

Soil drought increases atmospheric fine particle capture efficiency of Norway spruce

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Atmospheric fine particles from natural and anthropogenic sources reduce air quality and thus cause undesirable health and climate effects. Trees can act as obstacles to dispersal of particle pollution and thus remove a significant amount of particulate matter from the atmosphere. However, the significance of environmental factors in this context is not well understood. The effect of drought on fine particle capture efficiency (C_p) of Norway spruce (*Picea abies*) saplings was studied in controlled wind-tunnel experiments. The results showed that C_p of Norway spruce saplings with low soil water availability was 0.065% and well watered saplings 0.051%. Particle deposition onto all parts of the canopy was equally efficient with no difference in C_p between current- and previous-year needle generations. The results suggest that water availability significantly affects C_p of Norway spruce, which may be partly due to altered stomatal function.

Introduction

Fine particles have major adverse effects on air quality and human health (Pope and Dockery 2006). Atmospheric fine particles of diverse size categories are released from various sources, though most of the detrimental health effects are due to particulate matter with a diameter smaller than $2.5 \mu\text{m}$ ($\text{PM}_{2.5}$) (Schwartz *et al.* 1996). Road traffic, industrial processes, energy production and residential wood combustion produce most of the anthropogenic $\text{PM}_{2.5}$ in Europe and the USA (United States Environmental Protection Agency 2004, Karvosenoja *et al.* 2008). There is continuing interest to use traditional (e.g. wood)

and other forms of biofuels as energy sources in residential areas. The European Union has decided that in 2020 renewable energy sources should cover 20% of the total energy consumption. Residential wood combustion lacks proper filtering applications, thus, producing over 100-fold more fine particle emissions per watt generated than e.g. small scale industrial log-using firing plants (Ehrlich *et al.* 2007). Therefore, in the near future, particulate pollution emissions from bioenergy sources might increase.

Trees can retain particles from the air (Hori 1953, Beckett *et al.* 1998) and thus improve air quality. For example, in the Chicago city area, particle removal by trees was estimated to pro-

duce a million dollars worth of annual savings as compared with other emission controlling methods (McPherson *et al.* 1994). Coarse particles hit trees mainly because of gravitational settling and inertia, and consequently cannot follow the air stream that circulates around leaves and branches (Hinds 1999). Finer particles are mainly deposited on leaf surfaces by Brownian motion which means that when fine particles move close to a leaf surface they can turn towards the leaf and remain there. Beckett *et al.* (2000) showed that the complex shoot structures of coniferous Corsican pine (*Pinus nigra* var. *maritima*) and Leyland cypress (*X Cupressocyparis leylandii*) retained more PM₁₀ than broadleaved maple (*Acer campestre*), whitebeam (*Sorbus intermedia*) and poplar (*Populus deltoides* × *trichocarpa*). These findings were later confirmed in a field study where Corsican pine and Leyland cypress retained particles more efficiently than broadleaved species (Freer-Smith *et al.* 2005). In addition, Douglas fir (*Pseudotsuga menziesii*) reached the same particle capture efficiency level as Corsican pine in a wind tunnel experiment with a 3 m s⁻¹ wind flow, whereas the common European broadleaved species tested, oak (*Quercus petraea*), alder (*Alnus glutinosa*), ash (*Fraxinus excelsior*) and sycamore (*Acer pseudo-platanus*) showed noticeably lower capture efficiencies. Simple-structured and plain-leaved Tasmanian blue gum (*Eucalyptus globulus*) and weeping fig (*Ficus nitida*) showed even lower particle capture efficiencies than other species tested. Because of their more complex canopy structure, coniferous tree species are considered to be more efficient in capturing particles than broadleaved species (Beckett *et al.* 2000, Freer-Smith *et al.* 2004, Reinap *et al.* 2009). However, further research will be needed to confirm the factors related to efficient particle deposition in tree canopies and especially fine-particle (< PM_{2.5}) deposition efficiency needs further attention.

