



OPINION PAPER

A first assessment of the impact of the extreme 2018 summer drought on Central European forests

Bernhard Schuldt^{a,*}, Allan Buras^b, Matthias Arend^c, Yann Vitasse^d,
Carl Beierkuhnlein^e, Alexander Damm^f, Mana Gharun^g, Thorsten E.E. Grams^h,
Markus Hauckⁱ, Peter Hajek^j, Henrik Hartmann^k, Erika Hiltbrunner^c, Günter Hoch^c,
Meisha Holloway-Phillips^c, Christian Körner^c, Elena Larysch^l, Torben Lübke^m,
Daniel B. Nelson^c, Anja Rammig^b, Andreas Rigling^d, Laura Rose^j,
Nadine K. Ruehrⁿ, Katja Schumann^m, Frank Weiser^e, Christiane Werner^o,
Thomas Wohlgemuth^d, Christian S. Zang^b, Ansgar Kahmen^{c,*}

^aChair of Ecophysiology and Vegetation Ecology, Julius-von-Sachs-Institute of Biological Sciences, University of Würzburg, Julius-von-Sachs-Platz 3, 97082 Würzburg, Germany

^bLand Surface-Atmosphere Interactions, Technische Universität München, Hans-Carl-von-Carlowitz-Platz 2, 85354 Freising, Germany

^cDepartment of Environmental Sciences – Botany, University of Basel, Schoenbeinstrasse 6, 4056 Basel, Switzerland

^dForest Dynamics, WSL Swiss Federal Institute for Forest, Snow and Landscape Research, Zürcherstrasse 111, 8903 Birmensdorf, Switzerland

^eDepartment of Biogeography, Bayreuth Centre of Ecology and Environmental Research (BayCEER), University of Bayreuth, Universitätsstraße 30, 95447 Bayreuth, Germany

^fDepartment of Geography, University of Zurich, Winterthurerstrasse 190, 8057 Zurich, Switzerland

^gDepartment of Environmental System Science, ETH Zürich, Universitätsstr. 2, 8092 Zürich, Switzerland

^hEcophysiology of Plants, Department of Ecology and Ecosystem Management, Technische Universität München, Hans-Carl-von-Carlowitz-Platz 2, 85354 Freising, Germany

ⁱChair of Applied Vegetation Ecology, Institute of Forest Sciences, Faculty of Environment and Natural Resources, University of Freiburg, Tennenbacher Str. 4, 79106 Freiburg, Germany

^jDepartment of Geobotany, Faculty of Biology, University of Freiburg, Schänzlestr. 1, 79104 Freiburg, Germany

^kMax-Planck Institute for Biogeochemistry, Hans Knoell Str. 10, 07745 Jena, Germany

^lChair of Forest Growth, Faculty of Environment and Natural Resources, Albert-Ludwigs-University Freiburg, Tennenbacherstraße 4, 79106 Freiburg im Breisgau, Germany

^mPlant Ecology, Albrecht von Haller Institute for Plant Sciences, University of Goettingen, Untere Karospüle 2, 37073 Göttingen, Germany

ⁿKarlsruhe Institute of Technology (KIT), Institute of Meteorology and Climate Research - Atmospheric Environmental Research (IMK-IFU), Kreuzeckbahnstr. 19, 82467 Garmisch-Partenkirchen, Germany

^oChair of Ecosystem Physiology, University of Freiburg, Georges-Köhler-Allee 53/54, Freiburg 79110, Germany

Received 6 November 2019; accepted 10 April 2020

Available online 29 April 2020

*Corresponding authors.

E-mail addresses: bernhard.schuldt@plant-ecology.de (B. Schuldt),
ansgar.kahmen@unibas.ch (A. Kahmen).

