Working Paper

Cuticular Needle Erosion and Winter Drought in Polluted Environments - A Model Analysis

Annikki Mäkelä
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Abstract

A method is developed for analyzing the consequences of pollutant-imposed cuticular erosion for the tolerance of winter drought in coniferous trees. The erosion rate of cuticular wax is modelled in terms of the contact angle of water droplets, as a function of sulphur dioxide, air temperature and relative humidity. Whole tree transpiration during drought is considered, assuming that the state of erosion affects the cuticular resistance of each needle age class. A formula is derived to compare transpiration with the water available in foliage and stem storage. The derivations are applied to a numerical example concerning the transpiration during a warm spell in the spring. Under certain assumptions, increased cuticular transpiration may well give rise to increased winter drought damage. However, many of the parameters and processes still need to be more thoroughly investigated. The most critical open question appears to be the quantitative relationship between cuticular resistance and the state of erosion of the cuticle.

Preface

The Acid Rain Project at IIASA is concerned with long-term, regional scale ecological impacts of transboundary air pollution. The Regional Acidification Information and Simulation model (RAINS) developed by the project simulates pollutant emissions and transport and uses resulting deposition and concentration patterns as input to environmental impact models. With models for forest soil and lake acidification already in place, RAINS is now being extended to include the direct effects of sulphur on trees.

Annikki Mäkelä has led this effort at IIASA during her two-year period of affiliation (1985-1986). The paper before you is one of a short series reporting results of her work.

Leen Hordijk
Leader, Acid Rain Project

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List of Symbols

Symbol	Meaning	First Occurrence
C_i	storage capacity of i, i = t, f	(22)
c_i	specific volume of i, i = t, f	(17), (20)
c_p	specific heat of air	(7)
D_t	water vapour deficit during day t	(7)
$E(t)$	cuticular transpiration during day t	(7)
f	index referring to foliage	(13)
f_H	relative humidity stress	(5)
f_T	relative temperature stress	(5)
g_c	cuticular resistance	(6)
h	tree height	(20)
$k(t)$	coefficient depending on temperature during day t	(7)
LAI	leaf area index	(7)
Q	transpiration strain	(10)
q	contact angle	(1)
q_o	initial contact angle	(1)
q_{tf}	water flow between foliage and sapwood	(13)
q_w	contact angle with no wax	(1)
$\hat{q}$	contact angle at maximum age	(2)
R	relative erosion rate with no stress	(1)
R_o	actual relative erosion rate	(3)
R_{tf}	resistance of water flow between foliage and sapwood	(13)
S	sulfur dioxide concentration	(5)
t	index referring to sapwood storage	(13)
V_i	turgid volume of water in i, i = t, f	(14), (15)
x	combined erosion stress	(3)
α_H	half-value of humidity threshold	(4)
α_i	fraction of ith age class of potential transpiration	(8)
α_T	half-value of temperature threshold	(4)
β_H	width of humidity threshold	(4)
β_T	width of temperature threshold	(4)
γ	psychometric constant	(7)
γ_i	specific storage capacity of i, i = t, f	(23)
φ_H	relative significance of air humidity	(5)
φ_o	increase in relative erosion rate per unit increase in SO_2 concentration	(5) (5)
φ_T	relative significance of cold temperature	(5)
ψ_i	water potential of i, i = t, f, s	(13)
ρ_a	density of air	(7)

τ	maximum needle age	(2)
θ_i	relative water content of i, i = t, f	(14)

Cuticular Needle Erosion and Winter Drought in Polluted Environments - A Model Analysis

Annikki Mäkelä and Satu Huttunen

1. INTRODUCTION

Electron microscope studies have revealed that the surface structures of needles from sulphur polluted sites are considerably more eroded than normal needles of the same age, the stomatal areas being especially affected (Grill, 1973a; Huttunen and Laine, 1981; 1983; Cape, 1983). Studies on the chemical structure of the cuticular wax, also, show alterations under sulphur impact (Cape and Fowler, 1981; Huttunen, 1986; Cape, 1986). The erosion seems to be accelerated in relatively low concentrations, an annual average of 10–20 $\mu g\ SO_2/m^3$ already showing differences detectable against control experiments (Huttunen and Laine, 1981; 1983).

Since the cuticle protects the needles against water loss when water is not available from the roots (e.g. Kozlowski, 1971), the erosion of the cuticle can potentially lead to enhanced cuticular transpiration. Indeed, Cape and Fowler (1981) reported a decrease of cuticular resistance of needles along with the erosion of the surface structure. This can be fatal during long periods of drought when water is not available to replace the transpiration losses. Especially in the winter when soil frost prevents water uptake for a long period of time, even small increases in cuticular conductance of water have been observed to add up to winter desiccation (Molisch, 1897; Pisek, 1962; Bylinska, 1975; Tranquillini, 1979; Levitt, 1980).

Huttunen *et al.* (1981) compared the winter-time water economies of five Scots pine stands grown in unpolluted, slightly polluted and heavily polluted areas. They found that the water potentials of the foliage of the trees from both the slightly and heavily polluted sites dropped considerably during the late winter, as shown by Figure 1. The drop coincided with a warm spell during which the maximum air temperatures exceeded zero for about two weeks. They also observed that when brought to experimental conditions, the branches from the polluted areas started to transpire more rapidly than those from the control site.

The Acid Rain Project at the International Institute for Applied Systems Analysis (IIASA) is concerned with long-term, regional scale ecological impacts of transboundary sulphur. The RAINS (Regional Acidification INformation and Simulation) model developed by the project simulates sulphur emissions and transport as a function of energy use and sulphur abatement strategies, and uses the resulting deposition and sulphur concentration patterns as input to environmental impact submodels (Alcamo *et al.*, 1985; Kauppi *et al.*, 1986; Hordijk, 1986).

Currently the direct impacts of sulphur on forests are being incorporated in the model. The synergisms between sulphur and natural stresses are being analyzed, and scenario models of the geographic distribution of the combined stress are underway. As part of that work the objective of the present paper is to formulate a model for the erosion of surface structure in sulphur polluted air, and to analyze the consequences of accelerated erosion on the winter-time water balance in conifers. Special attention is paid to the applicability of the model for regional comparisons.