Particulate pollution has been shown to deposit more efficiently to leaf surfaces with increasing wind velocity (Beckett *et al.* 2000) — a circumstance whereby stomatal opening decreases (Grace 1988). It is also possible that other factors affecting stomatal regulation may have a significant effect on the particle cap-

ture efficiency of leaf surfaces. For example, in response to soil drought, plants close stomata to avoid disadvantageous water evaporation (Cornic 2000, Reynolds-Henne *et al.* 2010). Leaf surface structure including wax structure also affects particle deposition (Wedding *et al.* 1975, Burkhardt *et al.* 1995). Results of a study comparing particle deposition on silver fir (*Abies alba*), Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) showed that the amount of deposited particles was higher on structured wax areas than on flat shaped surfaces (Burkhardt *et al.* 1995). Leaf wax structure is deteriorated by aging and environmental factors such as air pollution, wind, rain- and snowfall (Grodzińska-Jurczak 1998). Thus, leaf age and environmental factors have the potential to affect stomatal function and surface characteristics that determine particle deposition.

The aim of this study was to find out if needle age and lowered water availability affect the capacity of Norway spruce (*Picea abies*) to collect fine particles from the atmosphere in a wind tunnel study. Norway spruce was selected as a test species, because it is widely distributed in boreal regions and some parts of central Europe, and as an evergreen species with long-living needles and a complex canopy structure (Beckett *et al.* 2000) it was expected to be an effective particle collector. Moderate drought stress was selected as an environmental factor, because it is and will continue to be a common stress in Scandinavia according to predicted climate warming (Alavi 2002, IPCC 2007).

Material and methods

Experimental design

An experiment was performed in February 2009 to investigate the efficiency of particulate matter capture by needle surfaces of Norway spruce saplings and the mechanisms involved. An additional testing of stomatal regulation and particle deposition at different branch locations, was done in February 2010. Studies were conducted in a straight-duct wind tunnel with a diameter of 0.50 m and a total length of 6 m. An axial fan was used to produce air flow of 3 m s⁻¹ through

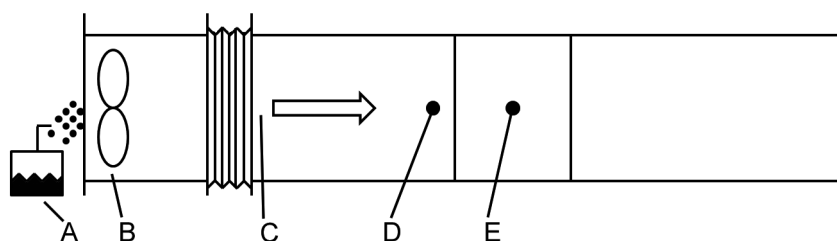


Fig. 1. A diagram of the aerosol exposure arrangements in wind-tunnel experiments. A: artificial NaCl particles were generated from aqueous salt solution and led into the airflow before the fan B for complete mixing. C: a honeycomb structure was used after the fan to balance the circulating air stream. D: particle number and mass concentrations were measured before the sapling. E: saplings were set one at a time to be illuminated in the test section for particle exposure. The arrow shows the direction of the air stream.

the tunnel. A circular air stream was balanced to turbulent flow (Reynolds number 100 000, Hinds 1999), with a honeycomb structure comprised of 18 smaller tubes with a 10 cm diameter installed next to the fan (Fig. 1). Saplings were placed one at a time into an illuminated section of the wind tunnel where they were irradiated with a greenhouse light (Philips Master Green Power 400 W) during the two-hour exposure period. Photosynthetically active radiation (PAR, LI-COR, model LI-185B, NE, USA) was $450 \mu\text{mol m}^{-2} \text{s}^{-1}$ at mid-canopy. Air temperature and relative humidity inside the tunnel were monitored during each test (Tinyview plus, Gemini Data Loggers Ltd., Chichester, UK). Air entering the tunnel was taken directly from the laboratory and exited the building at the end of the tunnel.

