Project Number 282910

ÉCLAIRE

Effects of Climate Change on Air Pollution Impacts and Response Strategies for European Ecosystems

Seventh Framework Programme

Theme: Environment

D 11.6 Parameterization of water use efficiency for model use under conditions of particle pollution

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CO	Confidential, only for members of the consortium (including the Commission Services)	☐

1. Executive Summary

Deposited aerosols on the surface of plant leaves have usually been considered inert, but recent measurements have shown that especially hygroscopic leaf surface particles may interact with plant water relations and may influence plant-atmosphere exchange of water vapor, CO_2, and other trace gases. Such interactions link aerosol pollution with plant drought tolerance, and can thus aggravate drought effects of climate change. Particle/plant interactions may also create feedbacks with relevance for models of biosphere/atmosphere exchange. Possible effects on plant water use efficiency WUE (i.e. the amount of carbon acquired per unit of water lost) would affect biomass production and the water cycle with likely relevance on regional and larger scales.

We studied the water relations of pine, beech, and sunflower plants under the influence of different particle regimes and by measurements of sap flow, gas exchange, and carbon isotopes. Particles were either excluded by air filtration, accumulated by rainfall exclusion, or added by singular events of spraying with salt solutions. We also studied the influence of vapor pressure deficit (vpd), as both plants and particles are known to react to changes of humidity. The detection and reaction of leaf surface particles as well as the spatial expansion of leaf surface particles under changing humidity was investigated, using an environmental scanning electron microscope (ESEM).

WUE generally decreased with the long term accumulation of particles on leaves, as measured by carbon isotope discrimination. By singular spraying with salt solution, no clear effects on WUE were observed. Although gas exchange measurements repeatedly showed increased transpiration after salt spray application, plants can stabilize WUE by reducing stomatal aperture. In dry conditions and on the long term, such reductions of stomatal conductance may reduce carbon uptake and could even lead to 'carbon starvation'. However, given the ongoing and expected increase of ambient CO_2 concentrations, reduced stomatal conductance may not be critical as long as stomata are not completely closed.

Particles on leaf surfaces are a so far underestimated and understudied environmental factor. The effects of particles on WUE depend on the concentration of these particles, on the isohydic/anisohydric behavior of the plant, and on vpd, and are thus difficult to predict. It is presently not possible to parameterize particle influence on WUE as was originally intended, due to the difficulties to determine long-term particle accumulation and the reported WUE stabilization by stomatal adjustment. On the other hand, our measurements of minimal epidermal conductance ($g_{min;}$ see Eclaire deliverable D 11.5) indicate that particle pollution may decrease plant drought tolerance and together with increasing drought periods may be a serious and so far undervalued cause of forest damage. g_{min} determination is based on closed stomata. Compared to WUE, g_{min} is therefore a better suitable parameter for defining critical particle pollution loads for plants.

2. Objectives:

- Evaluate the influence of leaf surface particles on the transpiration and water use efficiency (WUE) of pine, beech, and sunflower.
- Evaluate the influence of the origin and type of leaf surface particles
    - Long-term, ‘ambient’ deposition (assessed by aerosol exclusion and rainfall exclusion)
    - Short-term deposition by defined amounts of salts from salt spray application.
- Evaluate the effects of different salts, partly in combination with surfactants, regarding known effects of surface tension.
- Evaluate the impact of vapor pressure deficit (vpd) on the aforementioned effects, as vpd may affect both plant gas exchange as well as particle deliquescence.
- Study the expansion of leaf surface particles within the environmental scanning electron microscope (ESEM)
- Describe and parameterize the influence of specified particles on WUE.
- Suggest possible measurements for defining thresholds for particle effects on plants.

3. Activities:

Experiments were carried out in 2012 and 2013, using Scots pine (*Pinus sylvestris* L.), European beech (*Fagus sylvatica* L.), and sunflower (*Helianthus annuus* L.). Scots pine saplings (1+2 yrs), beech saplings (2 yrs), and sunflowers were grown in well watered soil. Sunflowers were also grown in hydroponic solution. The plants were grown in ventilated greenhouses (supplied with ambient air: AA or filtered air: FA) as well as outdoors under a plastic rainout shelter (OD) or unprotected from rain (OD-rain). The air in the AA greenhouse usually contained 10,000-20,000 particles cm^{-3}. The air in the FA greenhouse contained less than 100 particles cm^{-3}. The rainout shelter allowed free air flow from the sides and was situated on the university campus close to the greenhouses. Relative humidity (RH) and temperature were measured continuously in all environments and were used to calculate vpd. Photosynthetically active radiation (PAR) under the rainout shelter was 10-15 % higher than in AA/FA greenhouses. The ozone concentrations (measured by “Aeroqual Ozone Monitor Series 500") did not show any differences. The ion amounts present on AA, OD and OD-rain pine needles was determined by thoroughly rinsing a known needle surface area with a specified amount of deionized water, and measuring the ion concentrations using a pH electrode, ion chromatography (Cl, NO3, SO4), atomic absorption spectrometry (Mg), flame photometry (Na, K, Ca), and continuous flow analyzer (NH_4^+).

In addition to the long-term particle regimes, the trees were also sprayed once or twice per year by an automated spraying system (“Phytron Electronic”, developed by Agricultural Technology Institute, University of Bonn). The whole plants were sprayed with solution droplets having volumes of 0.5 - 5 µl until water holding capacity was exceeded, i.e. water had started dripping from the leaves or needles. Application to the soil was avoided by covering the pot and the first internodes header shoot by a thin plastic bag during spraying. Plants were sprayed with different salt solutions, some of them also containing an adjuvant (RSO5; 1g/L). Scots pine was sprayed twice in 2012 (JD 166, 206) by automated spraying with 50 mM salts ($(NH_4)_2SO_4$, NaCl, $NaNO_3$) ± RSO5 (1g/L). Beech seedlings were only sprayed once (JD 206) with 100 mM salt $(NH_4)_2SO_4$ with and without adjuvant in 2012. In 2013, plants were only sprayed once using 25 mM salt solutions: pine ($(NH_4)_2SO_4$, $NaNO_3$, NaCl,) with and without adjuvant; JD 155) and beech, ($(NH_4)_2SO_4$), $NaNO_3$ with and without adjuvant; JD 158). Sunflower plants were treated by hand sprayer, using 25 mM salt solutions ($(NH_4)_2SO_4$), KI; JD 158). All spraying treatments were accompanied by control treatments with deionized water.

