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Defense and avoidance of ozone under global change

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Modeling of ozone effects on plants should include a measure for the plant defense capacity.

Abstract

The level II approach of the critical loads concept adopted by the UNECE aims at a flux based evaluation and takes into account environmental factors governing stomatal conductance. These factors will probably be affected by global change. The flux concept predicts that a decrease in stomatal conductance would protect trees from air pollution effects by decreasing uptake. However, experimental evidence is inconclusive. Numerous results suggest that pollutants and factors subject to global change (drought, CO_2) may interact and even exacerbate effects, probably because antioxidative defense systems are involved in both, defense against pollutant effects and protection from natural stress. An effective pollutant dose, which is weighted by physiological defense capacity, would better predict such effects. In this review paper we argue that the flux-based approach is imperfect, because global change effects may also modify the physiological susceptibility to ozone. Instead, a flux concept weighted by defense capacity should be tested.

Keywords: Antioxidative defense; Drought; Elevated CO_2; Global change; Ozone flux

1. Introduction

While it is well known that increased tropospheric ozone (O_3) concentrations can be toxic to plants in general and to forest trees in particular (Reich, 1987; Ashmore, 2005), establishing clear cause and effect relationships for forest trees under ambient conditions is difficult (Manning, 2005). After decades of research it is perhaps surprising that the process base of ozone damage to plants is still not fully clarified (Matyssek et al., 2005). In addition to scaling problems from small seedlings typically subjected to experimental exposures to mature forest trees (Manning, 2005), interactive effects with other environmental factors come into play in natural stands. In particular, climate change and the increase in ozone concentrations have common causes in the burning of fossil fuels and have to be viewed concurrently. As a consequence, risk assessments at natural stands are difficult and ambiguous and often do not reflect the observations made in the field (Matyssek and Innes, 1999; Loibl et al., 2004).

The approach of ''Critical Levels for Ozone'' introduced by the UNECE originally defined exposure-based threshold values of the AOT40 (accumulated dose over the threshold of 40 nl l^{-1}). Exceedance of this threshold would indicate a risk of biomass loss of more than 10% (LRTAB, 2004). In a level II approach of the Critical Levels concept a flux based evaluation is tested (Emberson et al., 2000; Ashmore et al., 2004). In such a model the external exposure – defined as the AOT40 – is translated to the dose actually taken up into the plants. For this purpose, environmental meteorological factors (e.g. ambient vapor pressure deficit, solar radiation) governing stomatal conductance can be taken into account, or a simple stomatal model can even improve the performance

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of the model (Karlsson et al., 2004). It is widely anticipated that these factors controlling stomatal behavior will vary in the future due to global change. In the view of the flux based concept, a decrease of stomatal conductance (e.g. due to increasing drought or elevated CO_2 as anticipated by many global change scenarios) would protect trees from certain air pollution effects through avoidance of uptake.

However, the experimental evidence does not always support this hypothesis. There are numerous results suggesting that pollutants and factors subject to global change (drought, CO_2) may interact in different ways and even exacerbate effects. The stress physiological basis thereof is that the antioxidative defense system comes into play in both, defense against pollutant effects, and protection from natural stress effects (e.g. drought). It has been suggested that an ''effective pollutant dose'', which is weighted by physiological defense capacity, would be more appropriate to predict such effects.

In this opinion paper (which is not meant to be an exhaustive review), we argue that that a flux-based approach alone is imperfect, because global change effects may also modify the physiological susceptibility to ozone. Instead, a flux concept weighted by defense capacity should be widely tested.

2. From ozone exposure to plant responses

Ozone effects on plants are the result of a three-step chain of events: exposure, uptake, and biological effect (Fig. 1). Only the amount of ozone arriving at the cell membrane or, perhaps, at the cell wall (apoplast), can have a biological effect on the tissue.