Artificial fine particles were produced from 10 g l^{-1} NaCl water solution by atomizing the solution with an aerosol generator (TSI 9306 Six-Jet Atomizer, TSI Inc., MN, USA) to form droplets. The droplets were fed into the wind tunnel prior to the axial fan to provide an even distribution of particles in the incoming air (Fig. 1). RH had to be below 40% during the experiments in order to be sure that NaCl particles were solid when they contacted the plants. At higher RH levels NaCl particles can be aqueous liquid droplets which have a larger size than dry particles (e.g. two times larger in diameter at 80% RH, (Joutsensaari *et al.* 2001)). Since particle size is one of the main parameters affecting their deposition, dry particles with known size were used. As RH could not be adjusted, the experiment was performed during winter, when RH is naturally low (mean RH = 11.1%, mean

temp. = $22.9 \text{ }^\circ\text{C}$). Particle mass concentration of $933 \mu\text{g m}^{-3}$ in the tunnel air was measured during every run just before the sapling with an isokinetic filter (Fig. 1) and particle number concentration of 2.5×10^5 (Fig. 2A) was monitored with a condensation particle counter (CPC 3022A, TSI Inc., MN, USA). Geometric mean diameter of the mass size distribution of the particles, $0.7 \mu\text{m}$ (geometric SD = 3.0), was measured with a cascade low pressure impactor (Dekati Low Pressure Impactor, Finland) three times during the test series (Fig. 2B).

Plant material and growing conditions

Two-year-old Norway spruce (*Picea abies*) saplings were provided by the Finnish Forest Research Institute Suonenjoki research unit in the summer of 2008. Saplings were re-potted in two-liter pots filled with a 2:1 mixture of peat (PP6, Kekkilä, Finland) and sand. During repotting, saplings were fertilized with 1 g of slow releasing N:P:K (9:3.5:5) fertilizer. After repotting, the saplings were maintained outdoors at the research garden of the University of Eastern Finland (Kuopio), were watered during dry periods and fertilized once a week with 0.1% N:P:K (11:4:25) fertilizer. Saplings were dehardened and allowed to complete new shoot growth in a greenhouse for two months before experiments. Saplings were three-years-old in the first experiment and four-year-old in the additional experiment. Prior to experiments, plants were transferred to growth chambers where light and temperature were adjusted to simulate average

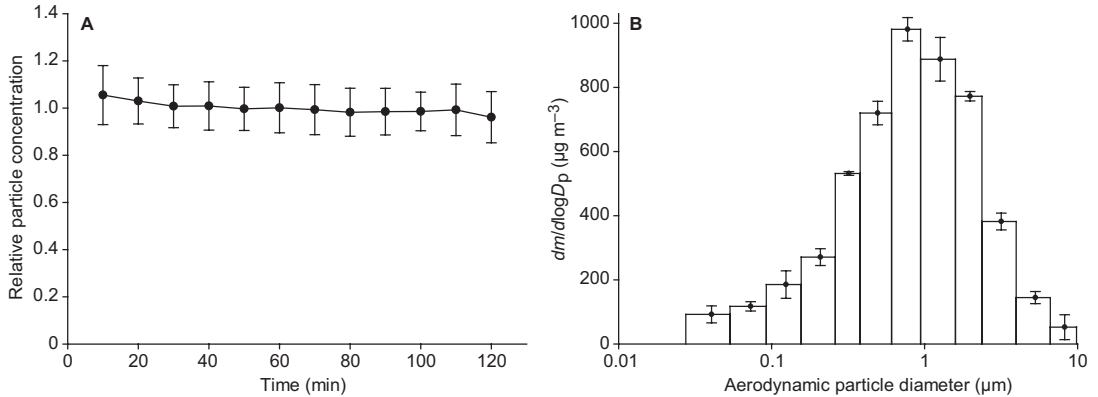


Fig. 2. (A) Relative particle number concentration (mean ± SD, $n = 10$) throughout the exposure period (120 min). Measured concentrations were divided by the average concentration of all the exposures. (B) Mass size distribution of the particles (mean ± SD, $n = 3$) with an aerodynamic diameter determined with the impactor.

