

Quantifying the direct effects of SO₂ and O₃ on forest growth

G.M.J. Mohren^a, I.T.M. Jorritsma^a, A.W.M. Vermetten^b, M.J. Kropff^c, W.L.M. Smeets^d and A. Tiktak^e

^a *Institute for Forestry and Nature Research (IBN-DLO), P.O. Box 23, 6700 AA Wageningen, Netherlands*

^b *Department of Air Pollution, Wageningen Agricultural University, P.O. Box 8129, 6700 EV Wageningen, Netherlands*

^c *Department of Theoretical Production Ecology, Wageningen Agricultural University, P.O. Box 430, 6700 AH Wageningen, Netherlands*

^d *Research Institute for Plant Protection, P.O. Box 9060, 6700 GW Wageningen, Netherlands*

^e *Landscape and Environmental Research Group, University of Amsterdam, Dapperstraat 115, 1093 BS Amsterdam, Netherlands*

ABSTRACT

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The direct effects of sulphur dioxide (SO₂) and ozone (O₃) on the growth of two Douglas-fir stands are quantified from continuous measurements of the concentration of air pollution above the canopy combined with a quantitative description of the direct effects of gaseous uptake of pollutants on photosynthesis and respiration. Effects at the leaf level are scaled up to the stand level, using a deterministic model of forest growth that uses time steps of 1 day. This approach enables total uptake of gaseous air pollutants and their effects on canopy assimilation and growth to be quantified, taking ambient weather conditions and stand structure into account. By using a description of water balance in the model, the influence of limitations in soil moisture availability can also be incorporated, and the combined effects of air pollution and water shortage can be accounted for. Under Dutch conditions, with average daily concentrations of 10 µg m⁻³ for SO₂ and 50 µg m⁻³ for O₃, the short-term effects on tree growth appear to be minor, except near local sources, and during episodes of high concentrations under stable weather conditions. The possible magnitude of long-term effects of exposure to O₃ is assessed using a hypothetical relationship between dose (exposure multiplied by duration) and foliage loss. From this it is concluded that long-term effects may be significant in stands with a low leaf area index.

INTRODUCTION

Gaseous air pollutants such as sulphur dioxide (SO₂) and ozone (O₃) may harm plants by influencing physiological processes, or by causing leaf dam-

Correspondence to: G.M.J. Mohren, Institute for Forestry and Nature Research (IBN-DLO), P.O. Box 23, 6700 AA Wageningen, Netherlands.

age. Gaseous air pollutants are mainly taken up through the stomata; the rate of uptake depends on the stomatal opening together with ambient concentration in the air surrounding the foliage (Unsworth and Black, 1981). The degree of the stomatal opening mainly depends on the rate of photosynthesis, the vapour pressure deficit of the surrounding air, and the water status of the foliage (Meinzer, 1982; Morison, 1987). Thus, CO₂ assimilation, transpiration, and the uptake of gaseous air pollutants are strongly interconnected. Air pollutants may affect physiological processes such as photosynthesis, respiration, stomatal regulation and phloem loading (see review by Darrall, 1989). The metabolism of both broadleaved and coniferous trees is influenced by SO₂, resulting in decreased photosynthesis and accelerated ageing of leaves and needles (Freer-Smith and Mansfield, 1987; Lange et al., 1989). Ozone is a strong oxidant, extremely reactive, and capable of disrupting a range of physiological processes by reacting with organic compounds. Leaves exposed to large doses of O₃ display typical symptoms of mottling, with decreased photosynthesis and increased dark respiration (Berry and Hepting, 1964; Skeffington and Roberts, 1985; Posthumus et al., 1989).

Air pollutants can interact with more traditional growth-influencing factors (such as temperature, light, and water and nutrient availability) in many ways (Darrall, 1989). These interactions are difficult to study under controlled conditions. Simulation models can be used to assess the magnitude and relevance of growth disturbances induced by uptake of gaseous air pollutants by quantitatively evaluating individual growth-influencing factors (Mohren and Rabbinge, 1990). These models enable the effects of air pollutants to be quantified while simultaneously accounting for the effects of other environmental factors. In situ measurements of air pollution can be combined with a detailed submodel of the physiological effects of pollutants taken up by the foliage which is then integrated in a carbon balance model of forest growth; this enables experimental results obtained under controlled conditions to be scaled up and extrapolated to the level of the whole stand.

The model used here to quantify the uptake and effects of SO₂ and O₃ is derived from an earlier model for forest growth (Mohren, 1987), itself derived from a summary model of crop growth (Spitters et al., 1989). For a detailed technical description of the model see Mohren et al. (1991) and Jorritsma et al. (1992). The basic growth model has been extended with submodels that account for short-term effects on photosynthesis of SO₂ (Kropff, 1989a) and short-term effects of O₃ on photosynthesis and maintenance respiration (Smeets et al., 1990). The resulting combined model simulates the carbon balance of an entire stand with time steps of 1 day, accounting for diurnal variation of radiation and temperature by using a Gaussian integration scheme over the day and over the foliage layers inside the canopy (Goudriaan, 1986; Spitters, 1986; Spitters et al., 1989), and it applies to an entire stand of Douglas-fir. This approach also enables the total amount of air pol-

lutants taken up to be estimated. The analysis presented in this paper is mainly concerned with the short-term effects of SO₂ and O₃, but a tentative quantification of possible long-term effects of O₃ on ageing and foliage loss has been included as part of a general sensitivity analysis.