<https://doi.org/10.1016/j.baee.2020.04.003>

1439-1791/© 2020 The Author(s). Published by Elsevier GmbH on behalf of Gesellschaft für Ökologie. This is an open access article under the CC BY license. (<http://creativecommons.org/licenses/by/4.0/>)

Abstract

In 2018, Central Europe experienced one of the most severe and long-lasting summer drought and heat wave ever recorded. Before 2018, the 2003 millennial drought was often invoked as the example of a “hotter drought”, and was classified as the most severe event in Europe for the last 500 years. First insights now confirm that the 2018 drought event was climatically more extreme and had a greater impact on forest ecosystems of Austria, Germany and Switzerland than the 2003 drought. Across this region, mean growing season air temperature from April to October was more than 3.3°C above the long-term average, and 1.2°C warmer than in 2003. Here, we present a first impact assessment of the severe 2018 summer drought and heatwave on Central European forests. In response to the 2018 event, most ecologically and economically important tree species in temperate forests of Austria, Germany and Switzerland showed severe signs of drought stress. These symptoms included exceptionally low foliar water potentials crossing the threshold for xylem hydraulic failure in many species and observations of widespread leaf discoloration and premature leaf shedding. As a result of the extreme drought stress, the 2018 event caused unprecedented drought-induced tree mortality in many species throughout the region. Moreover, unexpectedly strong drought-legacy effects were detected in 2019. This implies that the physiological recovery of trees was impaired after the 2018 drought event, leaving them highly vulnerable to secondary drought impacts such as insect or fungal pathogen attacks. As a consequence, mortality of trees triggered by the 2018 events is likely to continue for several years. Our assessment indicates that many common temperate European forest tree species are more vulnerable to extreme summer drought and heat waves than previously thought. As drought and heat events are likely to occur more frequently with the progression of climate change, temperate European forests might approach the point for a substantial ecological and economic transition. Our assessment also highlights the urgent need for a pan-European ground-based monitoring network suited to track individual tree mortality, supported by remote sensing products with high spatial and temporal resolution to track, analyse and forecast these transitions.

© 2020 The Author(s). Published by Elsevier GmbH on behalf of Gesellschaft für Ökologie. This is an open access article under the CC BY license. (<http://creativecommons.org/licenses/by/4.0/>)

Keywords: Climate change; Drought stress; Hotter drought; Hydraulic failure; Normalized Difference Vegetation Index; Recovery; Temperate forests; Tree mortality; Vapour pressure deficit; Water potential

The severity of the 2018 drought event from a climatic perspective

Since the beginning of instrumental climate recording, Central Europe has experienced several extreme hot and dry summers (Schär et al., 2004; Orth, Vogel, Luterbacher, Pfister, & Seneviratne, 2016; Hanel et al., 2018), but the climatic conditions during the 2018 growing season were exceptional. Across Austria, Germany and Switzerland (named DACH region hereafter), the 2018 mean growing season air temperature (MGT; April to October) was the highest temperature ever recorded for that period (Fig. 1). It was 3.3°C higher than the long-term average from 1961 to 1990, and even 1.2°C higher than MGT of the record-breaking 2003 summer (Rebetez et al., 2006). The 2018 growing season is thus the latest peak in a trend of rapidly rising temperatures in the DACH region that commenced in the 1980s, with 10 out of the 12 hottest growing seasons in the past 120 years occurring since the year 2000 (Fig. 1).

Mean growing season precipitation (MGP; April to October) for the DACH region in 2018 was as low as during previous record drought events in 1911, 1947, 1976 and 2003 (Fig. 1). Although climate models predict a decline in MGP (e.g. Fischer, Sedláček, Hawkins, & Knutti, 2014), observational data cannot confirm this trend yet. However, the

combination of increasing MGT with overall stable MGP patterns has resulted in a consistent decline of the climatic water balance (CWB; precipitation – potential evapotranspiration) from April to October in Central Europe since the 1960s (Fig. 1). In addition, the 2018 growing season had the highest mean vapour pressure deficit (MVPD; April to October) and second most negative CWB ever recorded in the DACH region, which was even more negative than in 2003 (-238 mm versus -200 mm, respectively). The regional hydroclimate pattern of the 2018 growing season is consistent with a European-wide assessment of the 2018 drought event (Buras, Rammig, & Zang, 2020).

