

VARIABILITY IN CUTICULAR RESISTANCE OF *PICEA ABIES* (L.) KARST. AND ITS SIGNIFICANCE IN WINTER DESICCATION

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Abstract. The variability of cuticular transpiration resistance (r_c) was investigated in *Picea abies*. Needles of different crown positions, age, and air pollution load were measured. Cuticular resistance declined gradually with the needle age, so that in four-year-old needles it constituted about half of that in the current-year needles. In an individual tree, the values of r_c were much higher in the shade needles than in the sun needles. The experiments in which wax was removed with ether revealed that the role of epicuticular wax in the total r_c decreased with needle age. In the current-year needles, the resistance attributable to wax exceeded 40% of the total r_c ; in C+3 needles it was as small as 18%. At the sites with polluted air the decrease in r_c during needle ageing was faster than at the control site. Calculations with wintertime air temperature and humidity used in a model showed that damage resulting from decreased cuticular resistance and consequent needle desiccation may appear after 22 days of continuously frozen soil in the four-year-old needles from the polluted site. Sun and shade needles from the control site can tolerate periods of permanent frost for 37 and 60 days, respectively.

Key words: cuticular resistance, epicuticular wax, wintertime desiccation, *Picea abies*, air pollution.

INTRODUCTION

The rate of cuticular transpiration is considerably lower than the rate of stomatal transpiration, especially in xerophytes and conifers (Larcher, 1975). However, under extreme conditions small variations in wintertime water economy may have crucial effects on the survival of conifers, thus playing the main role in determining both the altitudinal treeline in the mountains and the polar timberline (Tranquillini, 1979, 1982). A similar term 'urban timberline' has been proposed (Laine et al., 1984) for localities where human impact is the most important stress factor determining the growth of trees.

Cuticular resistance to water vapour diffusion (r_c) decreases with needle age (e.g., Fowler et al., 1980; Cape & Fowler, 1981). This phenomenon has been attributed to the gradual degradation of the epicuticular wax (Grill, 1973; Sauter & Voß, 1986). Air pollution and acid rain increase the rate of wax erosion (Percy & Riding, 1978; Huttunen & Laine, 1981; Crossley & Fowler, 1986; Rinallo et al., 1986; Schmitt et al., 1987).

Thus it seems logical to assume that the rate of decrease in r_c during needle ageing could serve as an indicator of pollutant concentrations,

However, as Huttunen (1978) has stated, there may be great variability in cuticular resistance among individual trees. No investigations are known to us in which cuticular resistance of sun and shade needles has been studied on the same tree.

The aim of the present study was to investigate the variability of resistance to cuticular transpiration in different parts of an individual tree, the variability between trees of the same age, and the differences in r_c between trees growing under different air pollution loads.

We have analysed the role of epicuticular wax and cuticle in total cuticular resistance, and we have estimated the possible influence of the age- and pollutant-induced decrease in r_c on winter desiccation of needles.

MATERIAL AND METHODS

Sample trees. The data were gathered from the following four sources in Estonia:

(1) a 100-year-old tree of 38 m in height growing in a closed canopy stand in Roela 1 sample area, Vooremaa Ecological Station, 43 km north of Tartu. The shoots for measurements were taken from the upper (30 m) and lower (12 m) parts of the crown;

(2) five 12- to 15-year-old self-sown trees growing in a close group in the open near the main laboratory of the Vooremaa Ecological Station, 2 km from site 1. The shoots were taken from the western side of the crown, 1 m above the ground. These trees were used to estimate the variation in r_c amongst trees;

(3) an 80-year-old tree growing 2 km northwest of the Kiviõli Oil-Shale Chemical Plant, a region in which alkaline oil-shale dust is deposited. The pH of snow water can reach 11.3 in this region (Laur & Mandre, 1987);

(4) a 35-year-old tree from a hedge in the northern part of Tartu, a site with slight, complex air pollution (Frey et al., 1988).

Measurement procedure. Measurements were made on shoots of each of the four age classes: current year (C), and three previous years (C+1, C+2, and C+3). The measurements were made in the middle of May, two weeks before budbreak. Thus the C needles were almost one year old, C+1 needles two years old, etc.