June conditions in Finland. The light period in chambers started at 04:00 and reached a maximum level ($375 \mu\text{mol m}^{-2} \text{s}^{-1}$) at 06:00 which continued until 18:00. At 18:00, the light level started to decline until complete darkness was reached at 20:00. Chamber temperature was 12°C during night time (00:00–04:00) and linearly rose up to 19°C between 04:00 and 10:00. The temperature was maintained at 19°C until 18:00 and then decreased linearly to 12°C between 18:00 and 00:00. Relative air humidity (RH) was constantly 52%.

Effects of water availability

In the first experiment, capture efficiency of fine particles was determined with five replicates of well-watered Norway spruce saplings and five replicates exposed to mild drought stress. Well watered and drought stressed treatments were generated by splitting saplings into two groups; the first group was watered if soil moisture decreased under 20% (measured mean 23%) whereas the second group was exposed to drought stress (watering limit 10%, measured mean 11%). Soil moisture levels were controlled daily (ThetaProbe, Delta-T Devices Ltd., Cambridge, UK). The first saplings were used after 12 days of drought treatment and the last ones after 21 days of drought treatment. There were also five control saplings for each treatment that underwent the same watering regimes but were not exposed to

particles, thus providing data on the background particle levels. Saplings were selected for testing in a planned order so that well-watered, drought-stressed and control saplings were represented during a certain time of day, but within the groups saplings were picked randomly.

Stomatal conductance (g_s) and transpiration of saplings were measured (LI-COR, model LI-1600 Steady state porometer, NE, USA) from one current-year lateral shoot per sapling using a cylindrical chamber (LI-1600-07) before and after every run in the wind tunnel. Conductance and transpiration measurements were corrected by total needle area. After a 2-h exposure period in the wind tunnel, measured shoots were detached, dried and needles scanned using a flatbed scanner HP Scanjet 3670. The projected needle (leaf) surface area (PLA) of the scanned images was determined with the ImageJ program (ImageJ, U.S. National Institutes of Health, Bethesda, Maryland, USA). After Sellin (2000), the total needle (leaf) area was determined as follows:

$$\text{TLA} = 2.45e^{0.347D_1^{2.02}} \times \text{PLA} \quad (1)$$

where TLA is the total leaf area, D_1 is the minor needle width of the cross-section (anatomical parameter, mm) and PLA is the projected leaf area (cm^2). For D_1 determination, sections from the middle of the five randomly selected, fresh needles per shoot were cut with a razor blade and digitally photographed under a light microscope (Zeiss axiolab). Five shoots were scanned twice,

first fresh and then after drying to determine how much needle area decreases after drying. PLA values were corrected by the size reduction factor of 1.18. Minor needle width (D_1) and PLA were determined using tools within the ImageJ software.

For scanning electron microscopy (SEM), three needles from C and C + 1 shoots were attached to a double-sided tape and stored in desiccators at room temperature (+21 °C). Dry needles were coated with an approximately 50 nm gold-palladium layer (Automatic Sputter Coater B7341, Agar Scientific Ltd., Stansted, UK). Three needles from each sapling were examined at 200× magnification using SEM (Philips XL30 ESEM-TMP, FEI Company, Holland) and digitally photographed. Stomatal density was determined from these pictures with the ImageJ program by measuring the average number of stomata in an approximately 1100- μ m-long section of a needle. In addition, three randomly selected stomata per needle were photographed at 4000× magnification. Thus, nine photographs per needle generation per sapling were taken, yielding a total of 180 photographs. Epistomatal wax structures were evaluated using a classification method designed by Trimbacher and Eckmüller (1997). Five classes of wax accounting for coverage and morphology were used:

Class 1: well-preserved wax structures where the stoma area is fully covered with single wax filaments.

Class 2: wax filaments are aggregated in clusters on a total of 10% to 25% of the stoma area.

Class 3: wax clusters and more planar shapes cover 25% to 50% of the stoma area

Class 4: a total of 50% to 75% of the stoma area is covered by the planar and clustered wax structures.

Class 5: stoma area is almost completely covered by an amorphous wax layer.

Medians of classes per needle generation and sapling were calculated. Each of the nine photographed stomata was scored for absence (0) or presence (1) of salt particles, and the proportion of stomata with salt particles was calculated.

