinus taeda*[79].

The response of poplar cuttings to treatments with 0.25 ppm O_3 and 0.5 ppm SO_2 suggested that the two gases had an antagonistic effect upon growth. SO_2 seemed to reduce the toxic effect of O_3[52, 58]. *Pinus sylvestris* needles showed severe injury after fumigation with 0.25 ppm SO_2, no visible response to 0.29 ppm O_3 alone and an apparent antagonism of SO_2 and O_3[97].
From all this, it follows that a lot of factors need attention when one aims at establishing threshold levels of pollutants below which even the most susceptible stages of the plants will not be injured.

Stomatal effects

The stomata are the main entrance into the leaves for gaseous air pollutants. It has been shown for SO_2 that the cuticle is nearly impermeable for this gas. The same may be true for O_2[110].
Therefore the movements of the stomata play a major role in the susceptibility of the plant to air pollutants. Stomatal opening during a pollution episode favors the uptake of the gases into the leaves and promotes growth inhibition, leaf necrosis or abscission. If the stomata are closed, the pollutants are excluded and any stress induced by air pollution is avoided. Differential sensitivity in pine species has been found to be correlated to the number of stomata and the size of suprastomatal cavities[32, 93].
Pinus nigra, when subjected to air pollutants, revealed a resistance pattern under field and laboratory conditions that coincided well with the stomatal resistance of these plants[13].
Generally, the stomata are open in the light and closed in the dark. Their reactions are mainly determined by the photosynthetic activity and the water status of the plant. The degree of stomatal resistance is genetically fixed and varies with plant species. Unfortunately, pollutants may modify the behavior of the stomata. This is one reason why fumigation experiments sometimes lead to ambiguous results.
It has been shown that some plants tend to open their stomata during fumigation with SO_2 or O_3[11, 85, 87, 115], while in others the stomata close[96, 112, 116, 133]. A given pollutant, in fact, may act in the same plant species in a different manner, depending on the dose applied[99].
Recently, it has been emphasized that the stomatal resistance is the most important factor determining the uptake of pollutants by the plants, apart from the pollutant concentration and the duration of exposure. Experiments have also shown that the resistance of the boundary layer is of similar importance, because it is directly linked to the diffusion of pollutants through the stomata[95]. With a given amount of pollutants, the wind velocity largely determines the concentration of pollutants at the leaf surface. Thus the actual mathematical product: concentration multiplied by wind velocity, the so-called flux, is considered a better measure for predicting injury under field conditions than the dose, that means the product of concentration and time. This is an important piece of information for forestry[113]. Because wind velocity increases with increasing height of the trees, dominant trees that reach above the canopy are preferentially attacked by pollutants and the injuries may be greater than would be expected from the pollutant dose alone. The same is valid for border trees. Although the importance of the flux for the development of injury in plants is not under dispute, very few efforts have been made to carry out fumigation experiments in which the effects of flux can be studied.
In many cases the uptake of pollutants is registered by chemical tissue analysis. However, in any specific case a lot of factors have to be considered such as translocation of the polluting compound to other tissues, uptake by roots and transport to the analyzed tissue, destruction of the pollutant or lack of storage. Thus, important pollutants such as O_3 or NO_2 cannot be detected by chemical tissue analysis. In addition, we have to keep in mind that a successful detection gives only an indication of the presence of this substance. It is no proof that the plant has undergone any chemical or physiological change, although there is some evidence that absorption is directly related to susceptibility within a given plant species[29, 30].
Two processes contribute to the uptake of pollutants into plant tissues: absorption and adsorption. As has already been mentioned, the absorption of pollutants into the leaves depends on the degree of stomatal opening. In contrast, adsorption is related to the properties of the plant surface. In 10 fumigated coniferous and deciduous shade tree species, Elkiey et al.[31] found that the total sorption rates of the conifers were generally greater (at 60–400 ppb SO_2, 400 ppb NO_2, 250 ppb O_3). Where the adsorption rate could be separated from that of absorption, the adsorption rate was higher in most cases. Sometimes similar sorption rates were noted after treatment with single gases as compared with mixtures; sometimes those from mixtures were lower, depending on the plant species used.
Although it is evident that absorption is potentially more dangerous to plants than adsorption, the latter takes on more importance with rainfall or dew, when pollutants can go into solution and thus become available to the plants.
The opposite of sorption of pollutants by plants has been observed, as well. It has been shown by Hällgren and Fredriksson[40], that *Pinus sylvestris* fumigated with low concentrations of SO_2 (50–200 $\mu g/m^3$) in the field emits H_2S from the needles. This emission depends on light and SO_2 concentration. It is not known whether this is a detoxification mechanism of the plant or not.

