

Seasonal photosynthetic response of European beech to severe summer drought: Limitation, recovery and post-drought stimulation



Matthias Arend^{a,*}, Krunoslav Sever^c, Ellen Pflug^{a,b}, Arthur Gessler^a, Marcus Schaub^a

^a Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Zurich, Switzerland

^b Department of Environmental Sciences, Federal Institute of Technology Zurich, Zurich, Switzerland

^c Department of Forest Genetics, Dendrology and Botany, Faculty of Forestry, University of Zagreb, Zagreb, Croatia

ARTICLE INFO

Article history:

Received 24 June 2015

Received in revised form 7 September 2015

Accepted 12 January 2016

Keywords:

Photosynthesis

Drought

Recovery

Post-drought

Phenology

Beech

ABSTRACT

Trees experience frequent periods of severe drought during their long lives and must therefore be able to recover and compensate for the limitations of previous stresses. In this study, the response of photosynthesis to a severe, long-lasting summer drought and drought release was followed in saplings of a mesic and xeric provenance of European beech transplanted to mesocosms with experimentally controlled water supply. Photosynthesis was assessed in stressed and non-stressed saplings over the course of an entire vegetation season. The drought response was divided into three phases: (1) limitation, (2) recovery and (3) post-drought stimulation. Limitation of photosynthesis developed gradually and caused, in both provenances, a major loss of cumulated photosynthetic activity. It was accompanied by impaired PSII photochemistry indicating severe stress. Recovery started rapidly after re-watering and was fully accomplished within 20 and 10 days in the mesic and xeric provenances, respectively. After recovery, photosynthesis remained at high levels while decreasing in control trees. This post-drought stimulation was sustained until the end of the vegetation period, partly counterbalancing the previous loss of photosynthetic activity. It was attributable to an altered leaf ontogeny as indicated by a delay of autumnal leaf senescence. These observed responses might be important factors when modelling seasonal carbon uptake and phenology of forest ecosystem under future climate change.

© 2016 Elsevier B.V. All rights reserved.

1. Introduction

Drought is the major environmental constraint, causing physiological limitations on growth, reproduction and survival of plants worldwide (Boyer, 1982; Chaves et al., 2003). It has therefore been recognized as a serious threat to forest ecosystems (e.g. Allen et al., 2010). Forest trees are of particular concern as they experience frequent periods of severe drought during their exceptionally long life span. The strong reduction in primary productivity of forest ecosystems in wide parts of Europe due to the extreme summer drought in 2003 is one of the most prominent examples of the limiting effects of drought on trees (Ciais et al., 2005). An increased frequency and intensity of this type of extreme climatic condition is predicted for the near future together with a temporal and spatial change in precipitation patterns (IPCC, 2012). Hence, responses of trees to drought are studied intensely at different scales of plant

organization and function (e.g. Bréda et al., 2006; Rennenberg et al., 2006) to provide the scientific knowledge base for estimating the effects of climate change on forest ecosystems. However, physiological studies assessing the recovery phase and longer-term effects after drought are scarce.

Trees respond to drought with specific changes of physiological and metabolic activities constraining their functional integrity. Leaf photosynthesis is among the most seriously affected activities as it is tightly linked to tree water balances via stomatal control of CO₂ uptake (Hetherington and Woodward, 2003; Zweifel et al., 2007). Recently, mesophyll conductance for CO₂ has been recognized as a further cause of photosynthetic variation that responds to environmentally driven fluctuations in the internal plant water balance (Flexas et al., 2006, 2012; Hommel et al., 2014). With increasing drought intensities, metabolic limitations of photochemical reactions become more and more effective disturbing the biochemistry of the photosynthetic apparatus. The degree to which stomatal control, mesophyll conductance and metabolic limitations contribute to drought-induced impairments of photosynthesis is still a matter of debate and depends largely on the severity and duration of the experienced stresses (Grassi and Magnani, 2005). Photosynthetic

* Corresponding author. Tel.: +41 447392436.

E-mail address: matthias.arend@wsl.ch (M. Arend).

net CO₂ exchange is a physiological measure that integrates all these sources of photosynthetic variation and is thus a widely used measure of stress in eco-physiological studies on drought exposed plants. On an ecological scale, it represents the plant physiological determinant that drives the seasonal course of net ecosystem fluxes of CO₂ and its climate dependent fluctuation (Baldocchi, 2003; Xu and Baldocchi, 2003).

As photosynthesis, and the underlying physiological processes and metabolic reactions, are tightly linked to plant water status they attracted much attention in terms of acclimation and adaptation to drought. A large number of studies reported effects of natural or experimentally imposed drought on photosynthetic traits of potted or field-grown trees providing basic information on stomatal and non-stomatal restrictions of photosynthesis (e.g. Epron et al., 1993; Epron and Dreyer, 1993; Kubiske and Abrams, 1993; Schaub et al., 2003; Haldimann et al., 2008; Mitchell et al., 2013). The majority of these studies dealt with trees exposed to immediate drought while information gathered over a seasonal time scale and including processes of drought recovery is scarce. To date, there are only a few studies that addressed this fairly overlooked issue although the capacity to recovery is, in a broader sense, part of the tree's drought response (e.g. Kirschbaum, 1988; Gallé et al., 2007; Gallé and Feller, 2007; Liu et al., 2010; Vaz et al., 2010). Most of these studies focused on the early response to re-watering while information gathered over a longer time period and placed in a seasonal context is mostly missing.