Plant water relations were measured using $\delta^{13}C$ (pine, beech;sunflower, 2012 – 48 days after last treatment, 2013 – 75 days after trt), gas exchange (pine, beech 2012 (8 – 14 d after trt), (pine (35 d after trt), beech (49 d after trt, sunflower 2013 (4-7 d after trt)), osmotic potential (pine, beech, 2012), leaf area (pine, beech, 2012), leaf area related sapflow (2012 only in pine; 2013 pine, beech, sunflower) which have been described in detail previously (Pariyar et al. , 2013, Burkhardt and Pariyar, 2014). Photosynthesis (A), transpiration (E), and stomatal conductance (gs) to water vapor were determined by using a porometer (Li-cor 6400 portable photosynthetic system, LI-COR, Inc., Lincoln, Nebraska, USA). Water use efficiency was calculated as WUE = A/E. Sap flow of sunflowers was measured by a dynagauge system (32A, Dynamax Inc., Houston, USA) which is based on an energy balance method derived from a constant heat source (dynagauge) by which the shoot is mantled. The osmotic potential ($\Psi\pi$) was measured with a cryoscopic osmometer (Osmomat 030, Gonotec GmbH, Germany) by determining the freezing point depression. For further details see Pariyar et al. (2013). Due to limited capacity of the dynagauge system, the sap flow of the different treatments was usually recorded only by one sap flow device, respectively. Depending on the type of measurement, the other parameters were assessed using between 3 and 10, using different plants as repetitions.

Statistical analysis was performed using one way analysis of variance (one way ANOVA). The significance was estimated between the different treatment groups by comparing them in all pair wise comparisons using Student-Newman-Keuls (SNK) and Holm-Sidak Test. Wenn these test failed to analyse the pair wise comparisons due to the different sampling numbers, Dunn´s methods was used.

4. Results:

4.1 Leaf surface chemistry and ESEM

The washing solution from Scots pine needles showed considerably higher amounts of particles on sheltered outdoor plants (OD; 36.6 µg cm^{-2}), compared to ambient air greenhouse plants (AA; 2.6 µg cm^{-2}). Those plants standing outdoor but exposed to rainfall (OD-rain) showed a particle loading of 1.2 µg cm^{-2}. These differences were observed for all analyzed ions (Fig. 1).

It is likely that OD plants were receptors of large (> 10 µm diameter) particles with predominant gravitational deposition, probably from disturbed soils and activities from the experimental agricultural area nearby. Such large particles presumably did not pass the ventilation system into the greenhouse and therefore did not deposit to AA plants. On the other hand such large particles are easily removed by precipitation, leading to lower concentrations in OD-rain samples.

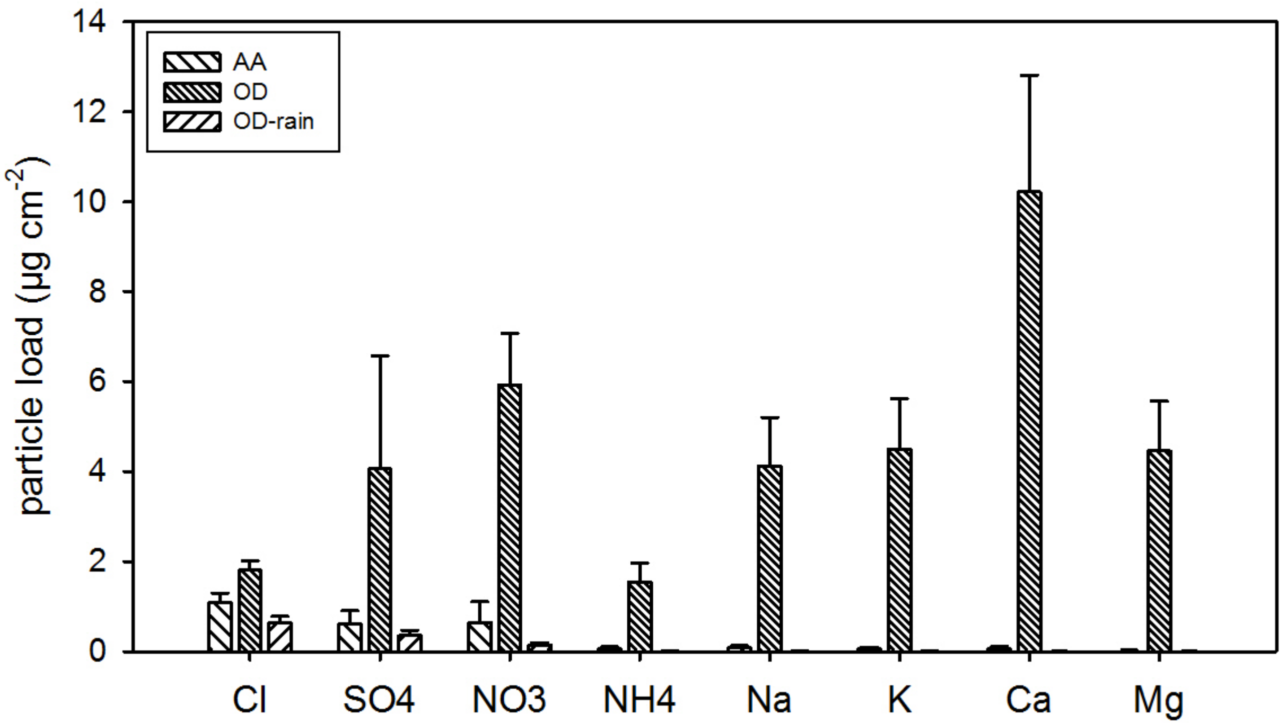

Fig. 1 Ion amounts from washing solutions, calculated as particle load per needle surface (µg cm^{-2}). Plants from ambient air greenhouse (AA), from outdoors, but sheltered from rain (OD), unsheltered plants from outdoors and exposed to rain (OD-rain).