The record-breaking drought of the 2018 growing season from April to October confirms projections from climate models that the future climate in Central Europe will be hotter, drier and will encompass more extreme climatic events (Samaniego et al., 2018; Trenberth et al., 2014; Zhou, Zhang, Park Williams, & Gentine, 2019; Zscheischler & Seneviratne, 2017). Prior to the 2018 drought, the 2003 summer was classified as the most severe drought event in Europe for the last 500 years according to historical archives (Camenisch et al., 2020; Luterbacher, Dietrich, Xoplaki, Grosjean, & Wanner, 2004; Orth, Vogel, Luterbacher, Pfister, & Seneviratne, 2016), exceeding the droughts of the years 1947 and 1976 in severity (Raspe, Grimmeisen, & Schulze, 2004). Since then,

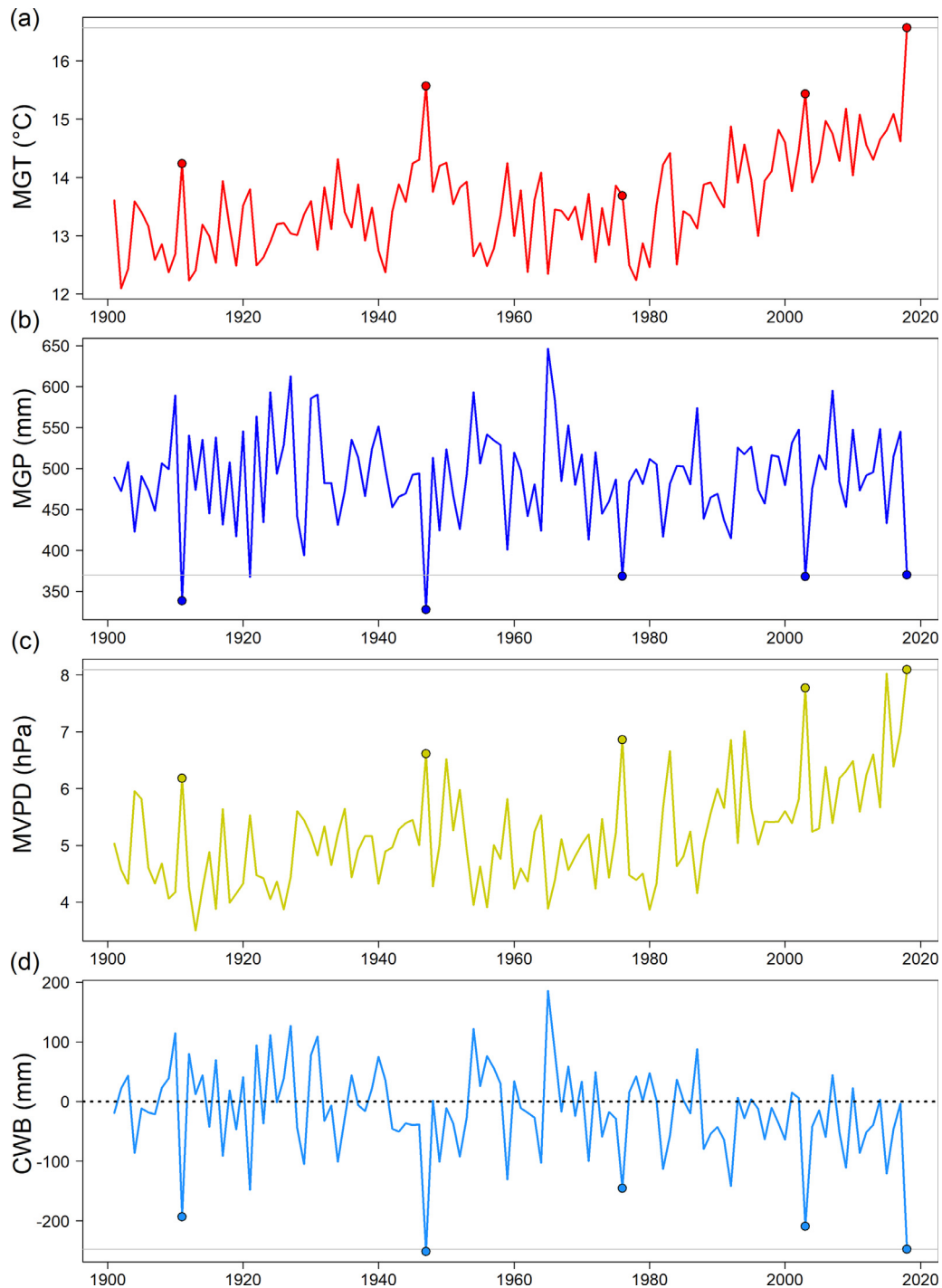


Fig. 1. Mean growing season air temperature (MGT; a), mean growing season precipitation (MGP; b), mean vapour pressure deficit (MVPD; c), and climatic water balance (CWB; d), i.e. precipitation minus potential evapotranspiration, for the DACH region in Central Europe for the period from April to October. Horizontal grey lines demarcate the corresponding value of 2018 for comparison with other record drought years in the DACH-region (1911, 1947, 1976, 2003), which are highlighted by dots in the corresponding colour. Data-source is the CRU version 4.03 gridded data-sets for minimum, mean, and maximum monthly air temperature, monthly precipitation sum, and monthly vapour pressure (Harris, Jones, Osborn, & Lister, 2014). To compute VPD, saturation vapour pressure was derived from monthly mean temperature using the approximation by Murray (1967), from which monthly vapour pressure was subtracted. For CWB, we computed PET by supplying minimum and maximum monthly temperature and precipitation to the Hargreaves equation (Hargreaves, 1994), and subtracting PET from monthly precipitation sum.

several additional drought events have occurred in the region. For example, 2011 had the third driest spring in the preceding 150 years in Switzerland (Meteo Schweiz, 2012), and in 2015 parts of the DACH region experienced the most severe drought event since 2003 (Hanel et al., 2018; Ionita et al., 2017; Orth, Zscheischler, & Seneviratne, 2016). Likewise, parts of Northern and Southern Europe were strongly affected by local droughts in 2016 and 2017 (García-Herrera et al., 2019). Thus, the 2018 drought was apparently not an isolated event but was consistent with a trend towards a different climate in the DACH region that includes a higher frequency of droughts at high temperatures. Importantly, “hotter droughts” (Allen, Breshears, & McDowell, 2015) might have more severe impacts on the terrestrial vegetation than “normal” droughts (i.e. droughts that occur at lower more typical temperatures). Since such hot droughts have previously not been documented in Central Europe, delineating the consequences of this climatic trend for the composition and functioning of Central European forest ecosystems will be crucial in the very near future (cf. Buras & Menzel, 2019).