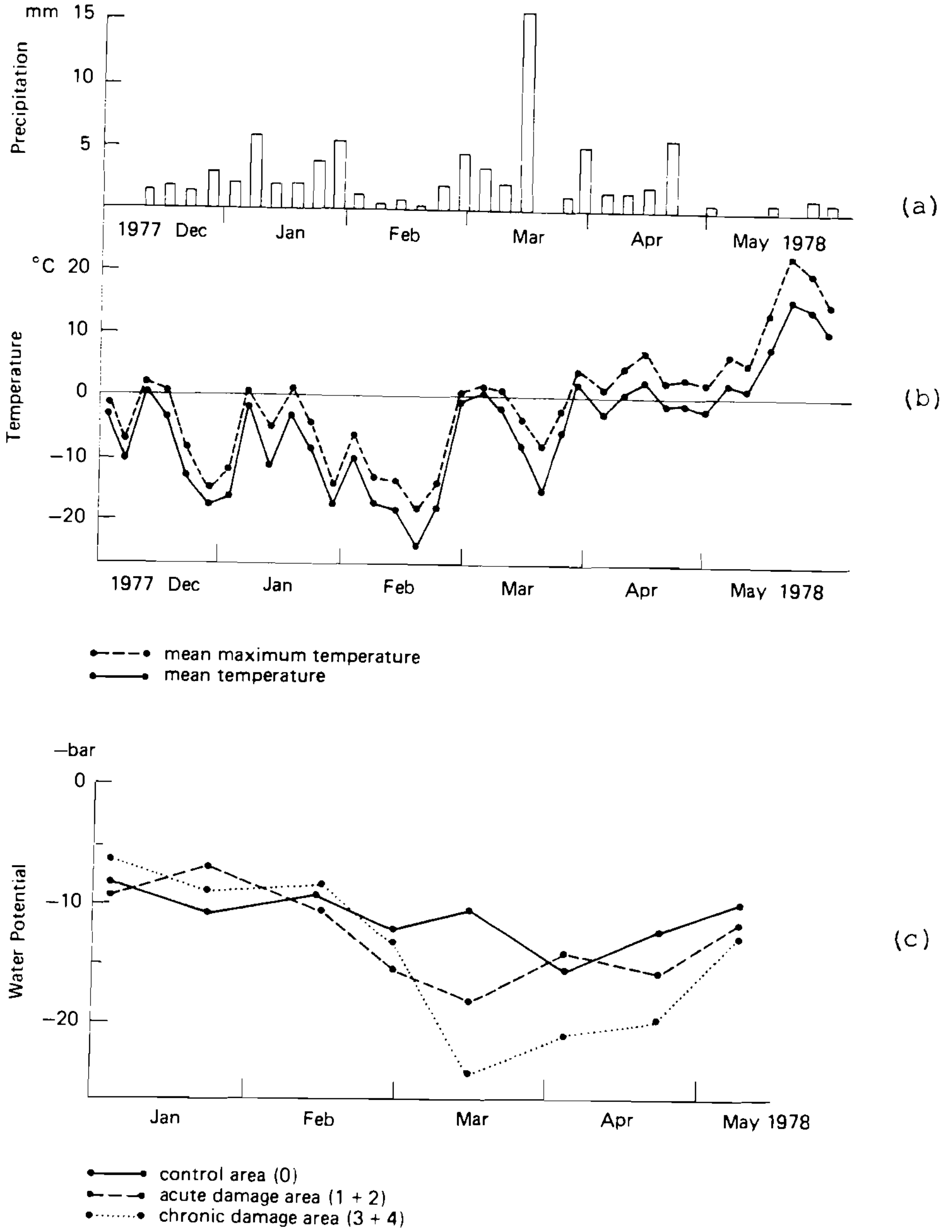


Figure 1. Precipitation (a), five-day means of average and daily maximum temperatures (b), and water potentials of Scots pine (*Pinus sylvestris*) branch tips in three test sites (c) in Oulu (65° N 25°30′E) in the spring of 1978. Reproduced from Huttunen *et al.* (1981).

2. MODEL DEVELOPMENT

2.1. Surface Structure Erosion

2.1.1. *Natural Rate of Erosion*

The structure of the surface waxes changes naturally when the needles age. The changes can be clearly observed in electron microscope photographs of needle surface (Grill, 1973b; Huttunen and Laine, 1981; 1983). In an analysis of the wax structure, Huttunen and Laine (1983) concluded that there was a significant difference in the structures of needles from different age classes. Cape (1983) quantified the change in terms of the *contact angle* of water droplets on the wax surface (Figure 2), and on the basis of empirical analysis, proposed an exponential model for the change of the contact angle. Let q denote the current contact angle, q_0 the initial contact angle and q_w the contact angle of a surface with no epicuticular wax. Then

$$\frac{d(q-q_w)}{dt} = -R\,(q-q_w) \quad ; \quad q_0 = constant \tag{1}$$

where R denotes the relative erosion rate. R varies geographically and between species.

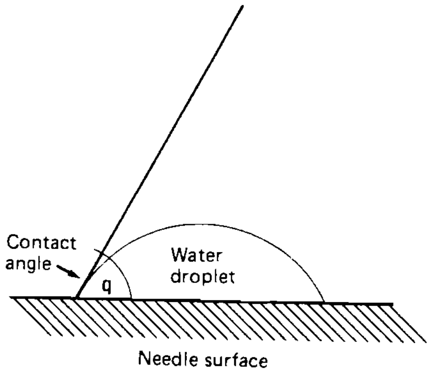


Figure 2. Definition of contact angle. Reproduced from Cape (1983).

2.1.2. *Regional Variation of Natural Erosion Rate*

The maximum lifetime of needles, τ, the relative erosion rate, R, and the maximum relative change in the contact angle during the life-time of the needles are related to each other by Eq. (1). If we solve the differential equation for q and equate the final contact angle, $\hat{q}$, with the solution at time τ, we obtain the following relationship:

$$R = \frac{1}{\tau} \ln \frac{q_0 - q_w}{\hat{q} - q_w} \tag{2}$$

Although the underlying mechanisms have not been explained, there is evidence that the rate of erosion of needle surface structure is functionally related with the average lifetime of needles. This observation has been reported both concerning natural variation (Grill, 1973b; Bligny *et al.*, 1973; Huttunen and Laine, 1983) and variation imposed by air pollution (Cape, 1983; Huttunen and Laine, 1983). Based on these observations, we calculate the natural relative erosion rate, denoted R_0, assuming a constant value for the ratio $(q_0 - q_w) / (\hat{q} - q_w)$ for each location. The regional differences in the natural erosion rate can hence be determined on the basis of information on the corresponding variation in the maximum life-time of needles.