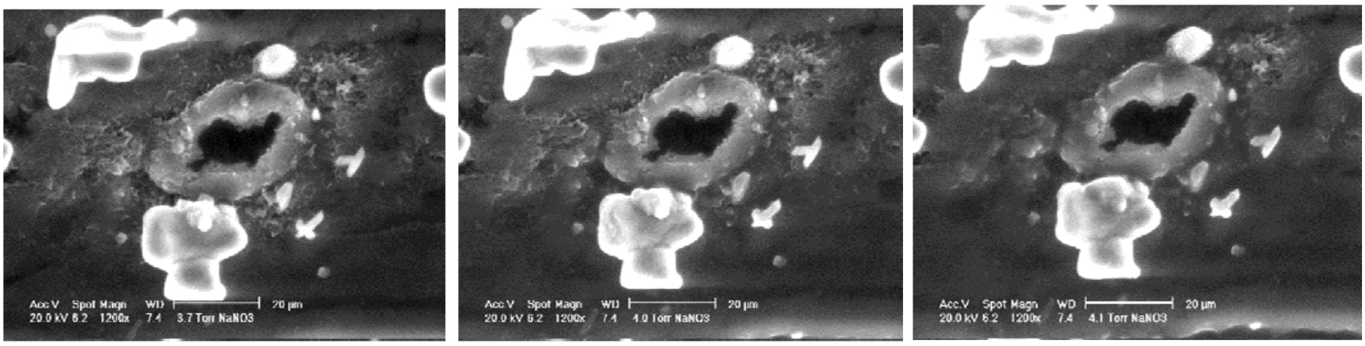

Fig. 2: NaNO3 particles becoming deliqescent on a pine needle, viewed by an environmental scanning electron microscope (ESEM), under increasing humidity (appr. 65 to 75% RH). Apart from small changes at the large particles, increasing wetness can also be noted in the area in between which becomes more amorphous.

The reported overall amounts of particles are in the range of earlier reported values (Burkhardt, 2010; Saebo et al., 2012). It is noteworthy that they equal or even exceed the amount of needle wax. In addition, particles on leaf surfaces are often difficult to recognize, because they become deliquescent from high humidity caused by leaf transpiration or ambient air, thus losing their crystalline form. Even after drying out, they quite often do not form new crystals, but amorphous salt crusts (Fig. 2).

They are only recognizable when they cause condensation within the ESEM significantly below 100% RH due to their hygroscopicity. A useful tool to detect this dynamic behavior under changing humidity is the visualization in videos (Burkhardt and Hunsche, 2013, Burkhardt and Pariyar, 2014). As a consequence we therefore argue that the repeatedly reported 'wax degradation' phenomenon might come from such amorphous structures formed by deliquescent aerosols, and that the amorphous appearance in scanning electron microscopes (working at high vacuum without the option to increase humidity as in the ESEM) has been repeatedly misinterpreted in the past.

4.2 Carbon isotope measurements

The carbon isotope measurements of beech, pine, and sunflower reflected the differences between the different growth environments. WUE was significantly lower for OD grown plants of pine compared to AA plants. Lower WUE was also observed for sunflower AA plants compared to FA plants (Fig. 3).

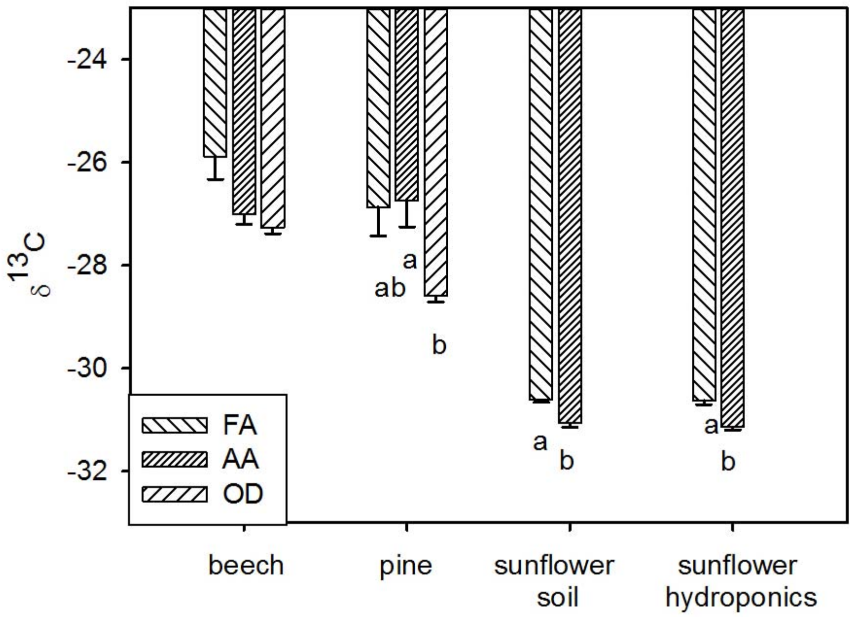

Fig. 3 Carbon isotope discrimination for beech, pine, and sunflower plants growing in particle free (FA) or ambient air (AA) ventilated greenhouses or below a rainout shelter (OD).

The $\delta^{13}C$ measurements from samples taken about two months after (the last) singular spraying with salt solution did not show significant differences compared to the control (Fig. 4).

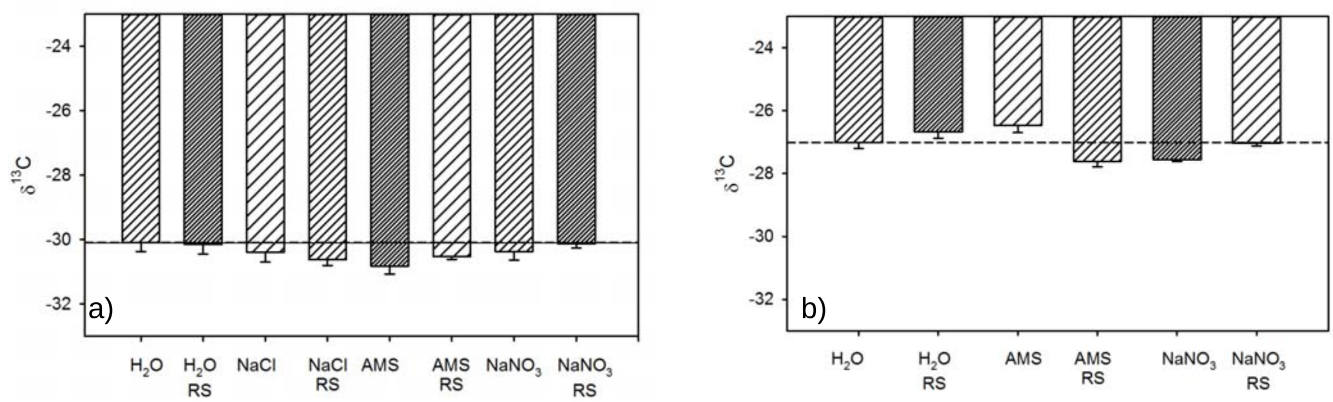

Fig. 4: *Carbon isotope discrimination for a) pine needles growing in ambient air greenhouse, one month after the last of two treatments with 50 mM salt solution and b) beech leaves growing in ambient air greenhouse, one month after a single treatment with 25 mM salt solution. RS: Combination of the salt solution with adjuvant RS. AMS: ammonium sulfate.*

4.3 Water potential, osmotic potential

The midday water potential of sunflowers grown in FA environment was higher (less negative) than for plants from the AA greenhouse for soil as well as for hydroponic plants, while both were indistinguishable in pre-dawn water potential (Fig. 5a). The osmotic potential of FA sunflowers was also higher than of AA sunflowers (Fig. 5b).