For each sample, r_c was estimated on ten separate shoots. The twigs were cut off from the tree, placed in a plastic bag, and taken to the laboratory. The shoots were detached from the twig and hung in the open air in the laboratory. The cut surfaces of the shoots were covered with latex glue to prevent evaporation. Air humidity and temperature in the room were measured with a ventilated psychrometer and the water vapour pressure deficit was maintained at about 1.0 kPa. As the boundary layer resistance at the air circulation rate in the laboratory ($0.2\text{--}0.4\text{ m}\cdot\text{s}^{-1}$) was negligible as compared to cuticular resistance (Jarvis et al., 1976), the cuticular resistance to water vapour diffusion was calculated as

$$r_c = (Q_{\text{sat}, T_n} - Q_{\text{sat}, T_a} \times RH) \times t \times A / \Delta m,$$

where Q_{sat} is the saturating water vapour concentration at needle (T_n) and air (T_a) temperature, RH —relative air humidity, Δm —water loss, t —time of the exposure, and A —the total needle surface area. Needle temperature was considered to be equal to air temperature. It was assumed that the stomata were closed completely and the cuticular phase of transpiration was reached after 4 hours of desiccation. The water loss was estimated by weighing the shoots on a torsion balance 4 hours after their detachment and again 10 hours later. The accuracy of weighing was

0.1 mg. Baig & Tranquillini (1980) have suggested that cuticular transpiration should be measured after a 24-hour initial desiccation period. We could not do this as by that time the shoots had started to shed needles, especially the older shoots from the polluted sites.

Total needle surface area was estimated by the bead method (Thompson & Leyton, 1971).

To determine the influence of epicuticular wax on r_c , the wax was removed by rinsing the shoots in ethyl ether for 1 minute.

The number of stomata was counted under the microscope at 1 mm intervals at the base, middle, and top of the four sides of the needles; five needles constituted a sample. Stomatal density was expressed on the total needle area basis.

RESULTS

Effect of needle age and position. In all the investigated trees the cuticular resistance decreased with needle age (Fig. 1). In general, the values of r_c in the four-year-old needles were half those in the current-year needles. There were pronounced differences in r_c among shoots from different crown positions in the forest-grown tree (Fig. 1). The shade needles from the crown base had much higher ($\times 1.6$ to 2.2) resistance in all age classes than the sun needles from the top of the crown.

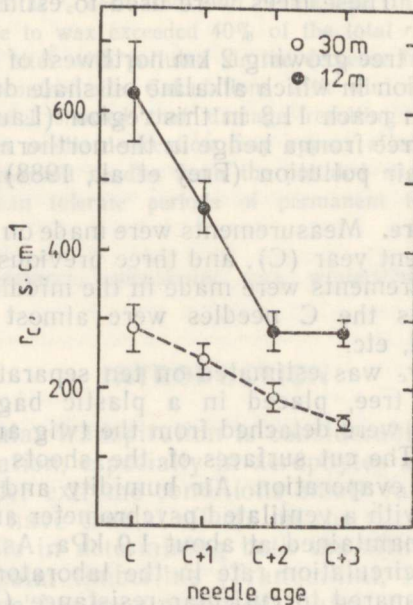


Fig. 1. Cuticular transpiration resistance of the shoots from the upper and the lower part of the crown of the 100-year-old tree. Error bars: \pm SE.

Variability between the trees. There were large differences in the r_c of C-needles of the five open-grown trees, the values of r_c varying from 650 ± 50 , 620 ± 60 , 440 ± 50 , 430 ± 20 to $420 \pm 30 s \cdot cm^{-1}$. On the average, however, r_c of the needles from young open-grown trees was closer to that of the shade needles rather than to the sun needles of the forest-grown adult tree (Fig. 2). There was no correlation between stomatal density and cuticular resistance.

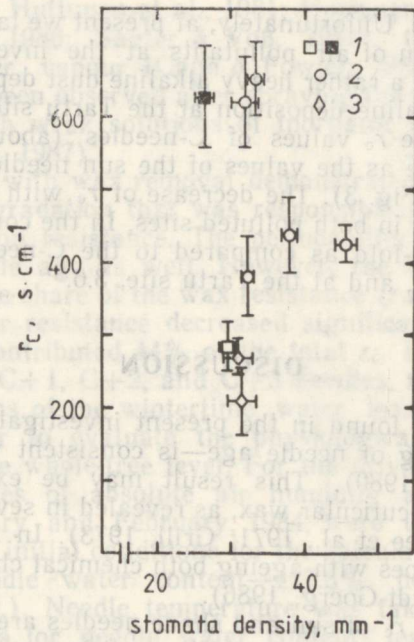


Fig. 2. The relationship between r_c and stomatal density in the current year sun (open symbols) and shade needles (closed symbols) of the 100-year-old control tree (1), 12–15-year-old trees (2), and a 35-year-old tree in a polluted area (3). Error bars: \pm SE.