Recently, seasonal drought development and recovery were studied in different European oak species, indicating that drought tolerant species resume photosynthesis faster than less tolerant species (Arend et al., 2013). There was also some indication that trees do not simply recover but retain a “memory” of drought in terms of overcompensating photosynthesis or delayed autumnal chlorophyll degradation. This idea is supported by previous studies on grassland and heath species that remained acclimated to drought and “remembered” earlier stresses when exposed to recurrent drought (Walter et al., 2011; Backhaus et al., 2014). These studies are included in the concept of an “ecological stress memory” describing any response of a plant after stress release that improves its response towards future stress experience (Walter et al., 2013). In this sense, it refers exclusively to improved tolerance upon exposure to recurrent stress while responses occurring without recurrent stress are not considered. The need for a broader concept of an “ecological memory” was only recently stressed by Ogle et al. (2015) to better understand and model current plant and ecosystem processes.

Responses of trees to drought are optimally studied under natural field conditions with slowly developing soil water shortage and including the whole sequence of seasonal drought development and drought recovery. Such an approach provides a realistic picture on the tree's drought resistance and resilience but comprises some difficulties in controlling drought conditions. In the present study, provenances of European beech (*Fagus sylvatica* L.) were transplanted into large model ecosystems with controlled water supply and subjected to a long-lasting drought and re-watering treatment. This approach combines the advantage of experimentally controlled conditions with a semi-natural growth environment and allows for studying the whole seasonal sequence of tree responses to drought and re-watering. European beech was chosen as model tree as it is a key species in European forests that is commonly considered to suffer from increasing drought (Ellenberg, 1988; Ohlemüller et al., 2006). Our study aims to (i) evaluate the effect of severe summer drought and re-watering on the seasonal course of photosynthesis and (ii) study the long term effects that modify the leaf physiological status and leaf ontogeny after recovery from drought. Provenances of mesic and xeric origin were included in this study as physiological drought responses may differ

among such provenances (Tognetti et al., 1995; Peuke et al., 2002, 2006).

2. Material and methods

2.1. Plant material and growth conditions

The present study was undertaken in the framework of the interdisciplinary beech experiment *BuKlim: beech in a changing climate*. In this experiment, saplings of twelve beech provenances were excavated in natural forest stands growing along steep precipitation gradients in two Swiss inner-alpine valleys (Table 1). From each provenance, 64 saplings with a size of about 20 cm were transplanted in spring 2011 in a randomized design to the model ecosystem facility MODOEK of the Swiss Federal Institute for Forest, Snow and Landscape Research WSL. The MODOEK facility comprises 16 large mesocosms with a height of 3.5 m and a plantable area of 6 m². Each mesocosm is equipped with an automated irrigation system and a sliding roof closing automatically at the onset of rainfall. Belowground, each mesocosm is split into two lysimeters with a depth of 150 cm one filled with an acidic (haplic Alisol), one with a calcareous (Fluvisol) forest soil (Kuster et al., 2013). In each mesocosm 2 saplings from each provenance were transplanted on acidic and calcareous soil, respectively.

From November to April, the sliding roofs of the mesocosms were kept open to allow natural precipitation. By closing the sliding roofs from May to October, natural precipitation was excluded. The mesocosms were irrigated every second or third day with 50 l m⁻² deionized water enriched with nutrients to simulate the average composition of ambient rainfall (see Kuster et al., 2013). During hot summer periods, the irrigation intensity and frequency was increased to counterbalance higher rates of evapotranspiration and hold the soil moisture at 10 cm soil depth above 20%. With this target value, soil moisture in deeper soil layers was above field capacity as indicated by a constant outflow of drainage water at the bottom of the lysimeters. In 2014, a severe, long-lasting summer drought was imposed in half of the mesocosms by withholding irrigation from 22 May to 2 August (Fig. 1). As evapotranspirational water loss was particularly high at hot days, intermediate irrigation was applied to avoid too fast/intense soil drying and irreversible drought damage of the saplings. After the first saplings reached predawn water potentials below -2.0 MPa, the mesocosms were intensely re-watered for 1 day with 200 l m⁻² and afterwards regularly irrigated as described above.

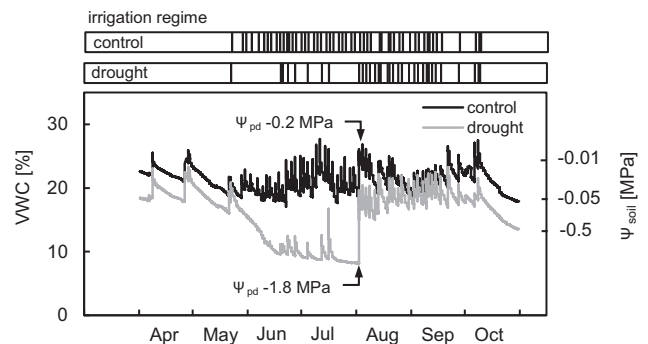


Fig. 1. Soil and plant water balances in irrigated and drought-treated mesocosms. Soil moisture was measured in 10 cm soil depth as volumetric soil water content (VWC) and related to soil matrix potential (Ψ_{soil}) and pre-dawn leaf water potential (Ψ_{pd} ; only shown before re-watering). Re-watering of drought-treated mesocosms started on 2nd August. Marks at the top indicate the temporal sequence of single irrigation events in control and drought-treated mesocosms. Soil and leaf data are means with $n = 8$ and $n > 13$, respectively.

Download English Version:

<https://daneshyari.com/en/article/6536995>

Download Persian Version:

<https://daneshyari.com/article/6536995>

[Daneshyari.com](https://daneshyari.com)