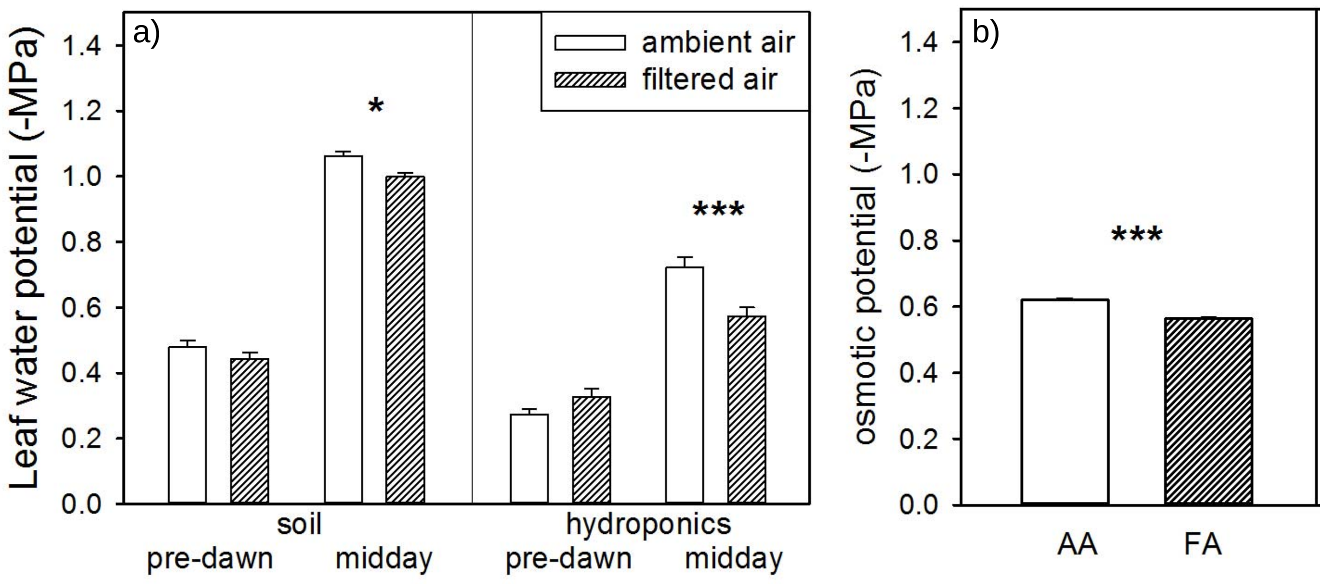

Fig. 5 a) Water potential of AA and FA sunflowers plants in soil and nutrient solution b) Osmotic potential of hydroponically grown sunflower plants (Pariyar et al., 2013).

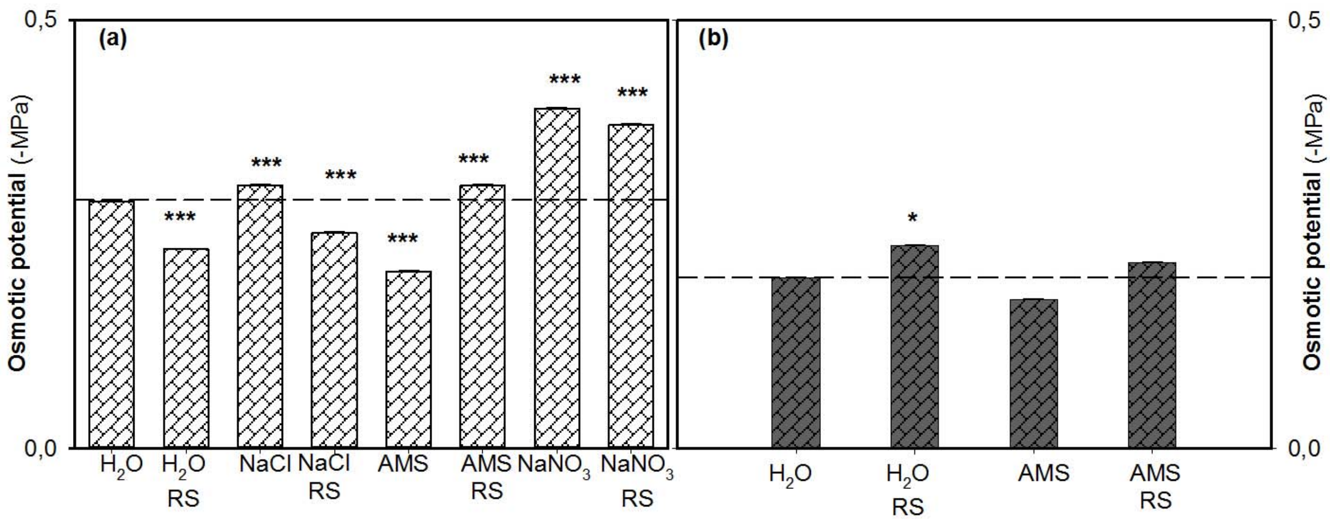

Fig. 6: a) Osmotic potential of AA a) pine and b) beech plants, as influenced by spraying with salt solutions

For single treatments with salt solutions, different effects in osmotic potential were observed. While the osmotic potential was higher for treatments with water and adjuvant for both, pine and beech, it increased for pine after spraying with NaCl + RSO5 and for ammonium sulphate (AMS), but decreased after spraying with AMS + RSO5, $NaNO_3$, as well as $NaNO_3$+ RSO5 (Fig. 6a,b).

4.4 Sap flow

Measurements of sap flow were in most cases not repeated simultaneously (n=1) due to restricted availability of the necessary devices. The amount of sap flow determined by the dynagauges was related to the total leaf area of the plant.