MATERIAL AND METHODS

In 1986, two Douglas-fir stands were selected to study the influence of air pollution on forest growth as part of the ACIFORN (ACidification of FOREst in the Netherlands) monitoring programme. Both these sites, 'Speuld' and 'Kootwijk', are located in the centre of the Netherlands, approximately 50 km from Wageningen. The weather and pollutant climate are virtually the same at both sites. The Kootwijk site is located on cover sand with limited water supply from the soil; the Speuld site consist of preglacial loamy sands (orthic podzol/luvisol), and is considered close to optimal for Douglas-fir growth under Dutch conditions. Details on soil moisture conditions are available from Tiktak and Bouten (1990). The geographical location of the sites is 52.1° N and 5.4° E. Altitude is 50 m at the Speuld site and 25 m at the Kootwijk site. The stands were 29 (Speuld) and 38 (Kootwijk) years old at the beginning of 1988. Stem densities were 886 trees ha⁻¹ and 992 trees ha⁻¹ for Speuld and Kootwijk, respectively, with basal areas of 33.4 m² ha⁻¹ (Speuld) and 28.7 m² ha⁻¹ (Kootwijk). At the height of approximately 18 m in both stands, the total stem volume was approximately 300 m³ ha⁻¹ in Speuld, and 245 m³ ha⁻¹ in Kootwijk. Both stands were fully closed, with leaf area index (LAI) estimated to be well above 6–7 m² m⁻² (approximately 8–10 m² m⁻² for Speuld and 7–8 m² m⁻² for Kootwijk). Total precipitation at Speuld was 1006 mm and 801 mm in 1988 and in 1989, respectively, and the corresponding figures for Kootwijk were 999 mm and 769 mm. Fig. 1 provides a summary of daily values for minimum and maximum temperature, global radiation, precipitation, wind speed and humidity as measured at Speuld in 1988 and 1989.

During an extensive monitoring programme, SO₂ and O₃ were continuously measured above and within the canopy at 30-min intervals, from a 30-m tall tower equipped with the necessary sampling and detection devices (see Vermetten et al., 1988, for details). The results of the SO₂ and O₃ monitoring programme for 1988 and 1989 for the Speuld site are summarized in Fig. 2. The results for the Kootwijk site, located within 20 km of Speuld, do not differ significantly from the results for Speuld. For the calculations presented here, the same input data set (Speuld) is used for both sites. The average SO₂ concentration was about 9.6 µg m⁻³ in 1988 and 10.6 µg m⁻³ in 1989. Incidental peak values occurred when strong inversions developed under stable conditions of high atmospheric pressure and no wind. Ozone concentrations are related to incoming solar radiation, and may build up on clear days. Ex-

