Environmental and Experimental Botany 88 (2013) 43–52

Contents lists available at SciVerse ScienceDirect

Environmental and Experimental Botany

journal homepage: www.elsevier.com/locate/envexpbot

The exclusion of ambient aerosols changes the water relations of sunflower (*Helianthus annuus*) and bean (*Vicia faba*) plants

Shyam Pariyar[a], Thomas Eichert[a], Heiner E. Goldbach[a], Mauricio Hunsche[b], Jürgen Burkhardt[a,*]

[a] *Plant Nutrition Group, University of Bonn, Institute of Crop Science and Resource Conservation, Karlrobert-Kreiten-Str. 13, D-53115 Bonn, Germany*
[b] *Horticultural Science Group, University of Bonn, Institute of Crop Science and Resource Conservation, Auf dem Hügel 6, D-53121 Bonn, Germany*

ARTICLE INFO

Article history:
Received 30 September 2011
Received in revised form
12 December 2011
Accepted 22 December 2011

Keywords:
Plant transpiration
Ecophysiology
Gas exchange
Atmospheric aerosols
Salt
Night time transpiration
Tree drought mortality

ABSTRACT

Aerosols are an ubiquitous component of the atmospheric environment of plants but their ecophysiological role is largely unknown. Here we address this role by comparing the water relations of plants grown in ventilated greenhouses with ambient air (AA), and filtered air (FA) where particle concentrations had been reduced by more than 99%. Beans and sunflowers were grown in well watered soil or hydroponics. Humidity response curves of gas exchange were recorded along with sap flow, water potentials, and osmotic potentials.

Hydroponically grown FA sunflowers and FA beans showed 20–40% lower stomatal conductance and lower transpiration compared to the respective AA plants under identical conditions. In sap flow measurements, the leaf-area related transpiration of soil-grown FA sunflowers was about 20–30% lower than for AA plants, partially due to lower night time values. Midday water potentials as well as osmotic potentials of FA plants were higher compared to the respective AA plants, while pre-dawn water potentials did not differ.

Reduced transpiration of FA plants with stable photosynthesis was observed for beans and can be explained by the “hydraulic activation of stomata”, where deposited hygroscopic aerosols form liquid water connections along the stomatal walls, thereby forming a second, liquid-water type of stomatal transpiration. Simultaneously decreased transpiration and photosynthesis were observed for sunflower and point to a smaller stomatal aperture of FA plants. To our knowledge, this is the first study allocating an important functional role to natural aerosol concentrations. It further supports the idea that particulate air pollution may decrease the water use efficiency and the drought tolerance of plants.

1. Introduction

Global change is accompanied by a strong anthropogenic increase of the concentrations and hygroscopicity of atmospheric aerosols, resulting mainly from industrialization and land use change (Mulitza et al., 2010; Neff et al., 2008; Tsigaridis et al., 2006). Because the physical, physicochemical, and nutritional properties of aerosols may influence vegetation, aerosol/plant interactions have recently been reviewed (Burkhardt, 2010; Grantz et al., 2003; Ravi et al., 2011). Plant surfaces are a major sink for aerosol deposition, but deposited particles have usually been considered as inert, in contrast to trace gases. However, many particles are hygroscopic and may become deliquescent within the humid leaf boundary layer due to plant transpiration, thereby creating a (microscopic) leaf surface wetness. Such highly concentrated solutions may then interact with leaf surfaces and influence plant water relations (Burkhardt, 2010).

The few published experiments which studied the interactions between particles and plants focused on the addition of particles to leaves by spraying them as dry particles (Burkhardt et al., 2001b; Gmur et al., 1983; Hirano et al., 1995; Thompson et al., 1984). However, residues of sprayed and evaporated salt solutions also remain as hygroscopic particles on the leaf. Therefore, experiments involving such solutions and even the fumigation with some trace gases (e.g. simultaneously with NH_3 and SO_2) (Dueck et al., 1990) may be considered as experiments testing the interaction of leaves with accumulated hygroscopic aerosols. Such experiments quite often led to an increase in transpiration (Beasley, 1942; Burkhardt, 2010; Burkhardt et al., 2001a; Eveling, 1969; Hirano et al., 1995). An extreme example is the use of chemical desiccants in plant breeding and practical agriculture where the application of concentrated