After sampling for SEM, samples were collected to analyze the amount of captured NaCl;

20 branch pieces, each 1-cm long, were cut from different sides of the saplings and C and C + 1 shoots put into separate beakers. Needles and stem were not separated, because capture efficiency of stems is known to be less than 1% of the total capture efficiency (Freer-Smith *et al.* 2004). Branch pieces were rinsed for 10 minutes with 40 ml of ion exchanged water in a shaker (Certomat S, type 886072/6, UK). After the washing procedure, a 10-ml sample of the water was filtered through a syringe filter (pore diameter 0.40 μ m) and collected in a sample tube. Chloride ion concentrations in the water were analysed by ion chromatography (Dionex DX-120 with AS40 autosampler, USA). Chloride amount of control samplings (background particle level) were subtracted from samples with particle exposure. Washed branch pieces were oven dried (60 °C, 3 days) and the needle area was determined as described above.

The unitless ratio of particle capture efficiency (C_p) of Norway spruce was calculated with the following equation that Beckett *et al.* (2000) showed to be functional in wind tunnel studies:

$$C_p = \frac{N}{X_u A} \quad (2)$$

where N is the mass of NaCl deposited on the needle surface in a certain exposure time, X_u is a function of the NaCl mass concentration (c) in air, the duration of the exposure (t) and average wind speed (u), i.e. $X_u = ctu$, and A is the total needle area (TLA) (Reinap *et al.* 2009). Thus the value of C_p is the proportion of particles deposited on the needle surface to all the particles available for capture estimated from the total surface area of the needles (*see* Reinap 2009).

Stomatal regulation in the wind tunnel

Our first experiment showed that stomatal conductance decreased in the wind tunnel (Table 1). It was not clear whether the stomatal closure was caused by wind or change in relative humidity. Relative humidity in the wind tunnel was very low (RH% < 15), while in the growth chambers it was 52%. Therefore, it was necessary to find how fast this change in humidity-

affected stomatal conductance. These measurements could not be performed during the previous experiment, because the tunnel fan had to be stopped for measuring stomatal conductance which would have disturbed particle collection. Instead, different saplings were used to examine stomatal function in the wind tunnel. Six well-watered four-year-old Norway spruce saplings (from the same batch as in the first experiment, but one year older) were grown in two chambers. The first chamber was adjusted to have a 19 °C day temperature and a relative humidity of 52%. A second-chamber ran the same program but with relative humidity reduced to 24% (a technical minimum). Saplings were placed one at a time in the wind tunnel and g_s of the C needles was measured sequentially at the starting point and then after 5, 10, 15 and 30 minutes. Wind velocity of 3 m s⁻¹ was used.

Particle capturing on needle surface in relation to wind direction

The particle capturing efficiency of needle surfaces in relation to wind direction was tested in

2010 using 12-well-watered 4-year-old Norway spruce saplings, which were exposed to the same conditions in the wind tunnel as those used in the 2009 experiment. After treatment, needle samples of mixed generations were collected from both the front and back sides of the wind-exposed trees. The percentage of the total particle capture of the front and back sides (Cs) was calculated as follows:

$$Cs = \frac{N_x}{N} \times 100 (\%) \quad (3)$$

where N_x is the mass of NaCl deposited on the needle surface at either front or back sides of the sapling in a certain exposure period.

Statistical analyses

Statistical analyses were conducted using the SPSS PASW 18.0 program (SPSS Inc., Chicago, IL, USA). Assumptions necessary for the variance analysis were tested with the Shapiro-Wilk test (normality of the data) and Levene's test (homogeneity of variances). Stomatal conductance data from the 2010 experiment were

Table 1. Soil moisture and stomatal parameters of the well watered and drought stressed Norway spruce saplings (mean ± SD, $n = 5$ except ^a $n = 4$ and ^b $n = 2$. Stomatal conductance and transpiration were measured from current (C) shoots at the beginning (A) and at the end (B) of the 2-h exposure. Stomatal density, surface waxes of the stoma and frequency of particles on the stomatal surface were analysed both from current and previous year (C + 1).