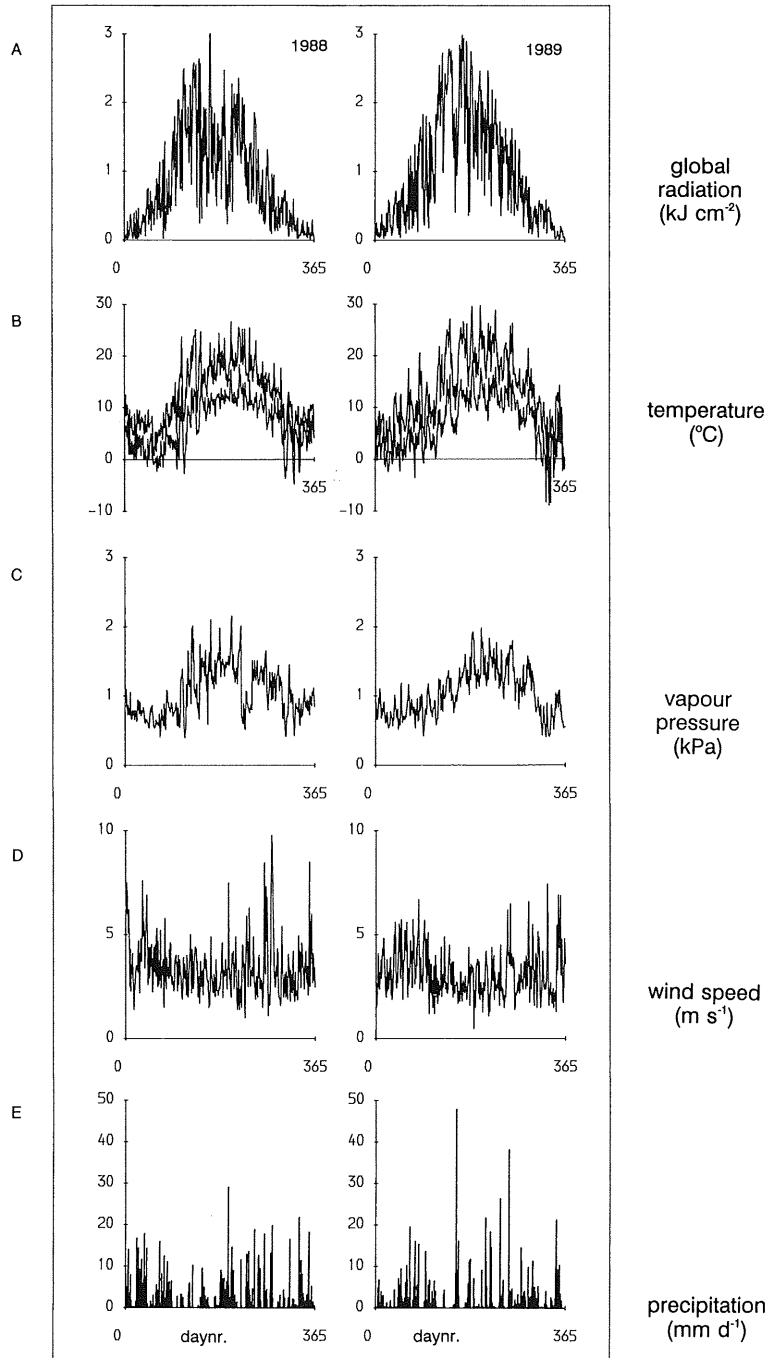


Fig. 1. Daily values for (A) global radiation (kJ cm^{-2}); (B) minimum and maximum temperatures ($^{\circ}\text{C}$); (C) humidity (kPa); (D) wind speed (m s^{-1}); (E) precipitation (mm) for the Speuld location in 1988 and 1989. Data from Vermetten et al. (1990) and Versluis et al. (1990).

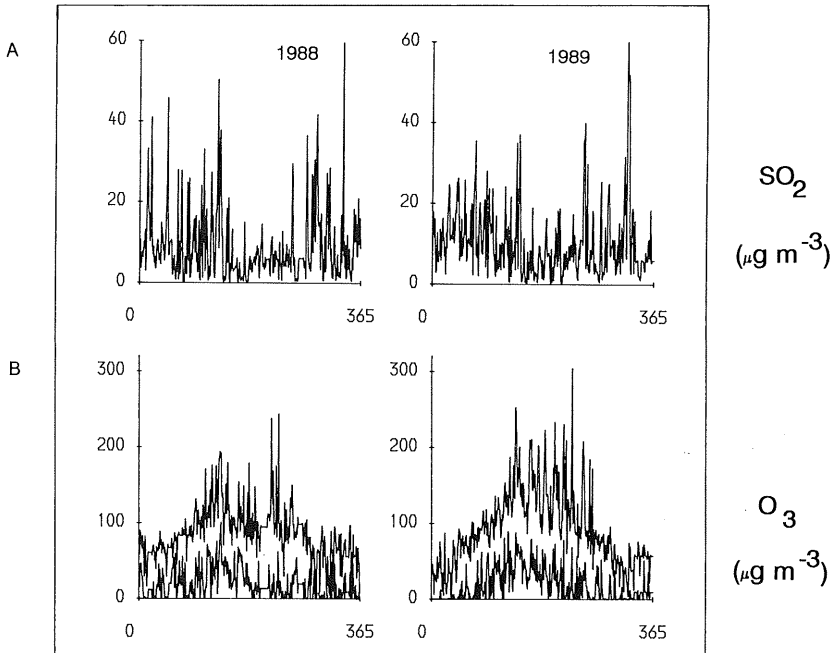


Fig. 2. Daily average values for SO₂ and daily minimum and maximum values for O₃ ($\mu\text{g m}^{-3}$) for Speuld in 1988 and 1989. Data from Vermetten et al. (1990) and Versluis et al. (1990).

amples can be seen in the Speuld data for May and August, 1989. Ozone concentrations have been increasing gradually since the 1950s and averaged about $50 \mu\text{g m}^{-3}$ in 1988 and 1989.

The concentration gradients of pollutants inside the canopy are small because of efficient mixing within the forest canopy, which has a low aerodynamic resistance ($10\text{--}20 \text{ s m}^{-1}$) in combination with rather high stomatal resistance of the conifers ($> 300 \text{ s m}^{-1}$); the differences between concentrations above and within the canopy were ignored. The weather data used to drive the carbon balance model consisted of daily total global radiation, and minimum and maximum temperature. The model includes an elementary description of water relations of the entire stand, accounting for interception loss, soil water balance, uptake by roots, and transpiration by the foliage. The transpiration estimate is based on a Penman–Monteith combination equation using net radiation, vapour pressure deficit, canopy resistance, wind speed above the canopy, and the aerodynamic exchange characteristics of the canopy as input variables. The canopy resistance for transpiration is derived from stomatal resistance, with stomatal resistance determined by photosynthesis (using a ratio of 0.6 between internal and external concentration of CO₂), vapour pressure deficit (Mohren, 1987; Van Hove, 1989), and the water po-

tential of the foliage (Hinckley et al., 1978). Soil water availability is simulated as a running balance, with net precipitation under the canopy as input, and uptake by the roots, evaporation from the soil, and drainage via groundwater when the rooted soil profile is saturated, as output variables. The parameter values used for the simplified simulation of soil water relations, were derived using a comprehensive soil water model (Tiktak et al., 1990). Total annual transpiration in 1988 and 1989 as simulated with the model was 300 mm and 387 mm, respectively for Speuld, and 275 mm and 310 mm for Kootwijk. As is clear from the transpiration rates, the Kootwijk site is drier, and during part of the growing season transpiration is restricted because of a limited supply of soil water. Field estimates of total annual transpiration were derived from detailed analysis of soil moisture dynamics, giving estimates for 1988 and 1989 of 316 and 380 mm for Speuld, and 285 and 340 mm for Kootwijk (Tiktak and Bouten, 1990). Hence, there was good agreement between the model calculations and the field estimates, indicating that stomatal resistance was accurately simulated.