Large-scale assessment of the 2018 drought impact on forest health

A prominent stress response of trees during the 2018 drought event was the widespread early discoloration and premature leaf senescence of dominant deciduous tree species, in particular European beech (*Fagus sylvatica*), which occurred at various sites in Central Europe across the DACH region and began as early as late July (Fig. 2). Aggravating this situation, coniferous tree species, primarily Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*), also showed signs of needle discoloration in the following months. Although various spatially representative

ground-based monitoring networks for the assessment of tree vitality are available across the DACH region, they are not suited to quantify drought-induced tree mortality at larger scales. Thus, the 2018 drought impacts on trees and forests mentioned here combine personal observations, reports of forest research institutes (e.g., ForstBW, 2018; LF-RP, 2018; NW-FVA, 2019) and the German report on forest conditions by the German Federal Ministry of Food and Agriculture (BMEL, 2019a). The BMEL report incorporates the pan-European International Cooperative Programme on assessment and monitoring of air pollution effects on Forests (ICP Forests) Level I plot network. The assessment presents an annual overview of crown conditions from repeatedly surveyed tree individuals since 1984 based on a 16 × 16 km grid (Michel, Seidling, & Prescher, 2018), and it provides a field-based evidence for the severe impact of the 2018 drought on forest health.

As field-based monitoring activities only produce temporally and spatially limited snapshots of forest stands or landscapes, remote sensing can critically complement field-based observations by assessments at higher spatial scale (Hartmann et al., 2018a; McDowell et al., 2015). Since physiological drought symptoms also change the light reflectance of leaves in affected trees, several remote sensing approaches are suited to assess the impact of drought events on forest health (Anderegg, Anderegg, & Huang, 2019; Anyamba & Tucker, 2012; Buras, Rammig, & Zang, 2020; Damm et al., 2018; Deshayes et al., 2006; Peng, Wu, Zhang, Wang, & Gonsamo, 2019; West, Quinn, & Horswell, 2019). Here, we employ satellite-derived Normalized Difference Vegetation Index (NDVI) data obtained from the long-term MODerate resolution Imaging Spectrometer (MODIS) dataset to assess the reduction in vegetation greenness of forests during the 2018 drought across the DACH region. The NDVI, originally developed by Rouse, Haas, Schell,



Fig. 2. Premature leaf senescence in a European beech (*Fagus sylvatica*) individual in August 2018 (left), followed by lacking leaf flushing and thus complete defoliation in the following year in May 2019 (right) in the Hardwald near Basel (Switzerland). Photo credits: Urs Weber.