There were systematic differences between the sap flow of pine and beech seedlings which are demonstrated in Fig. 7. The sap flow of beech seedlings reacted to vapor pressure deficit (vpd) in a almost linear way even at very high vpd's (Fig. 7a). The sap flow of pine seedlings also reacted to increasing and decreasing vpd, but usually after midday this reaction was less strong than in the morning, leading to disproportional behavior of transpiration (Fig. 7b). This behavior was observed for almost all types of short-term or long-term particle treatment. In a month-long evaluation of sap flow dependence on vpd, the hourly values of beech were strongly correlated with vpd, resulting in high correlation coefficients with r^2, usually exceeding 0.7 (Fig. 8a). For pine seedlings, the correlation coefficient was lower than 0.3 for all treatments (Fig. 8b).

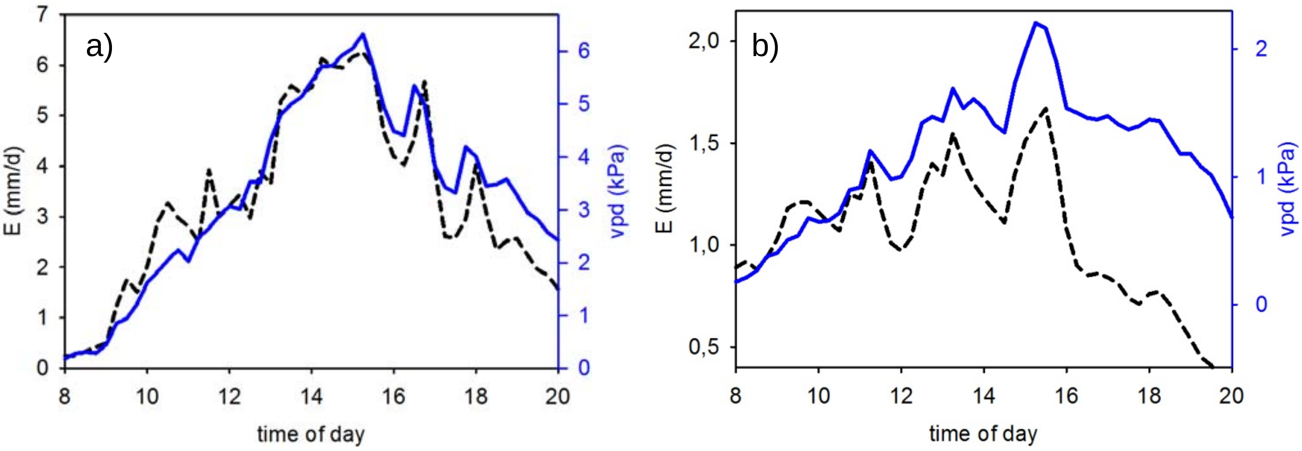

Fig. 7: Typical daily, species-specific transpiration behavior (black, slashed lines) and the corresponding vpd course (blue, solid lines, right axis), measured by sap flow (15 minutes values). a) beech seedling with strong coupling throughout the day. b) pine seedling, showing decreased coupling in the afternoon.

It is very likely that this behavior of pine seedlings is due to partial stomatal closure around midday, which seems to happen even at relatively low vpd's < 2 kPa and almost independent of particle load (Fig. 8b). This behavior confirms the known isohydric behavior of pine species (Klein et al., 2011).

On the other hand, the sap flow measurements indicate that even at high vpd, stomatal conductance of beech seedlings was almost unrestricted (Fig. 8). Again, this was similar for almost all particle environments and singular salt solution treatments. There was, however, a differentiation in the vpd response, as reflected in the slope (Fig. 8a). While in most cases, there was a slope of 0.3 mm d^{-1} kPa^{-1}, it was triple this value for $NaNO_3$_AA and twice this value for AMS_AA and $NaNO_3$_AA (Fig. 8a).