Direct effects of air pollutants

The physiological effects of air pollution must be related to the amount of gaseous pollutants taken up by the foliage, and to biochemical reactions within the foliage. These reactions can take the form of a short-term response such as decreased photosynthesis or increased respiration, and they may have long-term effects, e.g. accelerated ageing or reduced phloem loading and altered assimilate distribution. Here, short-term responses refer to effects that can be seen after short periods of exposure (hours to days), whereas long-term effects appear only after prolonged periods of exposure (weeks to months). Often the changes induced by the uptake of pollutants appear to be reversible, such as when photosynthesis is temporarily reduced because of build-up of toxic sulphite that results from the uptake of SO_2 (Kropff, 1989a, b; Kropff et al., 1989a; Lange et al., 1989); if the pollutant load is removed the amount of sulphite gradually decreases through detoxification, and the metabolism is able to recover. The maximum rate of detoxification determines whether cumulative effects occur with ongoing exposure; this rate depends on the detoxification capacity of the plant cell (possibly related to nutrient status) and on the speed of the biochemical reactions involved. These biochemical reactions are strongly dependent on temperature. For a more detailed discussion on biochemical effects see Kropff (1989b) and Kropff et al. (1990). If there is visible injury and increased foliage loss, the damage is irreversible.

Under conditions such as those measured at Speuld, the stomatal uptake of air pollution is the major pathway by which pollutants reach the leaf interior (Unsworth and Black, 1981; Freer-Smith and Dobson, 1989). The calculations of stomatal uptake are based on stomatal resistance to diffusion, de-

rived from the stomatal resistance to the transport of water vapour and carbon dioxide, accounting for differences in molecular weights of the different gases (Jorritsma et al., 1992). The cuticular uptake of pollutants is negligible compared with stomatal uptake, and it is further ignored in the calculations here. The uptake of SO₂ may influence photosynthesis, because SO₂ competes with CO₂ for the carboxylating enzyme. The magnitude of the reduction in photosynthesis depends on the rate of SO₂ uptake and the rate of detoxification via sulphite to sulphate. The total uptake of SO₂ at Speuld and Kootwijk is limited because the concentrations measured in the field are low and the stomatal resistance at maximum photosynthesis is high (300–500 s m⁻¹). The total amount of SO₂ taken up through the stomata at the ACIFORN sites was estimated to be 3.3 kg (SO₂) ha⁻¹ year⁻¹ in 1988 and 2.5 kg (SO₂) ha⁻¹ year⁻¹ in 1989 for Speuld, and 3.6 kg (SO₂) ha⁻¹ year⁻¹ in 1988 and 2.6 kg (SO₂) ha⁻¹ year⁻¹ in 1989 for Kootwijk.

The effects of exposure to O₃ on photosynthesis, dark respiration and transpiration of Douglas-fir needles were measured in controlled environments (Smeets et al., 1990), at different ambient concentrations of O₃. When the concentrations of O₃ were 200–800 µg m⁻³ in the air surrounding the needles, photosynthesis and stomatal conductance decreased proportionally, and dark respiration increased. These short-term effects occurred only when O₃ concentrations exceeded a threshold level of 200 µg m⁻³. Effects developed slowly and stabilised within 2–3 days after the start of the fumigation. The new physiological state, lower in net productivity but with the same water-use efficiency, was stable for an exposure period of at least 1 month; in this case, the damage caused by O₃ seems reversible. The total amount of O₃ taken up via the stomata, as calculated by the model, was 33.2 kg ha⁻¹ in 1988 and 35.0 kg ha⁻¹ in 1989 for Speuld, and 25.8 kg ha⁻¹ in 1988 and 24.4 kg ha⁻¹ in 1989 for Kootwijk. In the model so far, effects of O₃ have been related to external concentrations only, not to the amounts of O₃ taken up by the foliage. The ozone submodel used here is currently being replaced by a more dynamic model accounting for the diffusion of ozone into the leaf interior. As well as affecting photosynthesis and respiration, O₃ may influence water relations through the needle conductance (Freer-Smith and Dobson, 1989). After episodic exposure to very high concentrations of O₃, visible injury and premature shedding of needles may occur at the ACIFORN sites (see the episodes with high concentrations in May and August, 1989), but so far this has not been taken into account in the model.