Deering, & Harlan (1974) and first applied to drought monitoring by Tucker & Choudhury (1987), is a bulk information source representing vegetation greenness (i.e. leaf area combined with leaf chlorophyll content) as a function of spectrally contrasting red and near-infrared reflectance. Although the spatial resolution of MODIS is likewise limited, this mission has been ongoing since 2000 and thus allows a direct comparison between the 2003 and 2018 drought event. We computed NDVI quantiles over the period from 2000 to 2018 in order to rank the vegetation greenness relatively among all years (Buras, Rammig, & Zang, 2020; Orth, Vogel, Luterbacher, Pfister, & Seneviratne, 2016). This approach represents a modified version of the standardized vegetation index, which has been used earlier for monitoring drought stress on vegetation (Anyamba & Tucker, 2012).

NDVI quantiles across the DACH region clearly demonstrate the severe and widespread impact of the 2018 event on forest health and are in agreement with ground-based reports on early discoloration and premature leaf-shedding (Fig. 3). Under drought, lowest quantiles and thus lowest values of greenness in mid-August are the result of early leaf discoloration, premature leaf senescence, and may even indicate partial

or complete canopy dieback. Importantly, observed symptoms were more severe in 2018 than during the 2003 drought event. In fact, a detailed analysis of the NDVI data stratified into coniferous and deciduous forests empirically confirmed these observations (Fig. 4). In 2018, the area of deciduous trees that could be identified as experiencing the lowest NDVI quantiles and thus greenness was twice as large as in 2003, which is roughly 11,200 km² vs. 5600 km², respectively. In addition, low NDVI quantiles were spatially more homogeneously distributed across the DACH region in 2018 compared to 2003. This satellite-based assessment of drought impact illustrates the exceptionally strong effect of the 2018 drought event on forests in the DACH region and corroborates a recent European-wide assessment (Buras, Rammig, & Zang, 2020).

Tree mortality triggered by the 2018 drought

As a consequence of the extreme 2018 drought event, partial or complete canopy dieback was observed throughout the DACH region for a broad range of species in fall 2018, often followed by mortality of single trees, tree groups and even entire stands. Although to date no systematic and