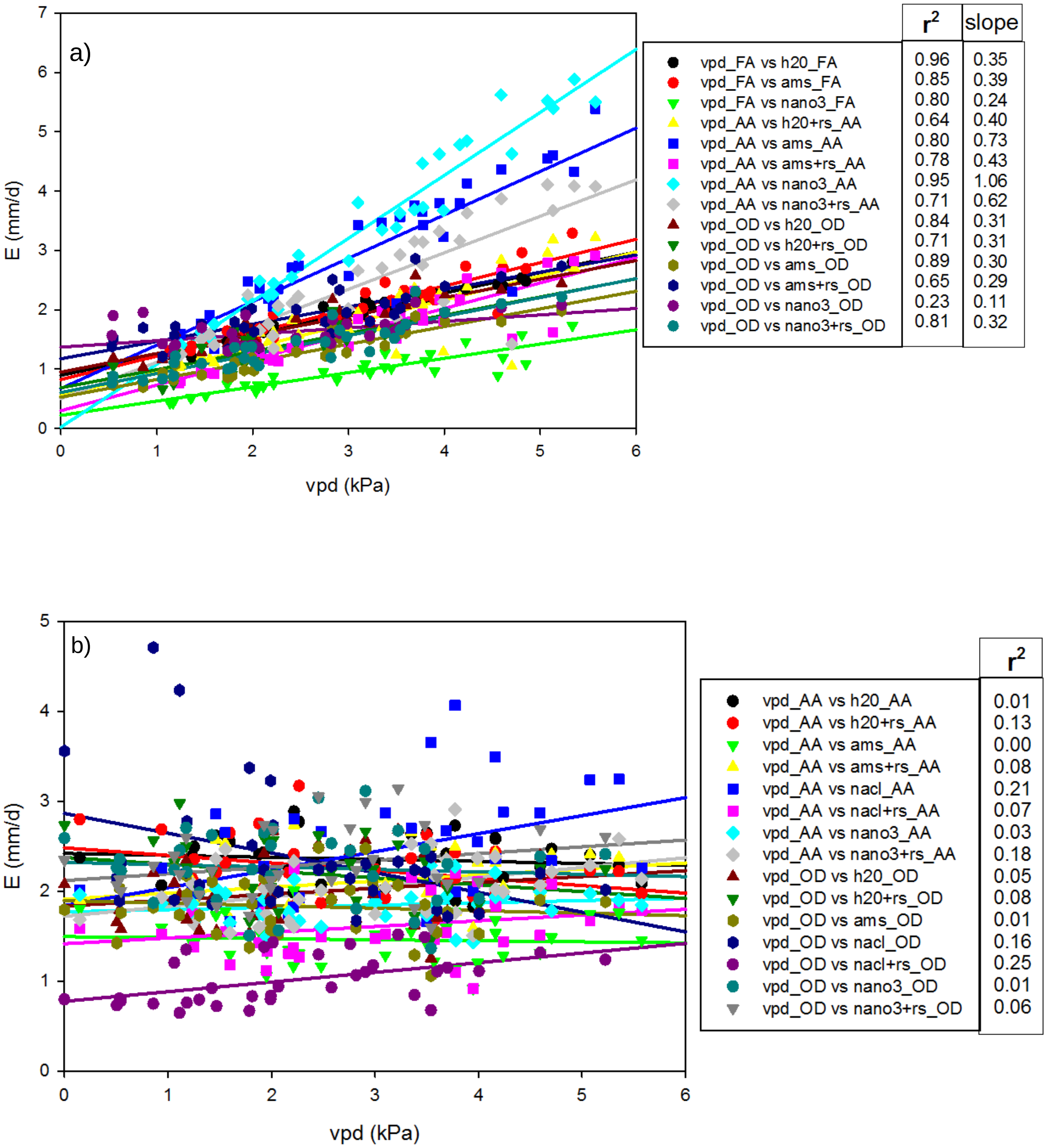

Fig. 8: Hourly values of leaf-area-related transpiration, calculated from sap flow measurements of tree seedlings (a) beech, b) pine), dependent on vapor pressure deficit. Measurements lasted for about 1 month, only daytime values (8 AM to 8 PM) were used. The treatments included combinations of long-term particle regimes (AA: ambient air, FA: filtered air, OD: outdoor, but covered by rainout shelter), in combination with sprays of different salt solutions. The vpd was separately measured in each particle regime. Linear correlations were calculated and the correlation factor r^2 is given. For beech, also the slope (mm d^{-1} kPa^{-1}) is given.

4.5 Gas exchange

Increasing transpiration with increasing vpd was generally observed for all treatments of beech (Fig. 9 a). For pine, transpiration was stable for most treatments, but some treatments of pine (NaNO3 OD, H2O AA) showed a tendency for a decrease of E at higher vpd (Fig. 9b). Others (NaNO3_RS OD, AMS OD, H2O OD) showed a tendency to increase. These observations are not significant due to a limited number of valid measurements.
The instantaneous WUE, determined from porometer measurements as WUE=A/E, generally showed a tendency to decrease with increasing vpd for beech, pine, and sunflower (Fig. 10).

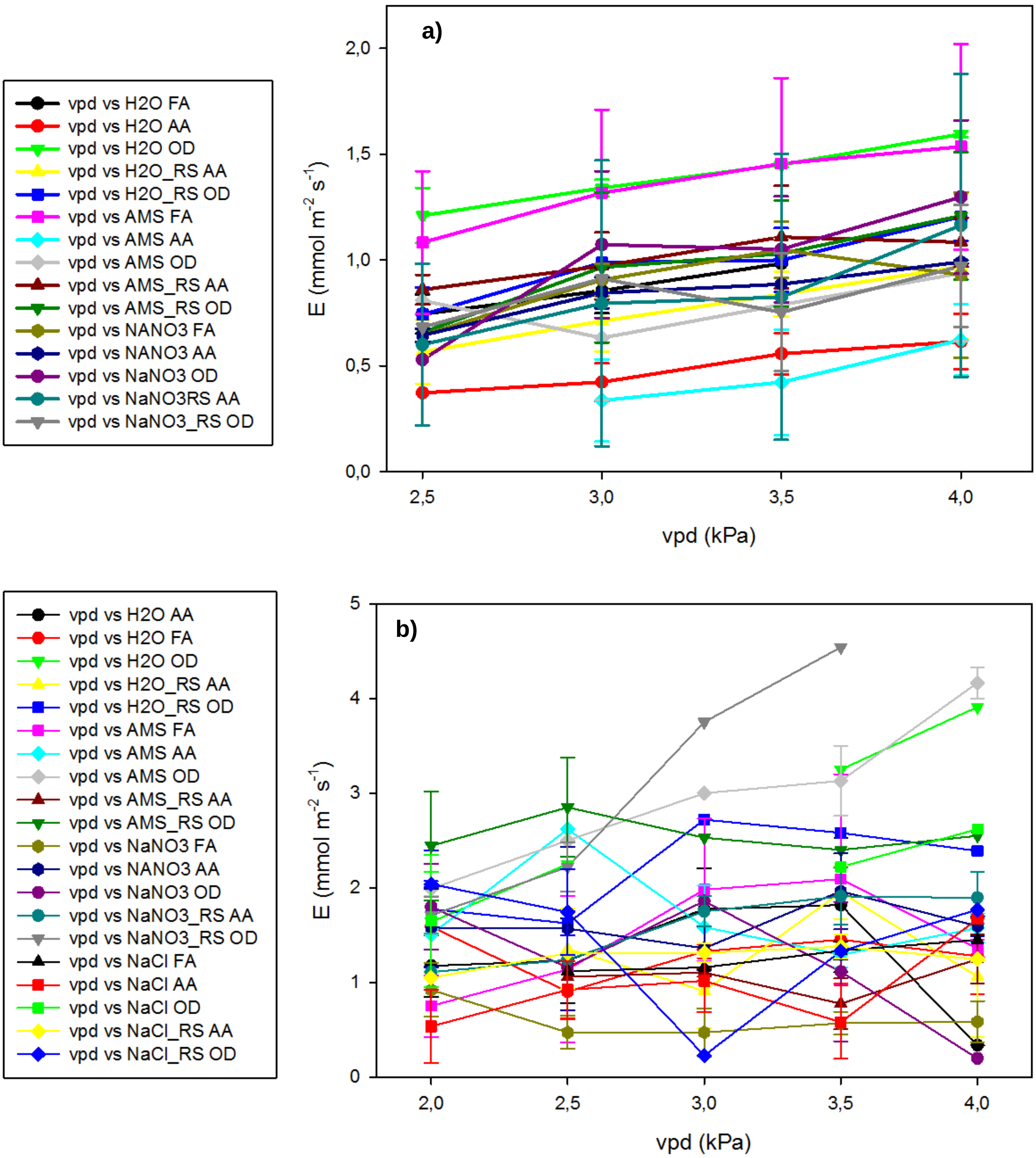

Fig. 9 Transpiration of leaves, measured by gas exchange at defined vpd values. a) beech, b) pine. Error bars indicate standard errors.