RESULTS AND DISCUSSION

Table 1 gives the magnitude of growth reductions that resulted from water shortage or from short-term effects of SO₂ and O₃, or both. The water shortage in the rooted soil profile reduced growth by 6% in Speuld and by 9% in

TABLE 1

Calculated growth rates as percent of potential growth in Speuld and Kootwijk during 1988 and 1989, accounting for water shortage and short-term effects of SO₂ and O₃

	Speuld		Kootwijk	
	1988	1989	1988	1989
Potential growth	100	100	100	100
Water shortage	94	85	91	72
Short-term effects	99	99	99	99
Water + short-term effects	94	84	91	72

The potential primary production, expressed as dry weight during 1988 and 1989, as simulated with the model amounted to 23.0 and 25.8 Mg ha⁻¹ year⁻¹ for Speuld and 22.3 and 25.1 Mg ha⁻¹ year⁻¹ for Kootwijk, respectively, corresponding to stem volume increment rates of 30–35 m³ ha⁻¹ year⁻¹. Actual stem volume increment rates varied from 20–25 m³ ha⁻¹ year⁻¹ in Kootwijk to 28–33 m³ ha⁻¹ year⁻¹ in Speuld

TABLE 2

Short term effects of SO₂ and O₃ on growth of a high productive Douglas-fir stand, for different combinations of SO₂ and O₃. Growth rates expressed as a percentage of the potential growth rate, using input data for the Speuld site

SO ₂ (μg m ⁻³)	O ₃ (μg m ⁻³)			
	0	50	100	300
0	100	100	100	77
50	100	99	99	77
100	99	99	99	76
300	97	97	97	75

Kootwijk in 1988. In 1989, the reduction in growth rate appeared to be around 15% for Speuld and 28% for Kootwijk. Using the models developed by Kropff (1989,a,b), Kropff and Goudriaan (1989) and Smeets et al. (1990) to quantify the short-term effects of SO₂ and O₃ at concentrations measured in Speuld during 1988 and 1989, the growth reduction caused by short-term effects of these pollutants appeared to be negligible. For the calculations for O₃, daily maximum values (based on hourly means) were used instead of daily averages (such as for SO₂) to account for the build-up of ozone during the day. From these simulation results it can be concluded that the low levels of air pollution to which the trees in the ACIFORN stands were exposed, together with the high stomatal resistance of Douglas-fir, lead to a relatively small uptake of pollutants, with only very limited short-term effects as a result. Table 2 indicates a general relationship between pollutant exposure and the resulting short-term effects of SO₂ and O₃, as derived with the model.

The long-term effects of exposure to air pollution are less well-defined than

the short-term effects, and are more difficult to monitor in the field, or to analyse experimentally under laboratory conditions. They either refer to changes in slow processes such as ageing and assimilate allocation, or relate to the gradual accumulation of toxic substances that influence metabolic processes. Evidence suggests that long-term exposure to low concentrations of air pollutants may lead to accelerated ageing and leaf shedding (Zajaczkowska et al., 1981; Kropff, 1990), thereby either shortening the growing season in annual crops and deciduous trees, or decreasing total leaf area in evergreen conifers. From analyses of the short-term and long-term effects in bean plants (*Vicia*) exposed to SO₂, Kropff (1990) concludes that short-term direct effects have a more limited influence on productivity than the long-term effect of yellowing and premature leaf fall. To date however, the metabolic responses to long-term exposure are hardly understood in any plant species. As long as the mechanism is not understood, it is difficult to define damage and measure its magnitude (Lange et al., 1989). A hypothetical mechanism for damage caused by long-term direct effects of SO₂, assumes that subtle injury induces accelerated ageing and leaf loss at low concentrations of SO₂. Under these conditions, the immediate effects on photosynthesis are minimal, with the possible exception of situations with low temperature and high humidity when stomata are open and metabolic activity is restricted (Freer-Smith and Mansfield, 1987; Kropff et al., 1990). Empirical evidence indicates that even at low levels of SO₂ (of 40–60 $\mu\text{g m}^{-3}$) the average lifespan of leaves is reduced and leaves fall prematurely (Kropff, 1990). In order to evaluate the possible magnitude of the long-term effect of exposure to and uptake of low concentrations of ozone, we ran the model described above with an empirical exposure index based on concentration (in $\mu\text{g m}^{-3}$) and time of exposure (in hours) (Reich, 1987; Lee et al., 1988; Posthumus et al., 1989). For reasons of convenience, the dose is simply expressed as $\text{mg (O}_3\text{) h m}^{-3}$. The relationship between dose (duration of exposure times concentration) and long-term effect that we used consisted of a threshold dose of 100 $\text{mg (O}_3\text{) h m}^{-3}$ below which no abnormal foliage loss occurs, a critical level of 400 $\text{mg (O}_3\text{) h m}^{-3}$ at which there is 10% more foliage loss than normal, and a doubling level of 800 $\text{mg (O}_3\text{) h m}^{-3}$ at which foliage loss is twice as high as normal (with linear interpolation between these levels and linear extrapolation beyond 800 $\text{mg (O}_3\text{) h m}^{-3}$). The total cumulative dose is estimated for each foliage age class separately, using 245 days in the year the foliage is formed, and 365 days in all other years. Daily exposure time is assumed to be 12 h, thereby ignoring the fact that short-term exposure to high concentrations is usually more deleterious than long-term exposure to low concentrations. For realistic concentrations of 50 $\mu\text{g m}^{-3}$ (25 ppb), this means that the critical level of 10% additional foliage loss will be reached after about 2 years of exposure. The threshold and critical levels for this type of dose estimation as reported in the literature, vary widely (Reich, 1987; Lee et al., 1988; Posthumus et al., 1989).