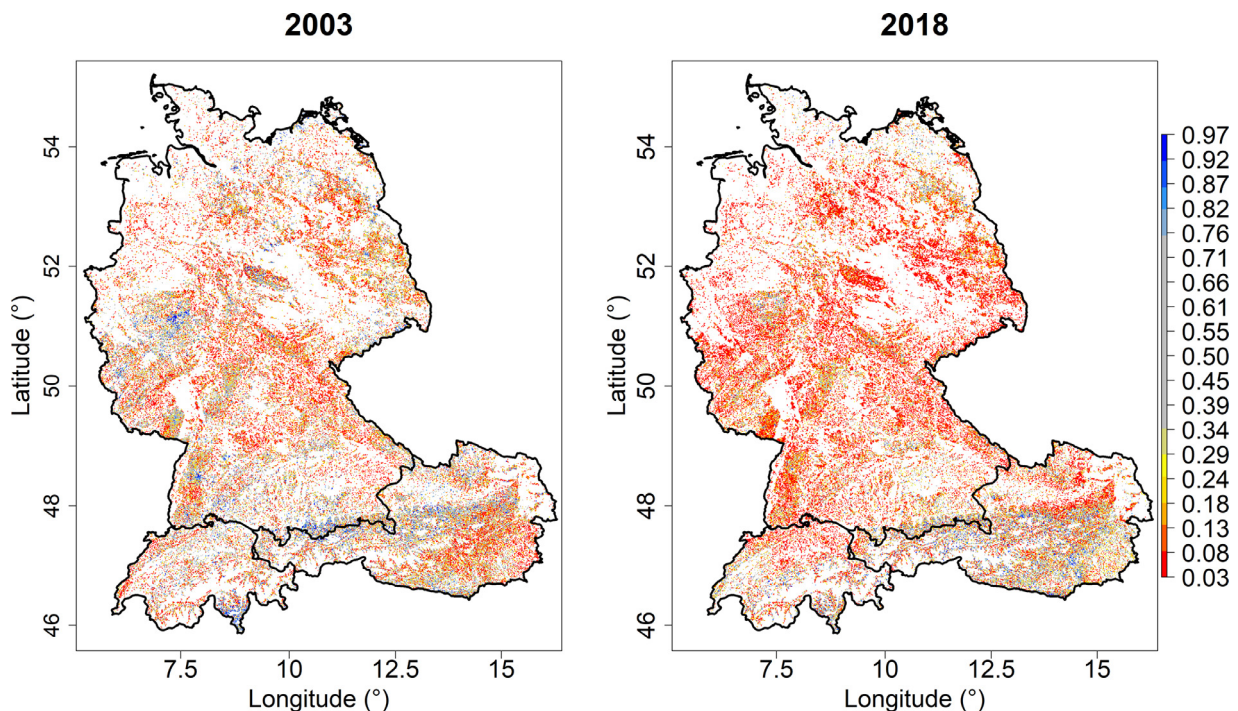


Fig. 3. Quantiles of Normalized Difference Vegetation Index (NDVI) for forested areas in Austria, Germany and Switzerland (DACH region). The quantiles have been derived from the MODIS satellite data and represent mid-August (DOY 225) relative greenness values of forests during the two drought events (2003, 2018). MODIS-NDVI data were provided by the Application for Extracting and Exploring Analysis Ready Samples (AppEARS) from the Terra satellite at a spatial resolution of 231 m x 231 m, and processed (gap-filtering and de-trending) as described in Buras, Rammig, & Zang (2020). NDVI quantiles of the drought years 2003 and 2018 were related to NDVI values of all years (2000–2018) to visualize the relative ranking of NDVI under extreme drought. Moreover, computation of quantiles for each pixel suppresses variability of the NDVI caused by superimposing effects (e.g. canopy structure, topography). Dark red colours represent the lowest quantile (0.03) and the lowest recorded greenness throughout the observation period (2000–2018), dark blue colours refer to the highest quantiles (0.97) and thus greenness values; grey values represent intermediate conditions.