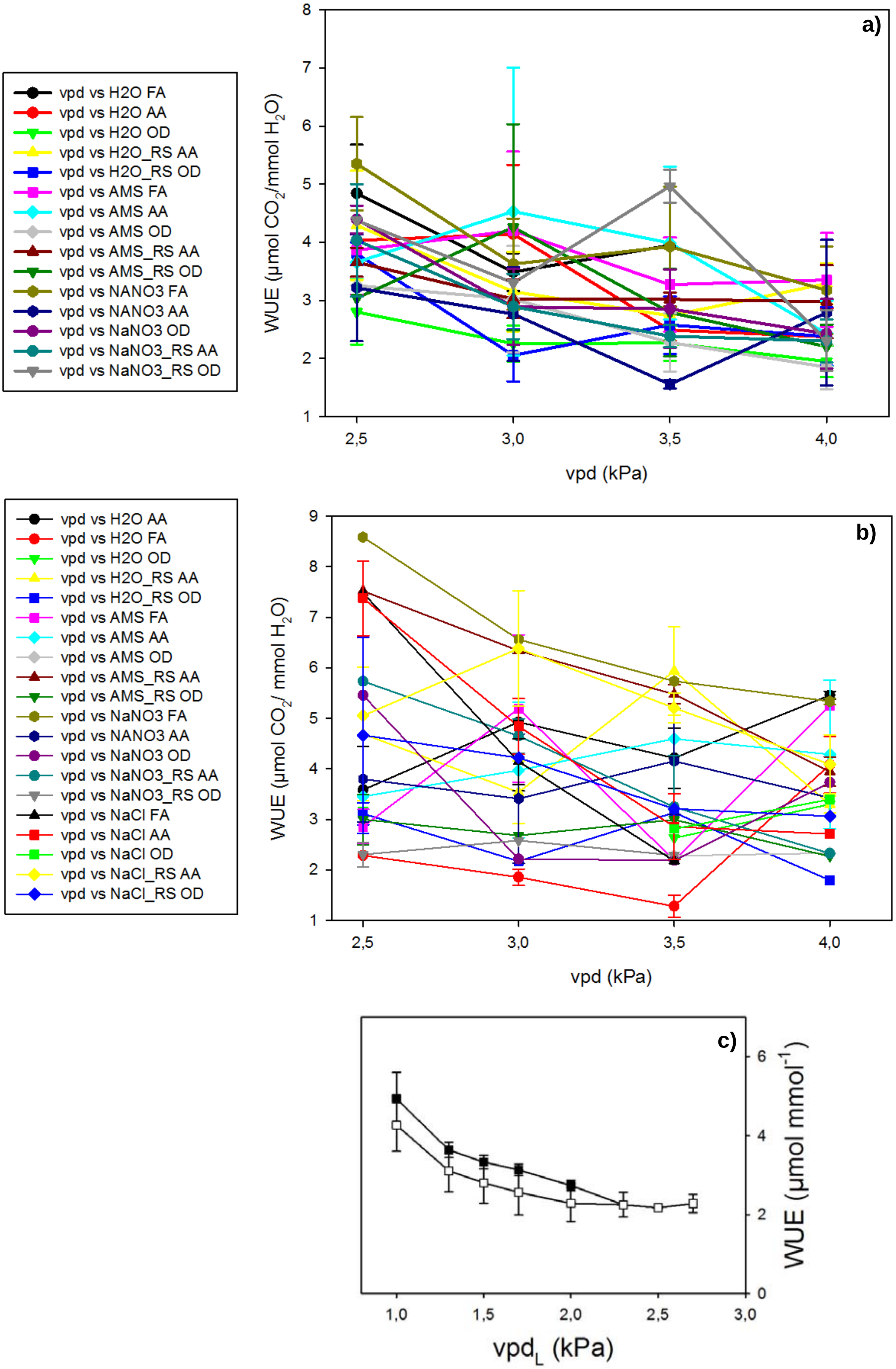

Fig. 10: Water use efficiency of leaves, measured by gas exchange at defined vpd values. a) beech, b) pine, c) sunflower: Filled squares: FA, empty squares: AA. Error bars indicate standard errors.

4.6 Discussion:

Different particle regimes were established by particle exclusion (FA), ambient air (AA), and rainfall exclusion (OD). OD caused the highest load of leaf surface particles, followed by AA and FA. The strong difference in particulate matter between OD and AA was likely due to the influence of large particles (> 10 µm), which is supported by the fact that the OD-rain samples had low concentrations. Large particles may come from disturbed soil or dust from activities nearby (experimental station). They settle by gravitation on the needles, but are not equally distributed by the ventilation system within the greenhouses. Small particles are often not washed down from leaves, even by strong or persisting rain (Freer-Smith et al., 2005). The formation of crusts is a possible reason, another one is that fine particles (< 1 µm) are almost not affected by gravitation and deposit as effectively to the lower side as to the upper side of leaves or needles whereas only small amounts of rainfall reach the lower side and with low intensity. The long-term measurements of carbon isotopes followed this ranking and further support an influence of particles on WUE.

The results for instantaneous WUE, measured by gas exchange and calculated by the ratio of net photosynthesis and transpiration (A/E) was less clear. For beech seedlings sprayed only with water, WUE decreased in the order FA – AA– OD, which did not change when additional salts were applied. For pine seedlings, the situation was different and e.g. for the water sprayed plants (controls) was reverse (Fig. 10). This might come from measurement errors and the fact that there were not enough valid data from repetitions. However, it may also reflect the influence of the different hydric types of plant species, the different functions which particles may have for them and how they interact with plant water relations. This is outlined in the following paragraph.

Beech and sunflowers are anisohydric as can be seen by the linear reaction to vpd. Pine is isohydric, and plants reacted by closing the stomata around noon. For both species, deliquescent particles may enter the stomata and establish thin water films along the stomatal walls (‘hydraulic activaton of stomata’ – HAS), which forms the basis for the transport of liquid water out of (and into) the leaf, as well as the establishment of hydraulic signalling across the stomata. The wick action of particles will increase the transpiration of the affected stomata. Anisohydric plants show little reaction to this and will generally transpire more. Isohydric plants will tend to react by stomatal closure, and may use the signal of HAS stomata as a ‘humidity sensor’ and reduce the aperture of surrounding stomata, possibly even to the degree that overall transpiration decreases (see a scheme of this mechanism in Burkhardt, 2010). By partial closing of stomata, plants can generally increase WUE (Lawson and Blatt, 2014), which can be seen as an adaptation to optimize plant water use. It is therefore possible that OD plants of pine had a higher WUE than FA plants, as the former received a signal to close the stomata, while the latter didn’t. Reduced trasnpiration after salt treatment might also account for the increased osmotic potentials observed for pine.