TABLE 3

Estimated magnitude of growth reductions, relative to potential growth rate, using input data for the Speuld site, at different exposure to SO₂ and O₃, and for stands with different initial LAI using the simulation model FORGRO

LAI (m ² m ⁻²)	O ₃ (μg m ⁻³)			
	25	50	100	300
7.5	--	-	-/+	++
4.5	-	-/+	+	++
3.0	-/+	+	++	++

For SO₂, only short-term direct effects have been taken into account, according to data from Smeets et al. (1990) and Kropff (1989a,b). For O₃ both short-term direct effects as well as possible long-term effects are taken into account as indicated in the text. In the case of ozone, simulation runs covered periods of 5 years. --, no effects; -, virtually no effects; -/+, some reduction, limited effect (0–3%); +, significant reduction of growth (at least 5–10%); ++, severe growth reductions (>20%), with likely tree mortality and stand decline

The values used here are not unrealistic, but the results should be interpreted with caution. Therefore, Table 3 contains an indication of the magnitude of the effect only. The results as presented in Table 3 indicate that the long-term effects of O₃ may very well be important under ambient conditions, as at the Speuld site, and should be investigated further. When expressed in terms of percentage reduction of dry matter increment, the calculations as presented here would indicate a loss of some 3–5% in the case of medium to high LAI under ambient O₃. At lower LAI, these tentative results indicate a somewhat larger effect, possibly around 10–20% loss. These values agree with estimates reported elsewhere (Van der Eerden et al., 1988; Tonneijck, 1989). At both the ACIFORN sites it seems unlikely that this phenomenon significantly influences productivity at present, because LAI is high. However, it may very well be important in stands with low LAI (such as Scots pine stands), or in deciduous trees (Mohren and Bartelink, 1990).

CONCLUDING REMARKS

When only the short-term direct effects of air pollutants on photosynthesis and respiration are studied, the resulting reduction in growth appears to be negligible for pollution conditions similar to those of Speuld in 1988 and 1989. The analysis of combined effects of water limitations and direct short-term effects of pollutants indicates that the resulting reductions in growth were dominated by the effect of water shortage (Table 1). Again, it should be noted that the effects of both SO₂ and O₃ relate to short-term influences on photosynthesis and respiration only. No long-term effects have been incorporated

in Table 1. However, the combinations of low temperatures, high humidity and episodic or local high exposure are likely to result in temporarily decreased photosynthesis, and irreversible, visible damage was not taken into account. Nutrient status of the trees has not been taken into account so far, although nutrient status is known to influence the susceptibility to effects of gaseous air pollutants (Jäger and Klein, 1976). The decreased oxidation of toxic anions such as sulphite and bisulphite, combined with decreased buffering capacity when metabolic activity is low, or because of imbalanced tree nutrition, may result in visible injury and foliage shedding near local sources of SO₂. Ozone undoubtedly has direct effects (decreased photosynthesis, increased maintenance respiration, and decreased allocation of photosynthates to the roots) during episodes of high exposure (200–300 µg m⁻³). These episodes may occur at times of great physiological activity (during the growing season), implying that stomatal resistance is relatively low and O₃ can be readily taken up by the foliage. Therefore, O₃ should be regarded as a primary risk factor, possibly resulting in acute damage and visible injury during episodic exposure to high concentrations. The magnitude of the effects of long-term exposure to a combination of gaseous pollutants remains unclear. Preliminary evidence indicates that accelerated ageing may lead to premature loss of foliage. In the case of conifer stands with high LAI, this may lead to only marginal effects, but in stands with a low LAI, and in deciduous forests, the effect on growth could be major (Mohren and Bartelink, 1990).

Our conclusions on the short-term and long-term direct effects of SO₂ and O₃ pollution on forest trees can only be tentative at this stage, because they are based on observational studies and short-term monitoring only and on an incomplete understanding of the underlying physiological processes. Especially the quantification of long-term exposure to low concentrations of air pollutants is lacking. Hence, predictions of the risk of future damage to forest trees inevitably include large uncertainties. Until this problem has been solved, it remains difficult to develop general relations between exposure to pollutants and the resulting effects on trees. Simulation models such as the one used in this paper have proved to be valuable in the quantitative analysis of short-term and long-term effects, by bridging the gap between controlled environment experiments and field studies, and by allowing the analysis of air pollution against the background of traditional growth-influencing factors such as water and nutrient shortage. We believe that using these models, it will become feasible to integrate direct effects from gaseous air pollutants with indirect effects such as those resulting from soil acidification. A multidisciplinary approach in which models are used to interpret and generalise results from controlled experiments will be required, and a wide range of field data would be used to evaluate model performance, test hypotheses and corroborate conclusions from detailed experimental investigations.