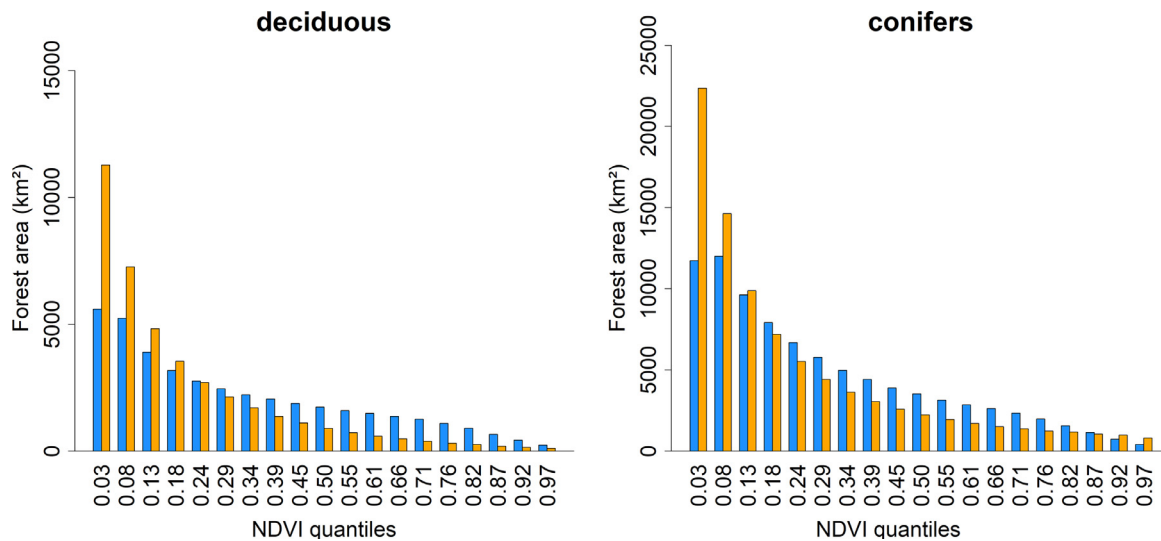


Fig. 4. Histograms of the nineteen MODIS-based NDVI quantiles corresponding to relative greenness values of forests for peak-season conditions for mid August (DOY 225) depicted in Fig. 3 but separated for deciduous and coniferous forests. Blue bars (left) refer to 2003, orange bars (right) to 2018. The separation into deciduous and coniferous trees was undertaken using the corresponding classes of the Corine Land Cover Classification (<https://land.copernicus.eu/paneurpean/corine-land-cover/clc-2012>). The lowest quantiles (0.03) refer to the lowest greenness values throughout the considered observation period (2003–2018), while the highest quantiles (0.97) represent the highest greenness values.

representative scientific assessment of the total number of affected trees is available, the German Federal Ministry of Food and Agriculture estimates that the damages caused by the 2018 drought affected millions of trees and at least 2,450 km² need to be afforested (BMEL, 2020). The most affected tree species were Norway spruce and European beech, but mortality was also reported for Scots pine, silver fir (*Abies alba*), and even sessile oak (*Quercus petraea*) and pedunculate oak (*Quercus robur*) (Fig. 5). Mortality of shallow-rooted and drought-sensitive Norway spruce was rather expected based on reports from previous heat waves and droughts (Zang, Rothe, Weis, & Pretzsch, 2011; Brinkmann, Eugster, Zweifel, Buchmann, & Kahmen, 2016; Vitali, Büntgen, & Bauhus, 2017; Brinkmann, Eugster, Buchmann, & Kahmen, 2019; Rigling et al., 2019; Vitasse et al., 2019). Furthermore, Scots pine on dry sites with limited soil water holding capacity had previously shown high mortality rates after intensive drought periods, for example in the Alps, Southern France and Southern Germany (Buras et al., 2018; Dobbertin et al., 2005; Etzold et al., 2019; Rebetez & Dobbertin, 2004; Rigling et al., 2013). The observed drought-induced mortality of European beech, silver fir, and partly even sessile or pedunculate oak, or the mortality of Scots pine on less drought-prone sites was, however, mostly unexpected (e.g. Leuzinger et al., 2005; Dietrich, Delzon, Hoch, & Kahmen, 2019; Vitasse et al., 2019). Especially the partial or complete canopy dieback of European beech trees in various stands across the region, often followed by the death of these tree individuals in 2019, was surprising. Notwithstanding, the future of this economically and ecologically important tree species has

already been intensively debated for years (cf. Ammer et al., 2005; Bolte, 2005; Leuschner, 2009; Rennenberg, Seiler, Matyssek, Gessler, & Kreuzwieser, 2004). Early senescence and partial branch dieback of European beech has also been observed during the 2003 drought (Breda, Huc, Granier, & Dreyer, 2006; Leuschner, 2009; Mayer, 2004; Raspe, Schulz, & Kroll, 2004). However, drought-induced mortality has not been documented for this species after the 2003 drought (Breda, Huc, Granier, & Dreyer, 2006).

The economic consequences of drought-induced tree mortality were severe for the forestry sector and have been estimated to amount to a loss of 3.5 billion Euros for the year 2018 in Germany (press release by the Association of German Foresters; BDF, 2019). These losses are due to the accumulation of meanwhile 160 million cubic meters of dead wood (BMEL, 2020). Aggravating this situation, millions of tree saplings planted over the past years in Germany have died due to the 2018 drought (BMEL, 2019b). The immediate and long-term consequences of the 2018 drought event on the forestry sector are substantial and are likely to increase under the predicted higher frequency of such "hotter droughts" in the near future.