2.1.3. *Impact of Sulphur on the Rate of Erosion*

Various observations indicate, that ambient sulphur dioxide accelerates the natural rate of erosion of the surface structure (Huttunen and Laine, 1983; Grill, 1973a; Cape and Fowler, 1981; Cape, 1983). In the lack of more accurate information, we shall assume that the impact of sulphur on the erosion rate is proportional to the natural erosion rate:

$$R(x(t)) = R_0(1 + x(t)) \tag{3}$$

where $x(t)$ is the *combined sulphur stress* which depends linearly on the sulphur dioxide concentration. This assumption gains support from the conclusions of Huttunen and Laine (1983) based on comparison of the electron microscope photographs of needles grown in different pollutant environments, and more quantitatively, from the observations of Cape (1983) on the development of the contact angle in different environments (Figure 3).

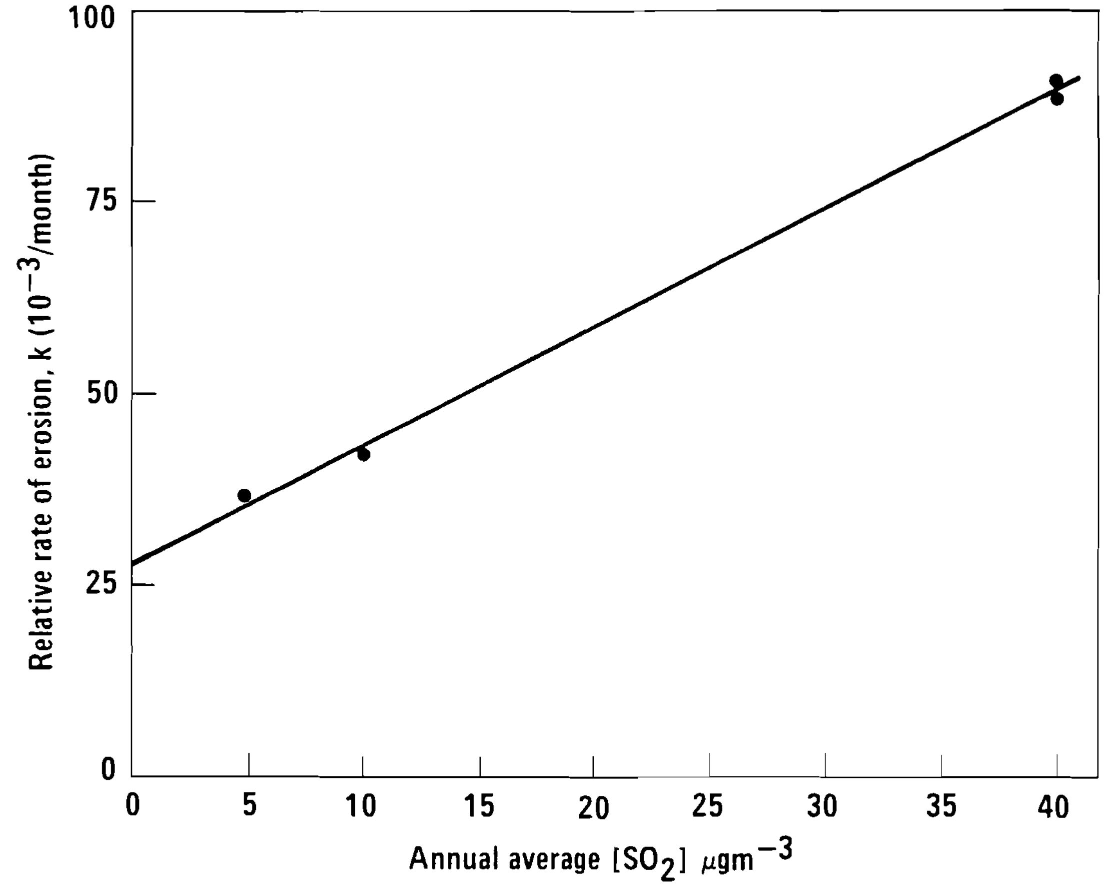
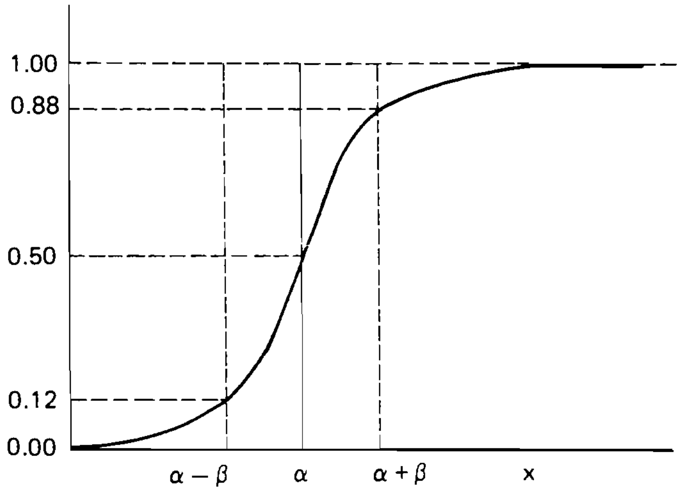


Figure 3. Relationship between the relative rate of erosion and annual average SO_2 concentration. In terms of Eq. (3), $[SO_2] = x(t)$, $k = R_o\,[1 + x(t)]$. Points from Cape (1983).

Some observations suggest that the erosion is further enhanced when sulphur occurs together with (1) low temperatures and (2) high relative air humidity. The former is probably due to physical stress, and the latter has been reasoned by the increasingly eroding impact when humid air or mist allows the sulphur to dissolve in water droplets. So as to incorporate these rather qualitative observations in the model, we shall simply assume that both impacts have an environmental threshold level at which the relative effect rapidly increases from zero to one. Such an impact can conveniently be described with the following logistic function:

$$f(x) = \{1 + \exp[-2(x-\alpha)/\beta]\}^{-1} \tag{4}$$

where x denotes the environmental variable and α and β are parameters (see Figure 4).



$f(x) = [1 + \exp(-2(x-\alpha)/\beta)]^{-1}$

Figure 4 Shape of the logistic function of Eq. (4) and the meaning of its parameters.