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REFERENCES

- Berry, C.R. and Hepting, G.H., 1964. Injury to eastern white pine by unidentified atmospheric constituents. *For Sci.*, 10: 2–13.
- Darrall, N.M., 1989. The effect of air pollutants on physiological processes in plants. *Plant, Cell Environ.*, 12: 1–30.
- Freer-Smith, P.H. and Dobson, M.C., 1989. Ozone flux to *Picea sitchensis* (Bong) Carr and *Picea abies* (L) Karst during short episodes and the effects of these on transpiration and photosynthesis. *Environ. Pollut.*, 59: 161–176.
- Freer-Smith, P.H. and Mansfield, T.A., 1987. The combined effects of low temperature and SO₂ + NO₂ pollution on the new season's growth and water relations of *Picea sitchensis*. *New Phytol.* 106: 237–250.
- Goudriaan, J., 1986. A simple and fast numerical method for the computation of daily totals of crop photosynthesis. *Agric. For. Meteorol.*, 38: 249–254.
- Hinckley, T.M., Lassoie, J.P. and Running, S.W., 1978. Temporal and Spatial Variation in the Water Status of Forest Trees. *Forest Science Monogr.*, 20, 72 pp.
- Jäger, H.-J. and Klein, H., 1976. Modellversuche zum einfluss der Nahrstoffversorgung auf die SO₂ Empfindlichkeit von Pflanzen. *Eur. J. For. Pathol.*, 6: 347–354.
- Jorritsma, I.T.M., Mohren, G.M.J. and van de Veen, J.R., 1992. FORGRO 3.3: A Quantification of Direct Effects of Air Pollutants on Forest Growth. Model Documentation and Listing. Institute for Forestry and Nature Research, Wageningen, Netherlands, in press.
- Kropff, M.J., 1989a. Modelling short-term effects of sulphur dioxide 1. A model for the flux of SO₂ into leaves and effects on leaf photosynthesis. *Neth. J. Plant Pathol.*, 95: 195–213.
- Kropff, M.J., 1989b. Modelling short-term effects of sulphur dioxide 2. Quantification of biochemical characteristics determining the effect of SO₂ on photosynthesis of leaves. *Neth. J. Plant Pathol.*, 95: 214–224.
- Kropff, M.J., 1990. The effect of long-term open-air fumigation with SO₂ on a field crop of broad bean (*Vicia faba* L.) III. Quantitative analysis of damage components. *New Phytol.*, 115: 357–365.
- Kropff, M.J. and Goudriaan, J., 1989. Modelling short-term effects of sulphur dioxide 3. Effects of SO₂ on photosynthesis of leaf canopies. *Neth. J. Plant Pathol.*, 95: 265–280.
- Kropff, M.J., Mooi, J., Goudriaan, J., Smeets, W.L.M., Leemans, A. and Kliffen, C., 1989a. The effects of long-term open-air fumigation with SO₂ on a field crop of broad bean (*Vicia faba* L.) II. Effects on growth components, leaf area development and elemental composition. *New Phytol.*, 113: 345–351.
- Kropff, M.J., Mooi, J., Goudriaan, J., Smeets, W.L.M., Leemans, A., Kliffen, C. and van der Zalm, A.J.A., 1989b. The effects of long-term open-air fumigation with SO₂ on a field crop of broad bean (*Vicia faba* L.) I. Depression of growth and yield. *New Phytol.*, 113: 337–344.
- Kropff, M.J., Smeets, W.L.M., Mooi, J., Goudriaan, J. and Leemans, A., 1989c. Growth and production of Faba bean crops exposed to SO₂ in the field: experimental data analysed with a simulation model. In: L.J. Brassler and W.C. Mulder (Editors), *Man and His Ecosystem*.