Physiological effects

Impaired growth or reduced vitality are symptoms of pollutant injury in plants, which may preceed visible foliar injury. Going on the assumption that any reductions in growth or yield are the result of previous biochemical or physiological alterations, many efforts have been undertaken to illuminate the first steps of pollutant action in metabolism. Most data are available on the effects of SO_2; there are some on the action of O_3, but NO_2 has usually been considered only in combination with the other two.
Despite the distinct chemical and physical properties of the individual pollutants, the disorders shown by plants

in different fumigation experiments are similar. The most common effects are a reduced photosynthesis and an altered water balance[43]. Nevertheless, many details are now known which may explain to a certain degree the lack of specific reactions in the cells under the influence of pollution.

It has been shown that SO_2 as well as O_3 induces the formation of highly reactive oxygen compounds in the chloroplasts. These compounds seem to play a key role in metabolism during fumigation. Oxidation of SO_2 by free radical mechanisms produces superoxide radicals, which are converted to hydrogen peroxide by either spontaneous or superoxide dismutase catalyzed reactions[2]. The phytotoxic action of O_3 is largely mediated by active oxygen radicals such as superoxide anions or hydroxyl- and perhydroxy radicals. Thus, plants with a high superoxide dismutase activity are considered to be more resistant to SO_2[122] or O_3[82]. However, McKersie et al.[89] could not establish any relation between O_3 sensitivity and superoxide dismutase activity in beans.

Peroxidase, a nonspecific indicator for a variety of plant stresses, has been suggested to be a valuable indicator for invisible injury in SO_2-treated plants[71] as well as in plants exposed to automotive traffic[88]. The role of peroxidase seems to be, at least partly, to detoxify hydrogen peroxide accumulated in the chloroplasts as a possible consequence of superoxide dismutase action. It has been shown that hydrogen peroxide even at low levels is inhibitory for chloroplast SH enzymes[56,111,124]. Thus, the inhibition of photosynthesis by active oxygen compounds, even in the case of SO_2, is thought to be more probable than that via the competitive inhibition of the ribulosediphosphate carboxylase[123].

It has been known for a long time that photosynthesis is a very sensitive indicator of plant injury[60,61]. Measurements of the photosynthetic activity allow the detection of early reversible changes in the plant metabolism, which are difficult to prove otherwise[9,10].

In *Fraxinus americana, Acer saccharum* and *Quercus velutina,* a fumigation with 0.5 ppm SO_2 or O_3, singly or in combination, reduced photosynthesis with or without visible symptoms. The inhibition was more pronounced in high air humidity. At light saturation the effect of SO_2 on photosynthesis depended on its concentration, whereas at lower irradiances it did not[17].

Phloem translocation of photosynthates in sensitive trees of *Pinus strobus* was impaired by increased ambient levels of O_3[92]. This inhibition was thought to be a consequence of high turnover rates of proteins in the needles[91]. Teh and Swanson[125] suggested that reduced translocation could be due to damage to the carrier molecules involved in phloem loading; thus, phloem loading could become an important limiting step in translocation. This inhibition may be greater than the reduction in photosynthesis. As a consequence, the levels of starch and sugars in the source leaves increase, as has been found by Koziol and Jordan[74], or they decrease in the roots[52].

According to Jones and Mansfield[55], however, the reduction in phloem transport cannot be fully explained by inhibition of phloem loading only. As in the case of increased peroxidase activity, reductions in translocation are not a unique feature of air pollution damage in plants. They may also be induced by other kinds of stress, particularly those caused by certain plant diseases[90].

The importance of pH in modifying the toxicity of SO_2 has recently been recognized[120]. Ionic disturbances of this kind seemed to be the most likely basis for the ultrastructural damage to thylakoids caused by acid gases like SO_2[134]. But there are some connections with the action of oxidants like O_3, too. In spinach leaves fumigated with 2 ppm(!) SO_2, malondialdehyde, a product of lipid peroxidation, was found[117]. This leads to the conclusion that the effects of SO_2 and O_3 on membranes are similar. The reaction of O_3 with leaf tissue induces a disruption of membranes, probably by the oxidation of unsaturated fatty acids, mediated by free radical reactions[89]. As a consequence of membrane damage, the efflux of solutes increases. This has been shown for SO_2[84] or O_2[6,89]. This leakage of solutes from damaged leaves, inforced by acid rain, is supposed to be a major reason for the nutrient deficiencies (Ca, Mg) observed at present in the injured forests of western Europe[108].