This hypothetical explanation has not been suffiently proven yet to enable the parametrization of WUE changes by particles, even if a division by hydric types would be made. It should be added, however, what happens if particle concentrations increase strongly and what effects this may have on the plant and for the definition of parameters to describe particle effects on plants. At high pollution levels, the isohydric plants may also transpire more, as the number of HAS-affected stomata will increase and the additional water loss will not be compensated by the reduction of stomatal aperture. In addition, a general and long-term reduction of stomatal aperture may considerably decrease CO_2-uptake and may lead to ‘carbon starvation’ (see MacDowell et al., 2008). These processes are driven and intimately linked with vpd, and can possibly help to explain the effects assigned to increasing vpd, especially forest decline or reduced biomass production of agricultural crops ((Breshears et al., 2013; Clifford et al., 2013; Lobell et al., 2014; Lawson and Blatt, 2014). The fact that minimum epidermal conductance (g_{min}) has consistently been found to increase by particle deposition (Burkhardt and Pariyar, 2014) suggests that there is additional transpiration of HAS affected stomata even when they are completely closed. It is therefore suggested to develop and use g_{min} rather than WUE for defining suitable thresholds and to evaluate the effects of particulate pollutants on plants.

5. Milestones achieved:

MS 50: Submission of data to database for modelling purposes

MS 51. Completion of analysis of water use efficiency, water deficit, analysis of gas fluxes

6. Deviations and reasons:

It was initially intended to study vpd as the main factor, which should be established by different ventilation strength in the greenhouses. It was assumed that vpd would determine the deliquescence and spatial extension of hygroscopic particles on the leaf surfaces, which then leads to the formation of wicks into the stomata and subsequently increased transpiration. When it turned out that only small vpd differences could be achieved by different ventilation, the program was shifted in the second year to a differentiation between different regimes of long-term accumulation of particles. The rain-out shelter was constructed and one half of the greenhouses received filtered air, thus forming three different aerosol regimes. The vpd-dependence was now studied as part of the measurements and within the data analysis of gas exchange and sap flow. Additional justification for this approach comes from the fact that the most likely factors which determine the dynamics of hygroscopic particles on leaves are stomatal transpiration and turbulence caused humidity fluctuations of the leaf boundary layer. This perception has been growing only throughout the last few years.

7. Publications:

Burkhardt, J., Basi, S., Pariyar, S. and Hunsche, M., 2012. Stomatal penetration by aqueous solutions – an update involving leaf surface particles. New Phytol., 196(3): 774-787.

Burkhardt, J. and Hunsche, M., 2013. "Breath figures" on leaf surfaces-formation and effects of microscopic leaf wetness. Frontiers in Plant Science, 4.

Burkhardt, J. and Pariyar, S., 2014. Particulate pollutants are capable to 'degrade' epicuticular waxes and to decrease the drought tolerance of Scots pine (Pinus sylvestris L.). Environ. Pollut., 184: 659-667.

Pariyar, S., Eichert, T., Goldbach, H.E., Hunsche, M. and Burkhardt, J., 2013. The exclusion of ambient aerosols changes the water relations of sunflower (Helianthus annuus) and bean (Vicia faba) plants. Environ. Exp. Bot., 88: 43-52.

Additional references

Breshears, D.D. et al., 2013. The critical amplifying role of increasing atmospheric moisture demand on tree mortality and associated regional die-off. Frontiers in Plant Science, 4.

Burkhardt, J. (2010). Hygroscopic particles on leaves: Nutrients or desiccants? *Ecological Monographs* 80**,** 369-399.

Clifford, M.J., Royer, P.D., Cobb, N.S., Breshears, D.D. and Ford, P.L., 2013. Precipitation thresholds and drought-induced tree die-off: insights from patterns of Pinus edulis mortality along an environmental stress gradient. New Phytol., 200(2): 413-421.

Klein, T., Cohen, S. and Yakir, D., 2011. Hydraulic adjustments underlying drought resistance of Pinus halepensis. Tree Physiol., 31(6): 637-648.

Lawson, T. and Blatt, M., 2014. Stomatal size, speed and responsiveness impact on photosynthesis and water use efficiency. Plant Physiol.; *doi:10.1104/pp.114.237107*

Lobell, D.B. et al., 2013. The critical role of extreme heat for maize production in the United States. Nature Clim. Change, 3(5): 497-501.

McDowell, N. et al., 2008. Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? New Phytol., 178(4): 719-739.

8. Meetings:

Results from the project were presented at the following international meetings:

IUFRO RG 7.01 International Conference 2012 ‘Biological Reactions of Forests to Climate Change and Air Pollution’, Kaunas, Lithuania, 18-27 May, 2012. J. Burkhardt: Direct interactions of hygroscopic particles with leaf/needle surfaces and plant water relations (oral presentation).

International Workshop and Meeting of the German Society of Plant Nutrition, Bonn, Germany, 5-7 September, 2012. S. Pariyar: Effects of ambient aerosol particles on the water relations of crop plants (oral presentation).

ECLAIRE 2nd GA, Edinburgh, UK, 15-18 October, 2012. S. Pariyar: Effects of aerosol deposition on stomatal functions (oral presentation).

Biohydrology Conference 2013, Landau, Germany, 21-24 May, 2013. J. Burkhardt: From leaf wetness to deliquescent leaf surface particles – microscopic water at the plant/atmosphere interface (oral presentation).

International Plant Nutrition Colloquium, Istanbul, Turkey, 19-22 August, 2013. S. Pariyar: Aerosol particles affect the water economy of plants (poster presentation).

Goldschmidt 2013, Florence, Italy, 26-30 August, 2013. J. Burkhardt: Aerosols and plant leaf surfaces (oral presentation).

Deutsche Botanikertagung 2013, Tübingen, Germany, 30 Sept – 4 Oct, 2013. J. Burkhardt: Hygroscopic leaf surface particles reduce the drought tolerance of Scots pine by deliquescence, stomatal penetration and the establishment of wick-like structures (accepted for oral presentation).

9. List of Documents/Annexes:

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