Effect of epicuticular wax. In all the samples measured, removal of epicuticular wax resulted in a decrease of the cuticular resistance (Fig. 3). However, the differences in r_c of the treated and untreated shoots decreased with needle age. The contribution of the wax layer to the total r_c in the C-needles was 44%, in the C+1 needles 33%, and in the C+3 needles only 18%.

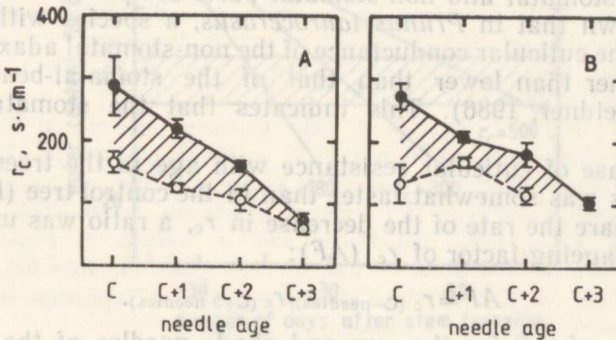


Fig. 3. Cuticular transpiration resistance of the shoots from Tartu (A) and from the oil-shale region (B). Dots denote untreated shoots, open circles mark epicuticular wax removed. The hatched area corresponds to the resistance of wax layer. Error bars: \pm SE.

Effect of air pollution. Unfortunately, at present we lack exact quantitative data on the deposition of air pollutants at the investigated sites. Pilot studies have revealed a rather heavy alkaline dust deposition at the Kiviõli site and a slight alkaline deposition at the Tartu site.

At both sites, the r_c values of C-needles (about 280–290 s·cm⁻¹) were almost the same as the values of the sun needles of the control tree from the Tartu site (Fig. 3). The decrease of r_c with needle age, however, was much more rapid in both polluted sites. In the control plot, r_c of C+3 needles decreased 1.9-fold as compared to the C-needles. At the Kiviõli site, the ratio was 2.7, and at the Tartu site, 3.6.

DISCUSSION

The general trend found in the present investigation—the decrease of r_c with the advancing of needle age—is consistent with earlier findings (e.g. Fowler et al., 1980). This result may be explained by gradual degradation of the epicuticular wax, as revealed in several other coniferous species (e.g. in Jeffree et al., 1971; Grill, 1973). In *Picea abies*, the epicuticular wax undergoes with ageing both chemical changes and reduction in quantity (Günthardt-Goerg, 1986).

The differences in r_c of sun and shade needles are not easy to explain. There may exist several processes which result in a more rapid degradation of the epicuticular wax and/or the cuticle in more exposed leaves. In the timberline ecotone the abrasion of cuticular wax by windborne ice crystals resulted in a decrease of the cuticular resistance of the wind-exposed needles of *Picea engelmanni* (Hadley & Smith, 1986). Baker & Hunt (1986) have demonstrated that the mechanical impact of rain droplets can cause the erosion of the crystalline wax structures of some species with glaucous leaves. These effects may lead to bigger differences in r_c of older needles from different crown positions. In our case, the situation was quite the opposite: the relative differences in r_c of the sun and shade needles were greater in younger needles (Fig. 1). One possible reason for the higher resistance of shade needles could be their somewhat lower stomata number per unit of the needle area. The stomata may close not tightly enough and there may occur water vapour diffusion through the stomatal apparatus during the desiccation experiment, which could be higher than that of the non-stomatal epidermis. The lack of correlation between stomatal density and r_c (Fig. 2) shows that this mechanism did not occur. We have no information on the differences in the diffusion resistance of stomatal and non-stomatal parts of epidermis in conifers. It has been shown that in *Prunus laurocerasus*, a species with hypostomatous leaves, the cuticular conductance of the non-stomatal adaxial epidermis is higher rather than lower than that of the stomatal-bearing abaxial epidermis (Meidner, 1986). This indicates that the stomata close very tightly.

The decrease of cuticular resistance with age in the trees growing in polluted areas was somewhat faster than in the control tree (Figs. 1, 3). In order to compare the rate of the decrease in r_c , a ratio was used that may be called the ageing factor of r_c (AF):

$$AF = r_c (\text{C-needles}) / r_c (\text{C+3 needles}).$$

The values of AF for the sun and shade needles of the control tree were 1.9 and 2.2, respectively; for the city-grown tree, 3.6; and for the tree from the alkaline-polluted site, 2.7.