Altered membrane permeability may be responsible for causing alterations in the proton gradients in photosynthetic membranes to which ATP formation is linked[128]. Field studies with *Pinus* hybrids showed a close relationship between a decline of ATP concentration in the needles and the SO_2 increase in the ambient air. However, this effect could be repeated in the laboratory only in exceptional cases. Since fumigations were performed under the same conditions, these differential responses imply that foliage grown in the field site or in the laboratory differ in its fundamental susceptibility to SO_2[41]. Until now, no specific biochemical or physiological parameters have been found which allow us to differentiate between several pollutants according to their action on plant metabolism. It is more likely that the influence of gaseous air pollutants causes a general stress situation in the plants[51]. The stress-induced ethylen emission observed during fumigation experiments with SO_2 or O_3 confirms this view[14,15,107].

Morphological and histological injuries

Hybrid poplar leaves which showed no typical pollutant injury symptoms revealed various crystalline-like inclusions within bundle-sheath extension cells exposed to O_3 and SO_2. The chloroplasts were located in the central region of the cells and were distorted and damaged. According to these results, Krause and Jensen[76] proposed scanning electron microscopy as a useful tool for the detection and diagnosis of plant injury due to the action of O_3 and SO_2. One has to keep in mind, however, that other factors may cause similar cellular destruction. In addition, this technique makes use of extremely tiny samples. This poses the question of how representative the samples are.

After a 5-month-exposure under ambient field conditions, *Acer rubrum* leaves showed collapsed epidermal cells and a lack of fluffy epicuticular wax. The cross sections through the polluted leaves revealed, further, an increase in vesicular activity of mesophyll cells, while plants grown in clean air appeared normal[75]. Thin sections of fumigated *Pinus strobus* needles exhibited a greater injury effect with O_3 than with SO_2, and the symptoms caused by the mixture resembled those produced with O_3[12].

Disintegration of circular chloroplast bodies was the first injury symptom observed in *Petunia* leaves fumigated with SO_2 and O_3. A differentiation of the SO_2 and O_3 effects was possible, because O_3 affected the chloroplasts in palisade cells and SO_2 those of spongy cells. Further detected cell damages were plasmolysis, aggregation of cytoplasmic content and disintegration of nuclei[126].

Visible symptoms

Visible symptoms of injury like chlorosis or necrosis are probably most often used in studies of pollution because of the easy detection of an effect. Thus symptoms caused by different pollutants or pollutant sources are described and well illustrated by colored photographs in books like those by Jacobson and Hill[50] or Malhotra and Blauel[87]. Both books, however, point to the fact that although symptoms may be typical, they are not necessarily specific, i.e. that different causes may produce the same effect. Any observer must be aware of this fact. On the other hand, there may be visible symptoms with unknown causes. In particular, when a specific pollutant is suspected, one may aim at producing the symptom by means of controlled fumigation. If it is possible to reproduce under laboratory conditions injury symptoms the same as observed in the field, there is a strong evidence for assuming that the injury-causing compound has been identified.

Thus, a foliar disorder of *Pinus nigra*, observed in the field, could be reproduced in fumigation chambers with the mixture of SO_2 and O_3[13]. But in *Pinus strobus*, SO_2 induced symptoms such as yellowish chlorosis, chlorotic mottling, necrotic banding or tipburn, which were indistinguishable from O_3-induced symptoms[137].

Due to the many factors producing injury symptoms, this approach often fails. The absence of visible symptoms of injury, however, must not be considered to be a proof of harmlessness. Trees with a long life span, in particular, may suffer during long or repeated pollution periods which decrease resistance and vitality without causing easily discernible signs such as necrosis or other visible symptoms. Low concentrations of e.g. SO_2 and NO_2 may interfere with physiological processes and reduce growth rate without producing identifiable physical damage[3].