Denote the daily average temperature by T, the daily average relative humidity by H, and the daily average sulphur dioxide concentration by S. We suggest the following model for the combined erosion stress caused by these factors:

$$x(t) = \varphi_o[1 + \varphi_T f_T(T) + \varphi_H f_H(H)]\, S(t) \tag{5}$$

where φ_o, φ_T and φ_H are scaling parameters.

2.2. Changes in Transpiration

2.2.1. *Cuticular Conductance*

Although there is empirical evidence that erosion of needle cuticle increases the cuticular conductance of water vapour (Cape and Fowler, 1981; Cape, 1983), this relationship has not been satisfactorily quantified. Since the erosion is not directly related to the thickness of the cuticle but rather to its structure (Cape and Fowler, 1981), the theoretical diffusion approach of Nobel (1974) is not applicable either. Therefore, we shall compare different possible functional relationships between the contact angle and the cuticular conductance.

Let us assume that the conductance is proportional to the p-th power of the difference between the initial contact angle, q_0, and the current contact angle, q. Therefore,

$$g_c = P_p(q_0 - q) \tag{6}$$

where g_c denotes cuticular conductance (mm/h) and P_p $(\cdot)$ is a p-th order polynomial.

2.2.2. *Whole-tree Transpiration during Drought*

Since the water economy of the whole tree is affected by all the needles present, and since the surface structure erodes with age, we have to consider the contribution of the different age classes to transpiration for estimating the impact of sulphur-imposed erosion on the whole-tree water economy.

The transpiration during day t, $E(t)$, of a coniferous canopy with leaf area index LAI (leaf area per unit ground area) and foliage conductance g_c can be described with an approximation of the Penman-Monteith equation:

$$E = k\,D\,g_c\,LAI \tag{7}$$

where

$$k = \frac{c_p\,\rho_a}{\lambda\,\gamma}$$

and c_p,ρ_a,λ and γ are physical parameters depending upon air temperature and D is water vapour deficit (Waring and Schlesinger, 1985).

Foliage conductance varies with foliage age. Additionally, the water vapour deficit varies along a vertical gradient in the canopy (Jarvis, 1979). Let us denote the conductance of age class i by $g_{c,i}$, and let us assume that this age class is subject to the average water vapour deficit D_i. Denoting the leaf area index of the age classes by LAI_i we can write

$$E = k\, D\, LAI \sum_{i}^{n} \alpha_i\, g_{c,i} \tag{8}$$

where

$$\alpha_i = \frac{D_i\, LAI_i}{D\, LAI}$$

and n is the number of age classes in the crown (cf. Jarvis, 1979). On the basis of this, we can equate the average foliage conductance to a weighted sum of the age classes:

$$g_c = \sum_{i}^{n} \alpha_i\, g_{c,i} \tag{9}$$

Substituting the cuticular conductance of Eq. (6) to Eq. (9) we can write the average foliage conductance as a function of the contact angles of the different age classes:

$$g_c = \sum_{i}^{n} \alpha_i\, P_p(q_0 - q_i) \tag{10}$$

Let us define the transpiration strain, $Q(x)$, as the ratio of the actual transpiration under stress x [see Eq. (5)] to the corresponding transpiration under unpolluted conditions:

$$Q(x) = \frac{E(x)}{E(0)} = \frac{\sum_{i}^{n} \alpha_i(x)\ P_p(q_0 - q_i(x))}{\sum_{i}^{n} \alpha_i(0)\ P_p(q_0 - q_i(0))} \tag{11}$$

Note that changes in α_i can include changes in the distribution of LAI into age classes, as a function of pollutant impacts. The transpiration under polluted conditions is therefore

$$E(x) = Q(x)\, E(0) \tag{12}$$

$Q(x)$ is hence a relative measure for the change in whole-tree transpiration during a drought period.

2.3. Resistance of Drought

Desiccation occurs when the water potential of the foliage descends below a threshold level. During the winter when there is no water uptake from the soil, this occurs when the cumulative transpiration exceeds the amount of water available from the reservoirs in the tree.

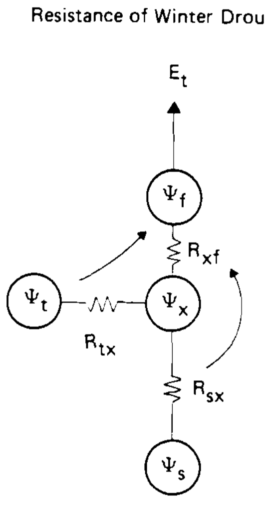


Figure 5. Water flows and reservoirs in a tree. ψ_f = water potential of the foliage, ψ_x = water potential of sapwood; ψ_t= water potential of the sapwood storage; ψ_s= soil water potential; R_{ij} = resistance to water flow between parts i and j; E_t = transpiration. According to Whitehead and Jarvis (1981).

Figure 5 shows the water flows and reservoirs of a tree (after Whitehead and Jarvis, 1981). Water is generally available to the foliage from the sapwood storage, and it is lost in transpiration. Let us denote the average water potentials of the foliage and sapwood by ψ_f and ψ_t, respectively. The volumetric flow of water from sapwood to foliage, q_{tf}, is proportional to the water potential difference and inversely proportional to the resistance of water flow, R_{tf}:

$$q_{tf} = \frac{\psi_t - \psi_f}{R_{tf}} \tag{13}$$

(Landsberg *et al.,* 1976). If we denote the turgid volume of the storage by V_t and its relative water content by θ_t, we can write the rate of change of the water content as

$$\frac{d\theta_t}{dt} = -\frac{1}{V_t}\frac{\psi_t - \psi_f}{R_{tf}} \tag{14}$$

Similarly, the change in the water content of the foliage is

$$\frac{d\theta_f}{dt} = -\frac{1}{V_f}\left[-E + \frac{\psi_t - \psi_f}{R_{tf}}\right] \tag{15}$$

where V_f is the volume of the foliage in full turgor pressure, and E is defined in Eq. (7).

The resistance of internal water flow depends on temperature. In very low temperatures, the movement of water in the xylem is prevented because of freezing, and the sapwood reservoir is not available for the foliage (Tranquillini, 1979). Thus, the foliage water content depends on the storage volume of foliage and the transpiration only:

$$\frac{d\theta_f}{dt} = -\frac{E}{V_f} \tag{16}$$

It seems reasonable to assume that foliage volume is proportional to leaf area. If we consider leaf area and volume per unit area, then

$$V_f = c_f LAI \tag{17}$$

where V_f is in units m^3/m^2.