- Proceedings of the 8th World Clean Air Congress 1989, The Hague, Netherlands, 11–15 September, 1989. Vol. 2. Elsevier, Amsterdam, pp. 29–34.
- Kropff, M.J., Smeets, W.L.M., Meijer, E.M.J., van der Zalm, A.J.A. and Bakx, E.J., 1990. Effects of sulphur dioxide on leaf photosynthesis: the role of temperature and humidity. *Physiol. Plant.*, 80: 655–661.
- Lange, O.L., Heber, U. Schulze, E.-D. and Ziegler, H., 1989. Atmospheric pollutants and plant metabolism. In: E.-D. Schulze, O.L. Lange and R. Oren (Editors), *Forest Decline and Air Pollution*. Ecological Studies 77, Springer, Berlin, pp. 238–276.
- Lee, E.H., Tingey, D.T. and Hogsett, W.E., 1988. Evaluation of ozone exposure indices in exposure–response modelling. *Environ. Pollut.*, 53: 43–62.
- Meinzer, F.C., 1982. Models of steady-state and dynamic gas exchange responses to vapor pressure and light in Douglas-fir. *Oecologia*, 55: 403–408.
- Mohren, G.M.J., 1987. Simulation of Forest Growth, Applied to Douglas-Fir Stands in the Netherlands. Ph.D. thesis, Wageningen Agricultural University, Wageningen, 184 pp.
- Mohren, G.M.J. and Bartelink, H.H., 1990. Modelling the effects of needle mortality rate and needle area distribution on dry matter production of Douglas-fir. *Neth. J. Agric. Sci.*, 38: 53–66.
- Mohren, G.M.J. and Rabbinge, R., 1990. Growth-influencing factors in dynamic models of tree growth. In: R.K. Dixon, R.S. Meldahl, G.A. Ruark and W.G. Warren (Editors), *Process Modelling of Forest Growth Responses to Environmental Stress*. Timber Press, Portland, OR, pp. 229–240.
- Mohren, G.M.J., Jorritsma, I.T.M., van de Veen, J.R., Bartelink, H.H. and Florax, J.P.G.G.M., 1991. FORGRO 3.0: A Basic Forest Growth Model – Model Documentation and Listing. Research Institute for Forestry and Urban Ecology “De Dorschkamp”, Wageningen, Netherlands, Report No. 524, in press.
- Morison, J.I.L., 1987. Intercellular CO₂ concentration and stomatal responses to CO₂. In: E. Zeiger and G.D. Farquhar (Editors), *Stomatal Function*. Stanford University Press, Stanford, CA, pp. 229–251.
- Posthumus, A.C., Tonneijck, A.E.G. and van der Eerden, L.J., 1989. Exposure–effect relationships for plants in relation to several air pollutants. In: L.J. Brassler and W.C. Mulder (Editors), *Man and His Ecosystem*. Proceedings of the 8th World Clean Air Congress 1989, The Hague, Netherlands, 11–15 September, 1989, Vol. 2, Elsevier, Amsterdam, Netherlands, pp. 13–18.
- Reich, P.B., 1987. Quantifying plant response to ozone: a unifying theory. *Tree Physiol.*, 3: 63–91.
- Skeffington, R.A. and Roberts, T.M., 1985. The effects of ozone and acid mist on Scots pine saplings. *Oecologia*, 65: 201–206.
- Smeets, W.L.M., Kropff, M.J., Meier, E.M.J., Bakx, E., van der Zalm, A.J.A., 1990. Quantitative analysis of the uptake of SO₂ and O₃ by Plants and Effects on Physiological Processes and Growth. Research Institute for Plant Protection, Wageningen, Netherlands, IPO Rep. R-89-11, 124 pp.
- Spitters, C.J.T., 1986. Separating the diffuse and direct component of global radiation and its implications for modelling canopy photosynthesis II: Calculation of canopy photosynthesis. *Agric. For. Meteorol.*, 38: 231–242.
- Spitters, C.J.T., van Keulen, H. and van Kraalingen, D.W.G., 1989. A simple and universal crop growth simulator: SUCROS87. In: R. Rabbinge, S.R. Ward and H.H. van Laar (Editors), *Simulation and Systems Management in Crop Protection*. Simulation Monogr., Pudoc, Wageningen, pp. 147–181.
- Tiktak, A. and Bouten, W., 1990. Soil Hydrological Characterization of the Two ACIFORN Stands Using Monitoring Data and the Soil Hydrological Model “SWIF”. Laboratory of Physical Geography and Soil Science, University of Amsterdam, Amsterdam. Dutch Priority Programme on Acidification, Rep. No. 102–01, 62 pp.

- Tiktak, A., Bouten, W. and Schaap, M., 1990. SWIF: A Simulation Model of Soil Water in Forested Ecosystems – Program Documentation and Example. Landscape and Environmental Research Group, University of Amsterdam, Netherlands, Rep. 44, 69 pp.
- Tonneijck, A.E.G., 1989. Evaluation of ozone effects on vegetation in the Netherlands. In: T. Schneider, S.D. Lee, G.J.R. Wolters and L.D. Grant (Editors), *Atmospheric Ozone Research and its Policy Implications*. Studies in Environmental Science Vol. 35. Elsevier, Amsterdam, pp. 251–260.
- Unsworth, M.H. and Black, V.J., 1981. Stomatal responses to pollutants. In: P.G. Jarvis and T.A. Mansfield (Editors), *Stomatal Physiology*. Cambridge University Press, Cambridge, UK, pp. 187–203.
- Van der Eerden, L.J., Tonneijck, A.E.G. and Wijnands, J.H.M., 1988. Crop loss due to air pollution in the Netherlands. *Environ. Pollut.*, 53: 365–376.
- Van Hove, L.W.A., 1989. The mechanism of NH₃ and SO₂ uptake by Leaves and its Physiological Effects. Ph.D. thesis, Wageningen Agricultural University, Wageningen, 131 pp.
- Vermetten, A.W.M., Hofschreuder, P. and Harssema, H., 1988. Air pollution monitoring in a Douglas-fir forest. In: P. Mathy (Editor), *Air Pollution and Ecosystems*. Proceedings of the COST-612 Symposium in Grenoble, 18–22 May, 1987. Reidel, Dordrecht, pp. 903–906.
- Vermetten, A.W.M., Hofschreuder, P. and Versluis, A.H., 1990. Air Pollution in Forest Canopies. Department of Air Pollution, Wageningen Agricultural University, Wageningen, Netherlands. Dutch Priority Programme on Acidification, Rep. 101–09, 58 pp.
- Versluis, A.H., Vermetten, A.W.M. and Hofschreuder, P., 1990. Air Pollution in Forest Canopies: Presentation of Selected Data. Department of Air Pollution, Wageningen Agricultural University, Wageningen, Netherlands, Dutch Priority Programme on Acidification, Rep. 101–10, 121 pp.
- Zajaczkowska, J., Lotocki, A., Morteczka, H. and Witkowska, D., 1981. Ageing of assimilatory organs of conifers under natural and polluted environmental conditions. *Pol. Ecol. Studies*, 7: 401–413.