	Well-watered	Drought	Significance of differences
Soil moisture (%)	23 ± 4	11 ± 2	$p < 0.001^1$
Stomatal conductance (cm s ⁻¹)			
A	0.08 ± 0.03	0.06 ± 0.03	ns ²
B	0.02 ± 0.01 ^a	0.03 ± 0.02 ^b	ns ²
Transpiration (µg cm ⁻² s ⁻¹)			
A	1.35 ± 0.19	0.94 ± 0.20	ns ²
B	0.33 ± 0.06 ^a	0.50 ± 0.22 ^b	ns ²
Stomatal density, (number per mm ⁻²)			
C	8.7 ± 0.5	7.8 ± 1.3	ns ^{3*}
C + 1	8.9 ± 0.7	8.8 ± 1.3	
Wax class [median (min, max)]			
C	1 (1, 2)	1 (1, 2)	ns ^{4*}
C + 1	1 (1, 2)	1 (1, 2)	
Stomata with salt particles (%)			
C	27 (20)	62 (33)	$p = 0.063^{5*}$
C + 1	27(10)	47 (25)	

¹ One-way ANOVA, ² independent samples *t*-test, ³ Mann-Whitney, ⁴ Wilcoxon, ⁵ mixed models, * data combined for statistical testing if no difference between year growth.

square-root transformed ($\sqrt{x} + \sqrt{x+1}$, Zar 1999) to fulfill the ANOVA assumptions.

The main effects of drought, needle age and their interaction on fine particle capture efficiency and quantitative stomatal density parameters of Norway spruce saplings under different soil-water treatments were tested with repeated measures ANOVA with needle age as a within-subject factor (i.e. repeated factor, C and C + 1 needles collected from the same tree) and drought as a between-subject factor. Stomatal conductance and transpiration were tested with an independent samples *t*-test. Differences in epistomatal wax classes between treatments were tested with the Mann-Whitney *U*-test and needle age with the Wilcoxon test. Settling of particles on needle surfaces in relation to wind direction (front-back) was tested with a paired *t*-test. The change in stomatal conductance over time of saplings from the two humidity chambers was tested by two-way ANOVA, with time and humidity as fixed factors. Sapling was included as a random factor. Standard repeated measures ANOVA could not be used because of the incomplete measurement series. Four Helmert contrasts, which compare the first sampling point with the average of the later sampling points was used to determine the time points at which changes in stomatal conductance occurred. In all statistical analyses differences were considered significant at $p < 0.05$. All the results are given in the form of mean \pm SD if not otherwise stated.

Results

Effects of needle generation and water availability

Efficiency of particle deposition onto needle surfaces was similar in both C and C + 1 needle generations (Fig. 3). Wax structure was also similar in both needle generations (Table 1). Overall, the stoma areas were covered by a single filament structured wax layer (median class 1) with some saplings having wax filaments clustered on small areas of stomata (median class 2). Needle age did not affect particle prevalence on the epistomatal area (Table 1). Stomatal density did not

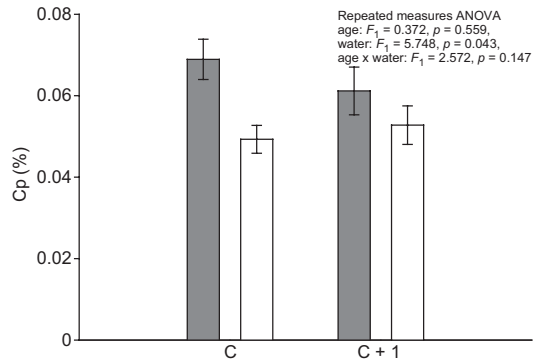


Fig. 3. Particle capture efficiency (C_p) (mean \pm SE, $n = 5$) of C and C + 1 spruce needles. White bars: well watered saplings, grey bars: drought-stressed saplings.

differ significantly between C and C + 1 needles either (Table 1).