Ozone exposure measurement is a physical rather than biological problem and reliable data can be measured or modeled in many instances. Much has been written about the preferred metric describing ozone exposure and the scientific community has generally adopted the AOT40 concept as a suitable descriptor (LRTAB, 2004), although it e.g. neglects night time exposure which may be significant in some cases (Wieser and Havranek, 1995; Matyssek et al., 1995; Grulke et al., 2004). While it may be difficult to condense the exposure characteristic, which is composed of time courses of ambient concentrations, into one representative value, we can safely accept that it is presently in principle possible to characterize the exposure in detail. However, a characterization of exposure alone is obviously not enough to conduct a meaningful risk assessment for biological systems.

The uptake of ozone is largely controlled by the stomata, the main entry pathway for ozone. Stomatal conductance (g_s) is the metric required to calculate the ozone flux into the leaf at a given external concentration. Current models describing ozone uptake into plant foliage usually build in environmental factors that control stomatal opening (e.g. a metric that allows for soil drought or air humidity) or use models for stomatal conductance (Karlsson et al., 2004).

Once ozone has entered the substomatal cavity it reacts quickly with molecules in the adjacent cell walls or with constituents of the outer cell membrane. The intercellular concentration of ozone is assumed to be close to zero because of the high reaction velocity of such chemical reactions (Laisk et al., 1989). However, the reaction products of ozone – reactive oxygen species (ROS) or oxidation products of biomolecules originating from the interaction of ozone with cellular redox systems – initiate or mediate reactions within the living tissues leading to known ozone effects such as decreases in photosynthetic rates, discoloration, and cell death. There is evidence that suggests than ozone interferes with a cell-death related signaling pathway, which uses ROS as trigger substances (Matyssek and Sandermann, 2003; Baier et al., 2005). More generally, ozone effects on living cells are related to

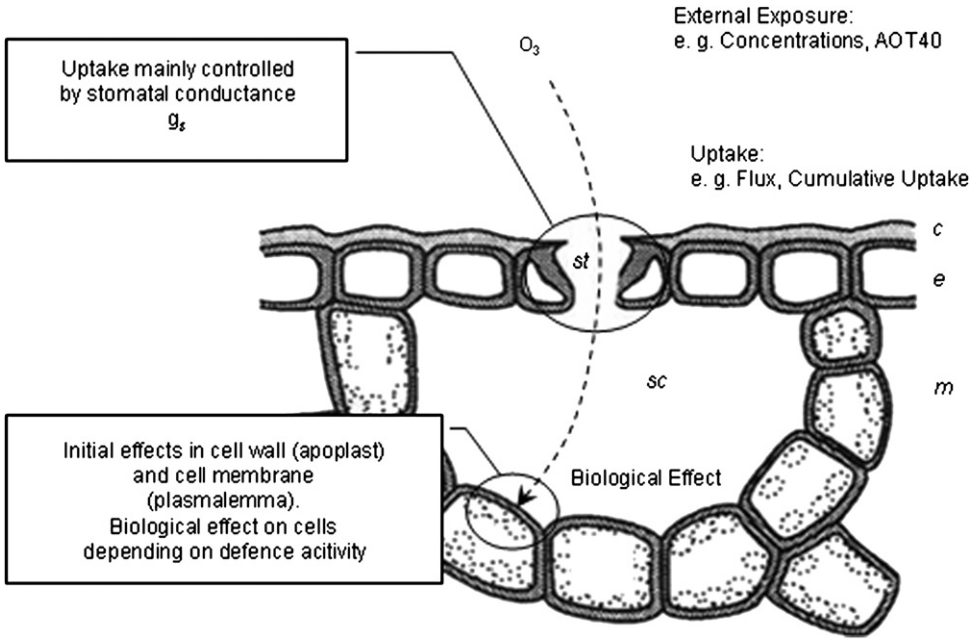

Fig. 1. Scheme of O_3 uptake and biological effect on leaves. st stoma, sc substomatal cavity, c cuticle, e epidermis, m mesophyll, g_s stomatal conductance.