If we use Equations (7) and (12) for E and substitute (17) into (16), then solving for θ_f we get

$$\theta_f(t) = \theta_f(0) - \frac{Q(x)\,g_c}{c_f}\int_0^t k(t)\,D(t)\,dt \tag{18}$$

where the initial time is the moment when water availability from sapwood to foliage becomes blocked.

Let us now consider the second possibility; viz., that water is available from the reservoir. In order to obtain a rough estimate of the drought tolerance, let us assume that foliage water potential is in equilibrium until the stem reservoir has been exploited (cf. Whitehead and Jarvis, 1981). This means assuming that a decrease in the water potential of the sapwood does not restrict water flow to the foliage until a threshold water potential is reached, whence the restriction becomes complete. Under this assumption, the system is governed by the following differential equation:

$$\frac{d\theta_t}{dt} = -\frac{E}{V_t} \tag{19}$$

Analogous to the above case, this implies that the storage volume of the sapwood is essential for drought resistance when water flow in the xylem occurs.

Sapwood volume is approximately proportional to the product of tree height and leaf area index (e.g. Waring and Schlesinger, 1985):

$$V_t = c_t h \, LAI \tag{20}$$

where h denotes tree height and V_t is in units of volume per unit area. In analogy with Eq. (18), we can solve for the water content of the reservoir at moment t:

$$\theta_t(t) = \theta_t(0) - \frac{Q(x)\, g_c}{c_t h} \int_0^t k(t)\, D(t)\, dt \tag{21}$$

Storage capacity, C_i, is the maximum amount of water that can be retained by the storage (Landsberg *et al.*, 1976). Denote the maximum and minimum water contents by $\theta_{i,max}$ and $\theta_{i,min}$, respectively. Hence

$$C_i = V_i \, (\theta_{i,max} - \theta_{i,min}) \tag{22}$$

Let us define the *specific storage capacity*, γ_i, as storage capacity per unit leaf area. Hence, by Eqs. (20) and (22),

$$\gamma_f = c_f \, (\theta_{f,max} - \theta_{f,min}) \tag{23a}$$

$$\gamma_t = c_t h \, (\theta_{t,max} - \theta_{t,min}) \tag{23b}$$

Eqs. (18) and (21) can now be used to calculate the critical limit of transpiration during a drought period. The critical limit will be reached when the cumulative transpiration per leaf area exceeds the specific storage capacity of the foliage, or the sapwood, respectively, i.e. when

$$Q(x)\, g_c \int_0^t k(t)\, D(t)\, dt \geq \gamma_i \tag{24}$$

This inequality allows us to determine the conditions under which drought damage is likely to occur, provided that γ_i, g_c and the time course of the driving variables of evaporation are known. The impact of sulphur stress on drought resistance can be conveniently analyzed with this formula by varying the multiplier $Q(x)$.

3. APPLICATIONS

3.1. Stress and Climate

According to the assumption of Eq. (5), the combined erosion stress is due to sulphur, cold temperatures and air humidity. In order to get some insight into the geographic variation of the combined stress, a numerical exercise was carried out. We calculated the relative stress x/S for various locations in Europe, assuming the parameter values given in Table 1. Selecting the parameters φ_i equal to 1 means assuming that in the presence of a certain ambient SO_2 concentration, either low temperature or high humidity alone will double the erosion stress. If both stress factors are active, the stress will increase by a factor of three. The temperature threshold was assumed to be -10°C, and the humidity threshold 90%.

Table 1. Parameter values.

Symbol	Explanation	Source	Value
φ_o	increase in relative erosion rate per unit SO_2 concentration	Cape 1983	$0.057\ y^{-1}$
φ_T	relative significance of cold temperature		1
φ_H	relative significance of air humidity		1
α_T	half-value of temperature threshold		-10°C
β_T	width of temperature threshold		-2°C
α_H	half-value of humidity threshold		90%
β_H	width of humidity threshold		5%
q_o	initial contact angle	Cape 1983	110°
$\hat{q}$	contact angle at maximum age without stress	Cape 1983	85°
q_w	minimum contact angle	Cape 1983	70°
τ	maximum needle age	choice	5

The calculations were based on long-term average monthly values of temperature and relative air humidity (Müller, 1982). Daily values were estimated from the monthly data by calculating a spline which follows the monthly values and has the same monthly averages (Henttonen and Mäkelä, 1987). The daily values were applied to Eq. (5) for calculating the annual average x/S. Table 2 shows the obtained x/S in several locations in

Europe, along with some additional climatic information of the stations.

Since the susceptibility of trees to air pollution has often been related to the climate in terms of the Effective Temperature Sum (ETS), the values of x/S thus obtained were plotted against this variable (Figure 6). The ETS was calculated from daily temperatures which were estimated from monthly averages using the same smoothing method as for the other variables (Ojansuu and Henttonen, 1983). The inland stations seem to manifest a fairly linear relationship between x/S and ETS, whereas the stations located by the ocean do not appear to follow any distinct pattern.

The result is sensitive to the values chosen for the parameters φ_i quantitatively, but the relationship obtained between ETS and the combined stress holds true, qualitatively, for a wide range of parameter values. As regards air humidity and thus particularly the oceanic stations, the results involve many uncertainties. However, at the moment we do not have more accurate information on the occurrence of fog and mist.

3.2. Whole-tree Strain

3.2.1. *Direct Strain*

The whole-tree transpiration strain, $Q(x)$, was analyzed as a function of the relationship between the cuticular conductance and contact angle, and as a function of different assumptions on the weight parameters α_i [Eqs. (6) and (7)].

We used the following simple form for the polynomial P_p relating the cuticular conductance and contact angle [Eq. (6)].

$$P_p(q_0 - q) \;=\; c\,(q_0 - q)^p \tag{25}$$

For the parameters α_i, we compared three alternative age class distributions. First, we set all α_i-s equal, corresponding to the situation that (1) there is no needle shedding until the needles reach the maximum age, and (2) the water vapour deficit, D, is constant in the canopy. Apparently an unrealistic case, this gives a lower limit for the strain $Q(x)$. Secondly, we calculated the α_i-s using a parabolic function of needle age, $f(\tau)$, as follows:

Table 2. Annual average relative sulfur stress, x/S, as calculated for various meteorological stations.