Abbreviations: *A*, net photosynthesis ($\mu mol\,m^{-2}\,s^{-1}$); AA, ambient air; *E*, transpiration ($mmol\,m^{-2}\,s^{-1}$); FA, filtered air; gs, stomatal conductance ($mol\,m^{-2}\,s^{-1}$); WUE, photosynthetic water use efficiency ($\mu mol\,mmol^{-1}$).

* Corresponding author. Tel.: +49 228 732186; fax: +49 228 732489.
E-mail addresses: spariyar@uni-bonn.de (S. Pariyar), t.eichert@uni-bonn.de (T. Eichert), h.goldbach@uni-bonn.de (H.E. Goldbach), j.burkhardt@uni-bonn.de (M. Hunsche), mhunsche@uni-bonn.de (J. Burkhardt).

0098-8472/$ – see front matter © 2011 Elsevier B.V. All rights reserved.
doi:10.1016/j.envexpbot.2011.12.031

solutions of specific salts or acids (but also NaOH) creates drought symptoms or causes the terminal drought of the leaves (Murphy, 1968; Nicolas and Turner, 1993). While this is the intended effect, it has not been shown by experiment whether it results from the specific chemical damage of certain ions affecting the leaf, or (as the wording suggests) from plant desiccation due to the hygroscopicity of the substances and their competition for water with the plants interior.

Aerosols in natural concentrations may also fulfill functions for the nutrition and the water relations of plants. They are essential for the nutrient balances of large ecosystems (Chadwick et al., 1999; Newman, 1995; Vitousek and Farrington, 1997) and it is likely that after deposition a considerable part of them is directly taken up by the leaves (Sparks, 2009). While foliar uptake has long been used for fertilization in practical agriculture and horticulture, there has been a long lasting debate whether it happens exclusively by the cuticles (Schönherr, 2006; Schreiber, 2005; Stevens et al., 1991) or also by the stomata (Burkhardt and Eiden, 1994; Eichert and Burkhardt, 2001; Eichert et al., 1998). With the proven stomatal uptake of fluorescent nanoparticles along the stomatal walls under natural conditions, i.e. without the use of specific adjuvants (Eichert et al., 2008), this debate has recently come to an end. The relatively thin liquid water connections along the walls of individual stomata with an estimated thickness of less than 100 nm may establish by the expansion of salt solutions (Burkhardt et al., 2009; Burkhardt, 2010), but other suggestions (bacteria, mucilage) have been made (Eichert et al., 2008; Zimmermann et al., 2007). Independently of the mechanism, this 'hydraulic activation of stomata' (HAS) creates a fundamental difference to common concepts of plant/atmosphere interaction. HAS enables the bidirectional transport of liquid water, solutes, dispersed substances, and information (hydraulic signals). It changes the view on a range of different phenomena, including foliar nutrition and the 'leaching' of passively transported ions from the plant apoplast to the leaf surface (Burkhardt, 2010; Sattelmacher, 2001; Tukey, 1970). It also establishes a second pathway of stomatal water loss, where liquid water is transpired almost independently of stomatal aperture, and where hygroscopic particles on the leaf surface form the outer end of a 'wick' (Burkhardt, 2010). In this way, hydraulic activation may increase stomatal transpiration, with the overall effect depending on the number of activated stomata. It has also been suggested that this mechanism, established in individual stomata, may explain the 'plant humidity sensor', including the 'feed-forward' response, where the stomata close with decreasing humidity of the ambient air, even to an extent that transpiration decreases (Burkhardt, 2010; Farquhar, 1978; Franks, 2004; Meinzer and Grantz, 1991; Monteith, 1995; Schulze et al., 1972). Given such functions and beneficial aspects, plants may even have adapted to constant aerosol regimes by evolution, possibly by developing functional leaf surface microstructures which are known to control aerosol deposition (Burkhardt et al., 1995). This generalizes the concept where plants have adapted to minimize particle accumulation by self cleaning ('Lotus effect') (Barthlott and Neinhuis, 1997).