Growth effects

In many cases where visible symptoms of injury are not appearing, effects of environmental pollution can be seen in decreased growth, depression of dry weight, needle length or foliage area, etc. *Liriodendron tulipifera*, for example, is one of the most sensitive species in terms of foliar injury, but it is most tolerant in terms of height and dry weight suppressions. It was shown by Garsed et al.[35] that European broadleafed species were more tolerant to SO_2 in terms of visible injury than conifers. And the significant effects of growth reductions seen in *Pinus taeda* and *Platanus occidentalis* were not accompanied by foliar injury during fumigation with low concentrations (0.05–0.15 ppm) O_3[80]. *Pinus ponderosa* and *Pinus monticola* also exhibited significant growth reductions in dry weight of roots and foliage after fumigation with O_3. In contrast, when measurements were based on foliar injury, *Pinus ponderosa* was shown to be very sensitive and *Pinus monticola* was considered to be insensitive[132].

Foresters measure tree growth mainly in terms of increased trunk diameter. Already in the last century it was observed that air pollution reduces ring width. Since the effect varies with the season, it has been studied with a spruce clone subjected to 10-week fumigations with up to 0.2 ppm SO_2[64]. Although trees do not grow in winter, and pollution during this 'dormant' season is considered unimportant for tree growth, it has been shown recently that even an constant fumigation with 0.025 ppm SO_2 during 3 months may have consequences for spruce growth in the following growing season[69]. Not only may the number of cells be diminished, but cell wall thickness also diminishes, which influences wood density[66,106,114] or the ratio early wood/late wood[83] may be affected.

The fact that all these growth reductions may not be accompanied by any visible symptoms means that it is very likely that the full impact of the damage to forests has not yet been recognized. Although it is not probable that gaseous air pollutants have a direct influence upon the roots, they may exert an indirect effect via the upper part of the plants. This occurs in the following situations: 1) the photosynthetic rate is decreased[37]; 2) there is an increase in respiration[10]; 3) there is an increase in the amount of photosynthates, used in repairing injured tissue; 4) a combination of these and other processes, e.g. a reduced translocation of photosynthates to the roots. As a consequence of reduced root growth, the uptake of nutrients and water is impaired too. In susceptible trees there is some evidence for root dieback as a probable result of reduced carbohydrate supply from affected tops[90].

It seems that root growth is even more susceptible to air pollution than is shoot growth. This was not only observed in annuals[45,54], but also in trees[65]. It therefore seems promising to study the effects of acid precipitation, which promotes soil acidification, by investigating the growth of fine roots[47].

Root symbiosis may have important effects on injury development as well. Extomycorrhized root segments of *Pinus taeda* were more resistant to the deleterious influence of O_3 and SO_2 (at 50 and 500 µg each) on respiration, compared with nonmycorrhized roots. This indicates that ectomycorrhizal development may afford some protection against feeder root damage from O_3 and SO_2. The greatest protection from O_3 was provided by *Telephora terrestris*, while root sections containing *Pisolithus tinctorius* were more resistant to SO_2 damage[18,33].

Resistance

Although there are a lot of factors which modify resistance, there have been numerous attempts to list species with different susceptibilities. Usually these lists are derived from field observations and are only of local value. When such a list, however, is derived from screen-

ing tests and aims at a broader usage, then precise expression of pollutant concentration becomes particularly important. Garsed[34] found 'a lack of relationship between the sensitivity of plants to acute injury at high SO_2 concentrations and the longer-term effects of low concentrations of SO_2 on growth'. When the SO_2 effect of 200 $\mu g/m^3$ and 8000 $\mu g/m^3$ on conifer populations was investigated, Garsed and Rutter[36, 37] observed different orders of sensitivity after 35 days and after 67 days and stated: '... the order obtained at 8000 $\mu g/m^3$ was virtually the reverse of that at 200 $\mu g/m^3$'. They concluded that the relative sensitivity depends almost entirely on the concentration and duration of exposure and that 'short-term fumigation at high SO_2 concentrations cannot be used to predict responses to long-term exposure to SO_2 in the field'.
Furthermore Yang et al.[137] found in their experiments with *Pinus strobus*, that the response even varies with the parameter used for sensitivity ranking. Thus needle length was an inconclusive measure on clonal pollutant sensitivity, whereas needle dry weight was best associated with susceptibility of the trees after fumigation with low doses of O_3, SO_2 and NO_2 (at 0.05 or 0.1 ppm each), singly or in combination.
Without enumerating the numerous pieces of literature on resistance further, we should keep in mind that the nature of the plants is somewhat more complicated than the picture we make of it.