No. of Station	Name	Location	Altitude	Annual Temperature Temperature m	ETS Humidity °C d	Annual Mean Mean %	x/S
6	Tromsö, Norway	69° 36'N/18° 57'E	115	2.9	695	77	1.011
7	Mo i Rana, Norway	66° 71'N/14° 08'E	20	2.9	967	79	1.046
11	Bergen, Norway	60° 12'N/5° 19'E	45	7.8	1327	78	1.012
14	Kristiansand, Norway	58° 10'N/7° 59'E	23	7.2	1527	76	1.023
27	Oulu, Finland	65° 07'N/25° 29'E	17	2.3	1066	80	1.216
30	Punkaharju, Finland	61° 48'N/29° 17'E	88	3.3	1260	78	1.186
46	Belfast, Northern Ireland	54° 39'N/6° 13'W	67	9.1	1693	83	1.169
50	Birmingham, England	52° 29'N/1° 56'W	136	9.7	1880	76	1.053
75	Hof, FRG	50° 19'N/11° 53'E	567	6.2	1487	81	1.123
86	Brocken (Harz), GDR	51° 48'N/10° 37'N	1142	2.9	786	87	1.297
97	Presov, CSSR	49° 00'/21° 15'E	270	8.3	2069	74	1.021
124	Vienna, Austria	48° 15'N/16° 22'E	203	9.8	2113	74	1.008
129	Debrecen, Hungary	47° 33'N/21° 37'E	123	10.3	2528	75	1.046
132	Iasi, Romania	47° 10'N/27° 36'E	101	9.4	2449	71	1.019
145	La Coruna, Spain	43° 22'N/8° 25'W	67	13.9	3109	78	1.011
149	Madrid, Spain	40° 25'N/3° 41'W	667	13.9	3258	65	1.002

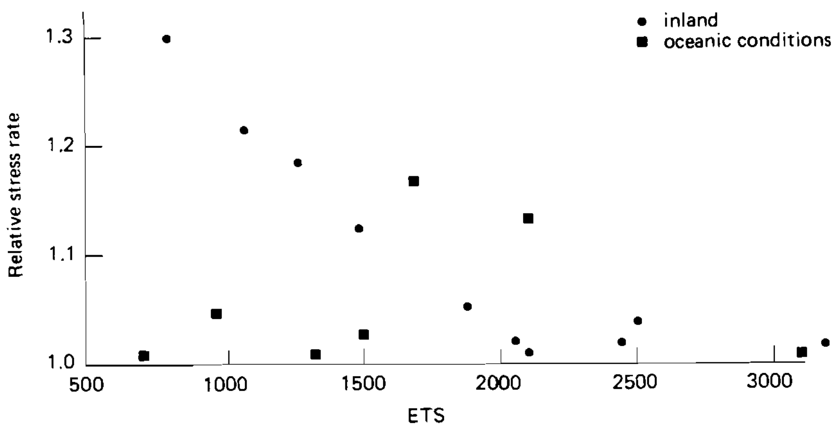


Figure 6. The relative stress, x / S, against effective temperature sum in various climatic stations (see Table 2). x as in Eq. (5), $S =$ annual average sulphur dioxide concentration.

$$\alpha_i = \frac{\int_{i-1}^{i} f(\tau)\, d\tau}{\int_{0}^{n} f(\tau)\, d\tau} \tag{26}$$

where n is the maximum needle age and $f(n) = 0$ (see Figure 7). This corresponds fairly well with some empirical observations on needle age class distributions on trees (Knabe, 1972; Flower-Ellis and Persson, 1980). In the third case, we substituted the parabolic $f(\tau)$ with a linear one, again assuming $f(n) = 0$. This curve combines the assumption that the water vapour deficit is greater the younger the needles are, due to more exposed average location, with the parabolic leaf area distribution.

The contact angles of the different age classes under the stress x were calculated solving Eq. (1), with R as follows from Eqs. (3), (4) and (5). A steady state was assumed, i.e. the needles in the i-th age class were assumed to have been subject to the stress x for i years. The values of the contact angle were calculated at the end of the year, corresponding to the late winter situation. The parameters used in the calculations are listed in Table 1.

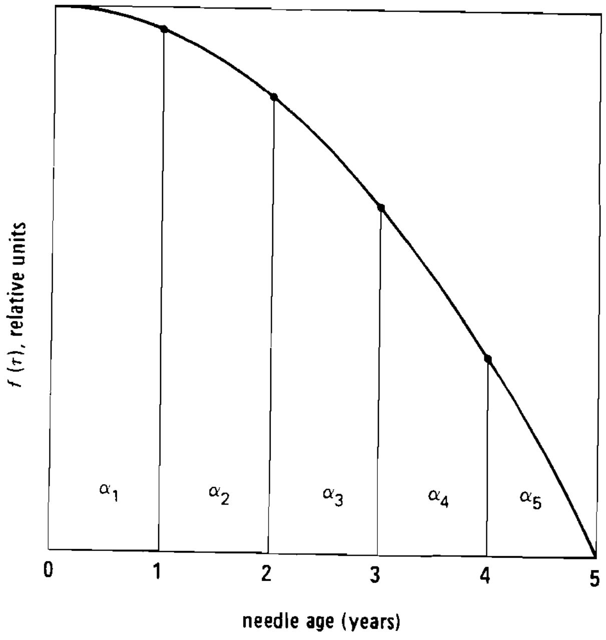


Figure 7. Example of the calculation of the weight coefficients α_i in the case of a parabolic distribution. α_i is the area below the curve between points $i-1$ and i, divided by the total area.

Figure 8 shows $Q(x)$ as a function of the combined stress, x, expressed as the equivalent annual average sulphur dioxide concentration when no other stresses are present. The linear distribution of α_i was used, and the parameter p of Eq. (6) was varied between 0.5 and 4. The figure demonstrates that the strain is very sensitive to the functional relationship between the cuticular conductance and contact angle.

Figure 9 compares the different weighting principles between the age classes. The value $p=2$ was used for the exponent. The uniform distribution gives a considerably lower strain, especially for the high sulphur concentrations, whereas the linear and parabolic distributions do not show significant differences.