Stomatal conductance was 25% lower and transpiration 30% lower in the drought-treated saplings (Table 1), but the differences were not significant either at the start or at the end of the test run. Drought significantly increased particle deposition onto needle surfaces: C_p of the Norway spruce saplings with low soil-water availability was 0.065% and well watered saplings 0.051% (Fig. 3). The effect of drought was independent of needle age. In addition, salt particles observed by SEM were insignificantly more frequent on needles exposed to drought (Table 1). This effect of drought was not significantly modified by needle age. Drought did not affect morphology and coverage of epicuticular waxes or the stomatal density (Table 1). All the salt particles examined by scanning electron microscopy (Fig. 4) had similar shape on needles from drought-treated and well-watered spruce saplings.

Stomatal function and the effect of branch position

The function of stomata in the wind tunnel was tested with saplings grown in 24% and 54% relative air humidity. As expected, stomatal conductance was higher, however not significantly, at high RH than at the low RH ($0.03 \pm 0.01 \text{ cm s}^{-1}$ and $0.02 \pm 0.01 \text{ cm s}^{-1}$, respectively). Stomatal conductance decreased similarly to 0.01 cm s^{-1}

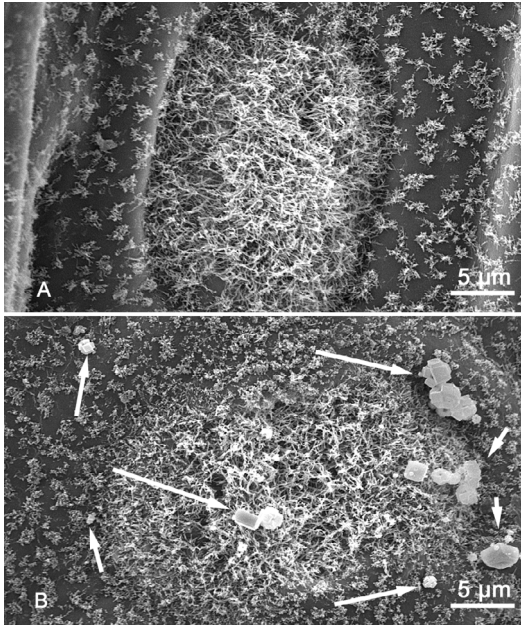


Fig. 4. SEM of the stomata of current-year needles of (A) well-watered and (B) drought-treated Norway spruce saplings. Note similar stomatal wax layers in A and B, and a greater frequency of salt particles (arrows) in B.

level in both treatments. The first two Helmert contrasts (0 min. *vs.* later; 5 min. *vs.* later) were significant (Helmert contrast: $F_1 > 39.847$, $p < 0.05$), but the latter two contrasts (10 min. *vs.* later, 15 min. *vs.* later) were not significant (Helmert contrast: $F_1 > 0.004$, $p > 0.05$) which showed that stomatal conductance decreased to the constant level about 10 minutes after saplings were placed inside the wind tunnel.

When studying branches in different positions, we found that $51\% \pm 17\%$ of the particles deposited to the side of the sapling that faced the wind and $49\% \pm 20\%$ of the particles deposited to the opposite side ($n = 6$). This small difference was not statistically significant.

Discussion

Particle capturing efficiency of Norway spruce

To our knowledge, this is the first study of fine particle capture efficiency by Norway spruce,

although Burkhardt *et al.* (1995) described the location of PM_{10} deposited on Norway spruce needles. In our experiments, the average particle size remained smaller than reported by others focused on particle capture efficiency of trees (Beckett *et al.* 2000, Reinap *et al.* 2009). Most of the particles were PM_{10} particles and almost all were $PM_{2.5}$ particles, which are classified as fine particles and are thus expected to have the most harmful health effects (Pope and Dockery 2006). C_p has only been published for a few other coniferous species studied in wind-tunnel experiments. Beckett *et al.* (2000) tested the particle capture efficiency of Corsican pine and recorded C_p of over 0.14% at the wind speed of 0.7 m s^{-1} , which is two times higher efficiency with four times lower wind speed than measured here. In the second experiment, where Beckett *et al.* (2000) used the same wind speed as we did here but with coarser particles, the C_p was over five times higher than we report. Freer-Smith *et al.* (2004) determined C_p separately for stem and needles of Douglas fir, but stem C_p values constituted only 0.7% of the total capture efficiency of 0.426%. Particle capture efficiencies measured for broad-leaved species at $3\text{--}5 \text{ m s}^{-1}$ wind speeds varied from 0.005% to 0.28% (Beckett *et al.* 2000, Freer-Smith *et al.* 2004, Reinap *et al.* 2009). It should be noted that capture efficiencies for coarser particles are generally higher than for fine particles and that higher wind speed increases particle capture (Hinds 1999, Beckett *et al.* 2000). As discussed by Reinap *et al.* (2009), also streamline posture of a sapling affects particle capture efficiency which is consistent with our results showing equally efficient particle collection on front and back sides of static spruces.