It has been demonstrated on several coniferous species that air pollution can cause an accelerated degradation of epicuticular wax structures

(Fowler et al., 1980; Huttunen et al., 1981; Huttunen & Laine, 1981, 1983; Crossley & Fowler, 1986; Sauter & Voß, 1986), thus increasing their permeability to water vapour (Cape & Fowler, 1981). Alterations in the wax structure have been observed after spraying the needles of *Abies alba* and *Picea abies* with weak solutions of inorganic acids (Rinallo et al., 1986; Schmitt et al., 1987).

Our experiments with wax removal demonstrated that it was not only epicuticular wax degradation that was responsible for the impairment of cuticular transpiration resistance. The permeability of the cuticle *per se* increased with needle age as well. However, the wax degradation was much faster. Thus the share of the wax resistance ($r_{\text{wax}} = r_c - r_{c, \text{wax removed}}$) in the total cuticular resistance decreased significantly with needle age. In C-needles, r_{wax} contributed 44% of the total r_c . Its share decreased to 41, 33, and 17% in C+1, C+2, and C+3 needles, respectively.

Model calculations of the wintertime water losses from the needles were made in order to evaluate the physiological significance of the decrease in r_c on the whole-tree level. For the driving force of transpiration the daily values of absolute air humidity and air temperature, averaged for January and February, 1984, were used (Метеорологический..., 1985). The initial conditions for the calculations were the following: the initial needle water content—117.5%, needle specific area— $50 \text{ mm}^2 \cdot \text{mg}^{-1}$ (d. w.). Needle temperature was taken equal to air temperature. The criteria for needle water content, leading to its sublethal damage and irreversible desiccation, were defined as the average values for *Picea abies* during the winter months according to Pisek & Larcher (1954).

Under these conditions the water content of the shade needles for the control tree ($r_c = 500 \text{ s} \cdot \text{cm}^{-1}$) would approach the limit of drought resistance after 47 days of permanent frost, and after 60 days the needles would desiccate to the critical damage level (Fig. 4). For the sun shoots of the control tree and shade C needles of the polluted trees ($r_c = 300 \text{ s} \cdot \text{cm}^{-1}$) these levels would be exceeded in 27 and 37 days, respectively. For C+3 needles of the polluted tree ($r_c = 180 \text{ s} \cdot \text{cm}^{-1}$) the initial damage would occur after 17 days and the critical limit of desiccation would be reached after 22 frosty days.

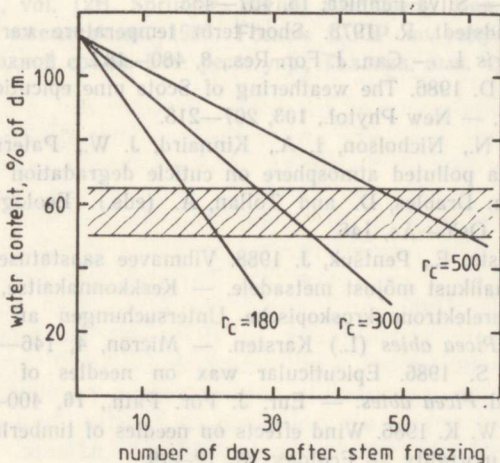


Fig. 4. Desiccation of needles with different r_c during a period of continuously frozen soil. The hatched area denotes the region of sublethal damage as defined by Pisek & Larcher (1954).

The above calculations are extremely simplified. In sunny and calm days the temperature of sunlit needles may rise about 7 to 8°C above the ambient air temperature (Christersson & Sandstedt, 1978), thus increasing drastically the driving force of transpiration. Hence, our estimation of the decrease of the needle water content may be considerably underestimated, especially for the exposed parts of the crown. On the other hand, the snow and hoarfrost, covering the shoots for extensive periods, may serve as protection against desiccation.

The decreased cuticular resistance of sun needles from the upper part of the tree combined with the high evaporation demand may be one of the mechanisms that lead to the well-known top-drying of conifers.

Huttunen (1978) has found great differences in air pollution effects of different provenances and even individual trees of *Pinus sylvestris* and *Picea abies*. We have noticed the high individual variability of trees with respect to their r_c , which may be one of the factors causing selective desiccation damage. This variability makes difficult to use r_c of randomly sampled self-sown trees as an indicator of the air pollution level. Further experiments with clone material are needed to evaluate this possibility.

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