The sensitivity of $Q(x)$ to the number of age classes was also analyzed, the result being that the sensitivity is very low. It seems, however, that the smaller the number of age classes, the higher the sensitivity to other parameters such as initial state. If the number of age classes is high, the uncertainties due to initial values average out when

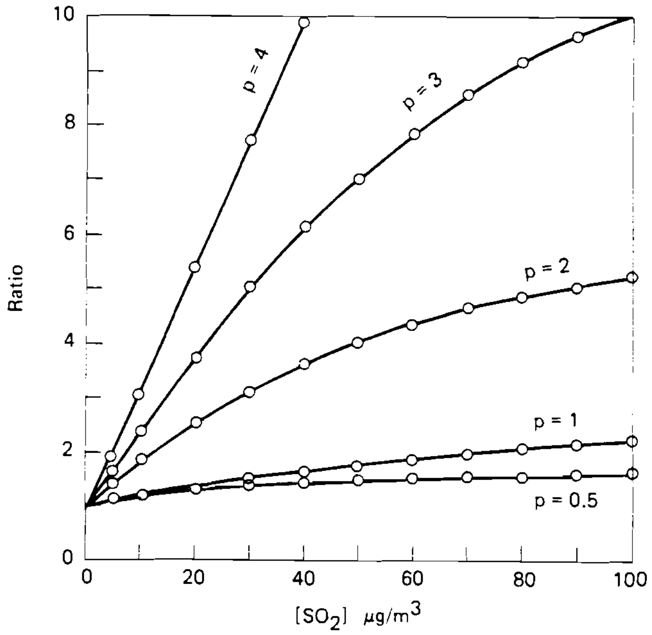


Figure 8. The ratio between actual and unpolluted transpiration $[Q(x)]$ assuming different functional relationships between cuticular resistance and contact angle (Eq. (25)] x = sulphur stress [Eq. (5)].

summing up the contact angles of the age classes, whereas for a low number of age classes, this averaging procedure is not very effective.

3.2.2. *Acclimatization to Stress: Shedding of Needles*

It has been observed that when exposed to sulphur stress, the rate of needle shedding increases and the maximum number of age classes decreases (Knabe, 1972; Grill, 1973b; Bligny *et al.*, 1973; Huttunen and Laine, 1983; Cape, 1983). At least in *Abies* and *Picea* families it appears that the needles are shedded when their state of erosion reaches that of the oldest needles under unpolluted conditions (Bligny *et al.*, 1973; Grill, 1973b). Although the shedding of needles is probably caused by several processes related to sulphur impact, it is interesting to use the model to experiment how well the phenomenon could be explained as an acclimatization to increased demand of cuticular transpiration. Since it is the oldest needles that have the highest cuticular conductance, it might be

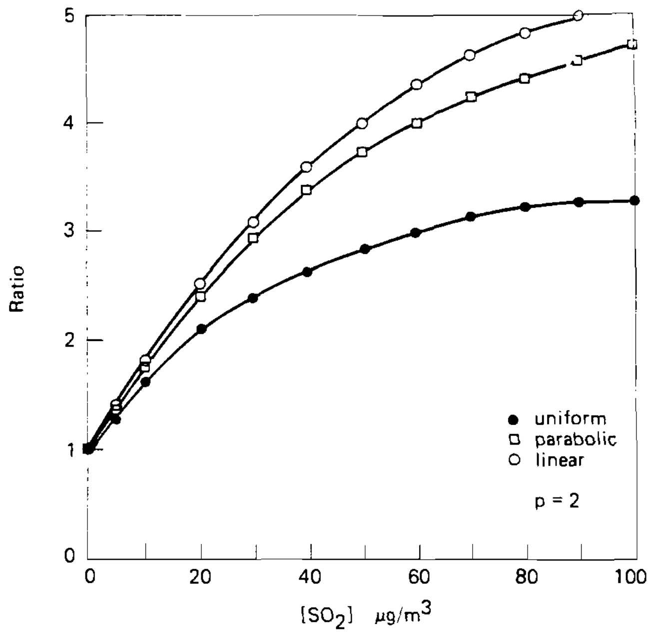


Figure 9. Comparison of different weighting principles of the transpiration of the age classes. Cuticular conductance is a quadratic function of the contact angle ($p = 2$).

profitable to shed those needles so as to retain the average cuticular conductance closer to the initial, normal level.

Figures 10 and 11 illustrate the situation that the damaged needles are shedded when their state of erosion reaches that of the eldest needles under unpolluted conditions, i.e when $q = \hat{q}$. In Figure 10 the resulting maximum age of needles, as a fraction of the natural lifetime, is shown as a function of sulphur stress. Figure 11 shows the corresponding value of $Q(x)$ for the linear and parabolic weighting factors α_i.

The conclusion is that shedding of needles indeed provides a potential decrease of the cuticular transpiration strain. The decrease of strain is the less effective, the more the relative contribution of the youngest age classes to transpiration.

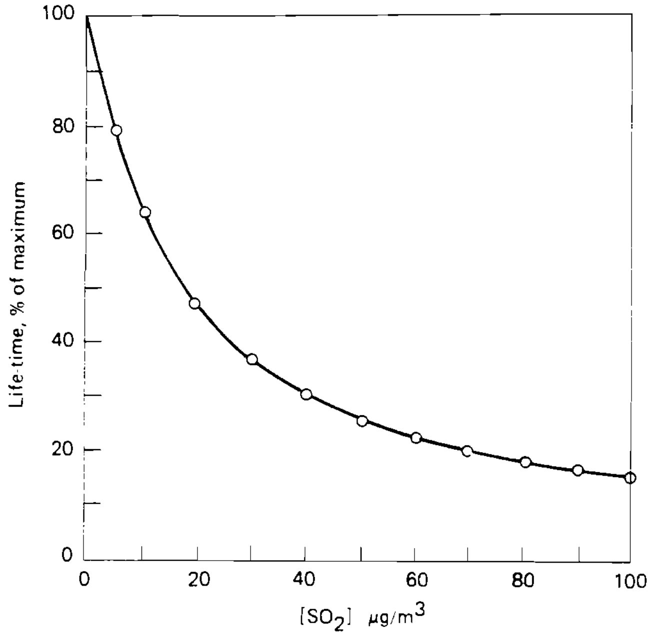


Figure 10. Acclimatization to higher cuticular conductance through shedding of those needles that have reached a critical contact angle: needle lifetime as percentage of the lifetime of healthy needles in relation to annual average SO_2 concentration.

3.2.3. *Transpiration and Reservoir*

During the water balance experiment illustrated in Figure 1, there was a warm spell in March which lasted approximately two weeks (Huttunen *et al.*, 1981). In order to get an idea of the potential water loss during this warm spell, we attempt to estimate the transpiration per leaf area during the period.