Separately collected C and C + 1 shoots of Norway spruces showed no variation in the particle load deposited on their surfaces. Burkhardt *et al.* (1995) reported greater particle deposition on surfaces of current-year than older needles and that this was due to a greater amount of epistomatal surface wax. In this study, C and C + 1 needles had equally well-preserved epistomatal wax structures and similar stomatal density, which is in line with the similar particle capture efficiencies measured. However, caution is needed when applying these results to field con-

ditions. Many pollutants and environmental factors can cause changes in surface wax morphology that can alter the particle capture efficiencies of different needle generations (Burkhardt *et al.* 1995, Viskari 2000). The saplings in this study had mainly grown in optimal greenhouse conditions, and natural deterioration of surface waxes had clearly not occurred.

Water availability affects the capture of particulate matter

Capture efficiencies of Norway spruce that had reduced water availability were higher than those of spruces with adequate soil moisture. We do not yet fully understand the reasons for the difference, but diffusiophoresis driven by water molecules (Hinds 1999) may explain some of it. Diffusiophoresis is the result of a water vapor concentration gradient causing a net transport of particles in the direction of the lower vapor concentration (away from the transpiration surface). Fine particles (aerosols) $< 1 \mu\text{m}$ tend to drift towards areas where their concentration is lower (Brownian diffusion), but water vapor coming through stomata pushes particles away from the stoma area (diffusiophoresis). Furthermore, evaporation of water also reduces deposition of particles by other mechanisms, e.g., sedimentation, impaction, interception, thermal and electrical forces. Water evaporation may explain some of the differences in measured C_p between spruce saplings with high and low soil moisture, because saplings with higher soil moisture evaporate more water through their stomata thus preventing particle deposition onto the surfaces of needles (Hinds 1999). The effect of diffusiophoresis was supported by the SEM analysis, which showed more salt particles on the epistomatal areas of drought-treated saplings. However, salt particles might have dissolved into water transpiring from stomata of the well-watered saplings, but this salt should have recrystallized when needles were dried for SEM, which was not observed. Thus, diffusiophoresis is a more likely explanation, although changes in the surface structure of needles due to water vapor might also have some effect on particle capture. Burkhardt *et al.* (1995) showed that

fine particles preferentially deposit on stomatal regions. In this study, the number of stomata was not altered and hence this does not explain the differences in capture efficiency. Water evaporation, or any other process regulated by stomata, must have occurred at the beginning of each test period, because saplings with higher soil moisture only keep their stomata more open than drought treated saplings during the first 10–15 minutes in the wind tunnel. The reason for stomatal closure in the wind tunnel may be that the wind speed and decreased humidity, both increase transpiration and thus induce stomatal closure (Kramer and Kozłowski 1960). It is also possible that captured salt particles at the beginning of the test run increased surface roughness, and thus induced more efficient deposition of particles onto the drought-treated saplings (cf. Burkhardt *et al.* 1995).

In conclusion, low soil water availability increases particle capture efficiency of Norway spruce, but the exact mechanism remains unclear. The most likely explanation would be that decreased stomatal conductance due to soil drought reduces the amount of evaporating water enabling greater amount of fine particles to be deposited onto needle surfaces. Higher particulate capture may be environmentally significant when trees are adapting to changing climatic conditions, including increased incidence of drought (IPCC 2007). However, further research with different conditions is needed to specify and confirm detailed mechanism of altered particle capture efficiencies of trees growing in different soil moisture levels.

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