Conclusions

There is a marked discrepancy between the complex way air pollutants act upon plants in the field and the mode of experiments that are carried out to investigate these effects in the laboratory. Unfortunately, mixed fumigations are difficult to handle and the many possible combinations and concentrations complicate the causal analysis of plant damage by air pollutants. Nevertheless, the progress in this discipline during the last years is evident. Today, reports of single gas treatments to study air pollution are still dominant. Furthermore, the concentrations of the pollutants are usually kept constant and they are in most cases too high compared with their ambient values. Such experiments may prove useful in establishing an unequivocal relationship between the pollutant and its effect on plant in a reasonable time. However, we should be aware of the fact that the transfer of such results from laboratory to field conditions is sometimes arbitrary or even impossible.
Much more research is needed to facilitate the diagnosis of plant damage, especially the delimitation of pollutant effects from other plant stresses.
Laurence[81] presented in his review a scheme for studying plant-pathogen interactions. His ideas are well-suited to carry out further research on air pollution effects upon plants. At least partly they are already realized. The problems can be approached in three ways: 1) growth chamber studies can be usefully implemented to investigate the interactions of air pollutants, singly or in combination, with biochemical or physiological processes in plants under different controlled environmental conditions. 2) Experiments with open top chambers are located between growth chamber studies and field observations. They allow the checking of results from growth chamber experiments under more field like conditions. On the other hand, they are well suited either to produce effects known from field-grown plants or to help to determine whether ambient concentrations of the air pollutants are sufficient to produce any effects in plants or not. 3) Finally, both types of experiments have to be compared with field observations which must include studies on the behavior of plants as well as measurements of pollutant concentrations under the different environmental conditions. This is the only way that air pollution research will attain more than purely academic importance.
There are some encouraging developments related, for example, to epidemiological or model studies, but work along these lines will have to be intensified. Much information also remains to be extracted from already existing data e.g. growth rates.

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Methods for evaluating and predicting forest growth responses to air pollution*

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Summary. The challenges of quantifying and characterizing recent broad-scale changes in forest growth are substantial and exciting. The implications of these declines to the future growth and stability of forests in both Europe and the United States are significant. While the role of anthropogenic pollutants in initiating or exacerbating observed changes in growth and mortality is not clearly established, the possible implications of erroneous decisions with respect to pollution abatement are enormous and call for concerted, imaginative, and multidisciplinary research to provide much needed answers in the shortest possible time frame. Proof of cause and effect in complex natural ecosystems will not be absolute; however, diverse approaches can lead cumulatively to strong inferential evidence that substantially reduces the uncertainities of such decisions.

Key words. Forest decay; forest growth response quantification; air pollution; anthropogenic pollutants.

Introduction

The documentation of widespread dieback and decline of forest trees in western Europe[5] and the northeastern United States[9] during the past decade has generated great concern that such changes are of anthropogenic origin and that they may intensify unless atmospheric pollution is reduced. While there are many current hypotheses about the possible causes of these changes, there is currently no proof that any single factor has been the predominant causal agent. Atmospheric pollutants associated with accelerated combustion of fossil fuels during the past three decades, including the gaseous pollutants, SO_2 and ozone, acid rain, and trace metals, have all been implicated as possible causative factors.

The occurrence of forest declines and their recent intensification in areas currently receiving high levels of deposition of anthropogenic pollutants provides only circumstantial evidence of a cause-and-effect relationship. While many possible physiological mechanisms of response of forest trees have been discussed[16,30], clear demonstration of the role of these mechanisms in reported declines has yet to be documented in the field. The present lack of scientific proof of a cause-and-effect relationship between atmospheric pollutants and these extensive forest declines must be considered from the perspective of two alternative hypotheses: 1) the declines may be of natural origin and totally unrelated to pollution stress, or 2) we have not yet adequately characterized and quantified the changes to a point where pollution effects can be separated from the myriad stresses and modifiers that normally control forest growth and development. In either case, broad-scale, imaginative, multidisciplinary research that focuses on multiple hypotheses is required to quantify the changes and identify the responsible mechanisms. The paper focuses on both conceptual and experimental approaches that may prove valuable in defining, quantifying, and understanding the basis of recent deterioration of some forested ecosystems.