In this paper, we report the effects of aerosol exclusion on plant ecophysiology in a greenhouse experiment. Former experiments with filtered air within cuvettes, open-top chambers, or greenhouses usually focused on the chemical aspects by the exclusion of trace gases or organic substances attached to atmospheric particles (Cape et al., 1991; Frey et al., 1996; Günthardt-Goerg and Keller, 1987; Günthardt-Goerg et al., 1993; Janson and Granat, 1999; Kaupp et al., 1994; Krause and Cannon, 1991; Percy et al., 1992; van Hove et al., 1999, 1992, 1991). Based on the HAS concept, this study focuses on the functional role of deposited aerosols for the water relations of plants including the humidity sensor, comparing plants grown in ambient air (AA) and in filtered air (FA). To our knowledge, this is the first time such an experiment is reported.

2. Materials and methods

2.1. Greenhouses

The experiments were conducted in Bonn, Germany, during the summer months of the years 2009 and 2010. Two greenhouses with forced ventilation were used, one supplied with AA, the other one with FA. The volume of air in each greenhouse was about 25 m^3, which was completely changed about 2 times per minute. In the FA greenhouse, the ambient air was filtered by a 2-stage filtering system consisting of textile filter bags in combination with high efficiency particulate air (HEPA) 13 filters (Buchholz and Meidt GmbH, Troisdorf, Germany). The greenhouses were within the city with typical concentrations of ambient aerosols between 10,000 and 30,000 cm^{-3}. In the FA greenhouse, particle concentrations were about 50–200 cm^{-3}, i.e. less than 1% compared to the AA greenhouse. Particle concentrations in both greenhouses were discontinuously monitored by an Aerosol Spectrometer Model 1.108 (Grimm Aerosol Technik GmbH & Co. KG, Germany). Temperature and humidity were continuously monitored in each greenhouse. Temperature and humidity were not completely equal as intended, but the air in the FA greenhouse was about 1 °C warmer and about 5% drier than in the AA greenhouse.

Sunflowers (*Helianthus annus* var. Heliaroc) and faba beans (*Vicia faba* var. Condor) were used. The experiments focused on atmospheric drought, and it was intended to keep root water and nutrient uptake as comfortable and stable as possible. This is best guaranteed by aerated hydroponic solution, which was used as the growing medium for beans and sunflowers. As an approach to more realistic conditions, sunflowers were also grown in well watered and well fertilized silty soil. Each group contained 10 plants in each greenhouse. For soil experiments, the seeds were directly sown in the pot. The soil pots were watered frequently with de-ionized water and soil moisture was maintained at 70% of the field capacity. Nutrient solution was added once a week to supply additional nutrients. Weeding was done once in two weeks. For hydroponic culture, the seeds of both *H. annus* and *V. faba* were first sown on sand for germination. At the 2-leaf stage, the seedlings were transplanted into hydroponic nutrient solution containing all essential macro- and micronutrients. Hydroponic solution was changed 2–3 times a week depending on the growth stages of the species. The root zone was aerated for 15 min every hour with the help of an external electric pump.

2.2. Gas exchange

Gas exchange was measured in *H. annus* and *V. faba* grown under treatment conditions, i.e. FA and AA greenhouses comprising of both growing media such as soil and hydroponic cultures in each greenhouse. 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.

Healthy and fully developed leaves, which were grown at least 3 weeks under treatment conditions, were selected for the gas exchange measurement. The leaves used were the third to fifth (sunflower) and sixth to eighth (bean) leaves from the base of the plant. Measurements were done at stable leaf temperature which was usually chosen between 27 °C and 32 °C in the morning according to the weather conditions, in order to keep a maximum stability throughout the measurements. The measurements were done at two different light levels, respectively, as it was assumed that the relative contribution of HAS mediated transpiration would be higher under low light than under high light conditions. 50 $\mu mol\ m^{-2}\ s^{-1}$ PAR (photoactive radiation) were