During the warm period, the maximum air temperatures reached +2°C, yet only one week earlier the temperatures had been below -20°C, and the night time temperatures were below freezing point throughout the period (Figure 1). This suggests a relatively low absolute air humidity, and consequently a low relative humidity during the hours of maximum temperatures. Assuming that on the average, temperature is +1°C, we obtain the values shown in Table 3 for the physical parameters required to calculate transpiration (Monteith, 1973; Table III). Putting $D = 0.5$ kPa and calculating the integral in Eq. (24) over 100h, corresponding approximately to 7 hours per day over two weeks, we get

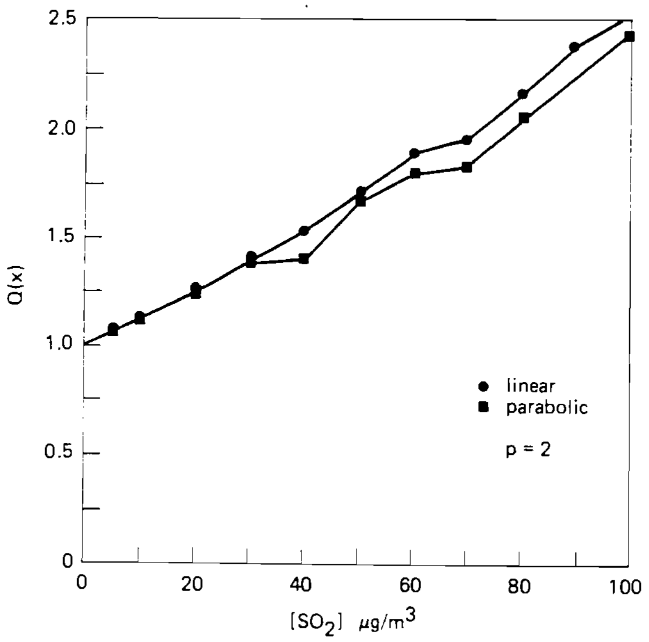


Figure 11. Increase in transpiration due to cuticular erosion, in the case of acclimatization through shedding of needles. Two weighting principles for the factors α_i have been compared.

$$\int_0^{100h} k(t)\,D(t)\,dt = 0.4\,\frac{\mathrm{kg}}{\mathrm{m}^3}\,\mathrm{h} \tag{27}$$

Table 3. Physical parameters for calculating transpiration at + 1°C.

Symbol	Explanation	Value	Units
c_p	specific heat of air	1.01	J^{-1} °C s^{-1}
ρ_a	density of air	1.27	$\mathrm{kg/m^3}$
λ	latent heat of vaporization	2500	$J\,g^{-1}$
γ	psychometric constant	0.647	$\mathrm{mbar°C^{-1}}$
γ_f	specific storage capacity of foliage	0.05	mm
γ_t	specific storage capacity of sapwood	0.15	mm/m
g_c	cuticular conductance	0.015-0.15	mm/s

The information on cuticular conductance in the literature is contradictory. According to Larcher (1980), the cuticular transpiration of evergreen conifers comprises about 3% of the corresponding transpiration with the stomata open. This, again, is approximately 50% of the transpiration of a winter-deciduous forest in the temperate zone. According to Gates (1980), the maximum stomatal conductance of the latter is in the order of magnitude of 1 mm/s, giving approximately 0.5 mm/s for conifers. However, Whitehead and Jarvis (1981) and Waring and Franklin (1979) report that the maximum stomatal conductance is 4 mm/s in some conifers. The two sources give a range of 0.015 - 0.12 mm/s for cuticular conductance. Furthermore, Major and Taylor (1977) indicate that cuticular conductance in spruce ranges from 0.003 to 0.01 mm/s. These were used by Sowell (1985) in calculations of cuticular transpiration at the timberline. If we set $g_c =$ 0.1 mm/s, and $Q(x) = 1$, we conclude that the corresponding cumulative water loss per leaf area is 0.15 mm. The variation in the estimates of cuticular conductance give a range 0.015 - 0.15 mm for this value.

We get an idea of the significance of the specific transpiration by comparing it with the specific storage capacity, as indicated in Eq. (24). Although there is little quantitative information on the storage capacities, some rough estimates can be found.

Waring *et al.* (1979) reported that the absolute storage capacity of young Scots pine stands, varied between 7 and 15 mm while the stocking density ranged from 600 to 3200 stems per hectare. Assuming leaf area indices of the order of 5 to 10 (cf. Jarvis, 1975) and tree height of 10 meters, we estimated that the specific storage capacity of Scots pine foliage and sapwood are of the order of 0.05 mm and 0.15 mm/m, respectively. A comparison of this with the specific transpiration estimated above shows that a doubling of the sulphur stress, $Q(x)$, which seems possible based on the results of Section 3.2, could already increase the water loss close to the critical level. Especially if several similar incidents occur during the winter, the increased susceptibility of the tree could be fatal. However, the conclusion largely depends on the estimate of cuticular conductance under natural circumstances.

4. CONCLUDING REMARKS

We have presented a method for analyzing the impacts of enhanced cuticular erosion, caused by airborne sulphur, on whole-tree transpiration and resistance of drought. Because both the rate of erosion and the synergistic impact of drought and sulphur depend on climatic variables, in connection with appropriate climatological data the method provides a tool for comparing the sensitivity of different climatic conditions to sulphur stress.

The derivation involved many assumptions based on suggestive relationships that have not been studied quantitatively before, and should therefore only be considered as tentative attempts to formalize the problem. In particular this is true of (1) the relationship of cuticular erosion with cold temperatures and relative humidity, and (2) the relationship between cuticular transpiration and the contact angle. The numerical values concerning the storage capacity of foliage and stem also, still remain to be validated. Further, the results are sensitive to the magnitude of the cuticular conductance, the reported values of which range from 0.003 to 4 mm/s for conifers. This area clearly deserves some more research. As regards the structure of the model, we treated the cuticle as a homogeneous medium, but more realistically the alveolar material should probably be distinguished from the ordinary cuticle.

Due to the many uncertainties, this exercise neither proves nor rules out the possibility that enhanced cuticular erosion leads to increased winter drought damage in conifers. Guided by earlier empirical studies the authors feel, however, that an increase in damage occurrence does seem likely at least in the most sensitive areas (e.g. Tranquillini, 1979). To get more insight into these questions, it is necessary to apply the model to a variety of climatic conditions, as well as to further investigate the most critical open questions.

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