Importantly, a comprehensive assessment of the extent of drought-induced mortality in forests of the DACH region is difficult because existing ground-based monitoring networks across Europe are largely not suited to consistently detect drought-induced damages at the level of individual trees over continuous areas due to their grid-based sample design. Data from existing networks therefore need to be complemented by long-term monitoring and inventory data

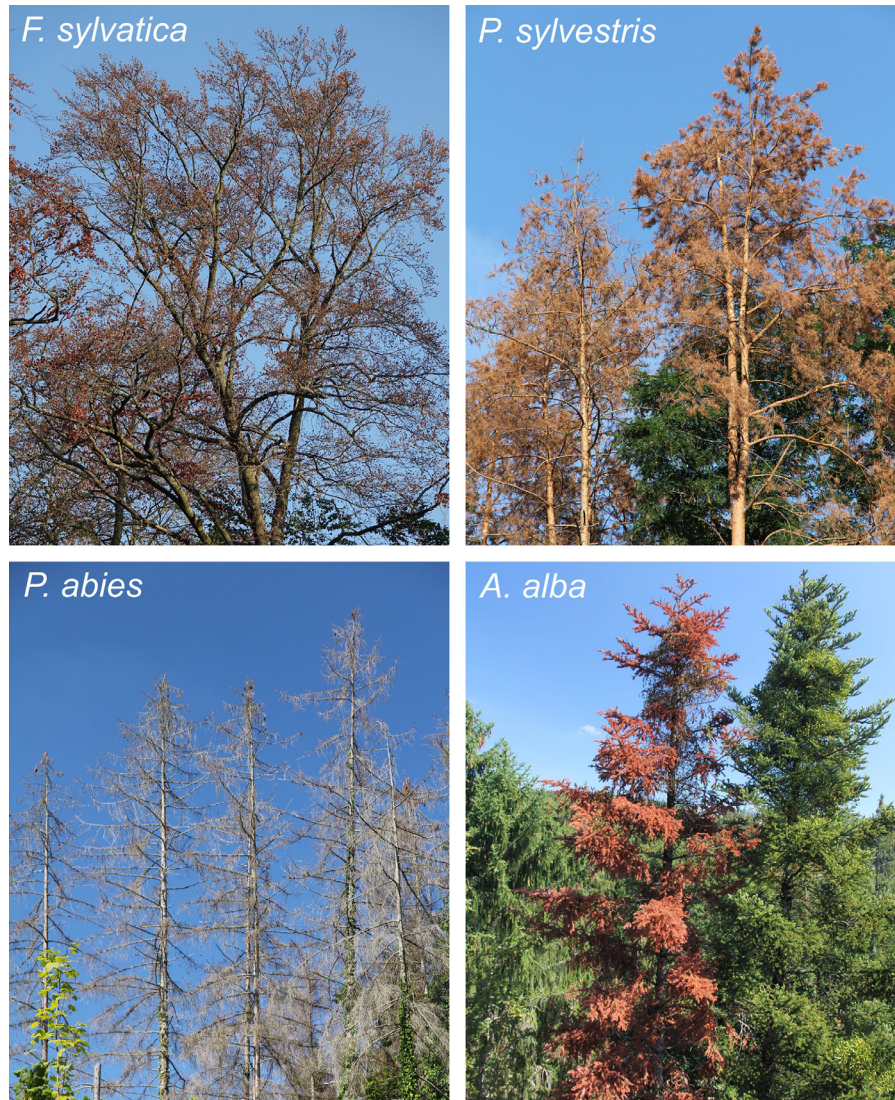


Fig. 5. Examples of drought-induced tree mortality triggered by the 2018 drought event for four important temperate European tree species at three different sites. *F. sylvatica* was observed in the Hardwald near Basel (Switzerland), *P. sylvestris* in the Vienna Woods near Tullnerbach (Austria), and *P. abies* and *A. alba* at the Swiss Canopy Crane II site in Hölstein (Switzerland).

that allow partitioning of drought-induced tree mortality and mortality rates depending on site conditions, species, tree ages or sizes, and other important parameters (cf. www.tree-mortality.net). The quantitative assessment of drought-induced tree mortality at the level of individual trees would yet be critical to detect mechanisms that influence tree survival or mortality at different temporal scales, and for characterizing the impact of forest management, sites and species on tree mortality during events such as the 2018 drought. Because such detailed assessments are highly labour demanding, ground-based plot networks need to be supported by remote sensing products with high spatial and temporal resolution (Buras, Rammig, & Zang, 2020; Damm et al., 2018; Hartmann et al., 2018a; Stovall, Shugart, & Yang, 2019). The recently released forest condition monitor (www.waldzustandsmonitor.de/en) may be

considered a first step in the direction of a near-real time monitoring of the state of European forests to identify potential early-warning indicators of tree mortality (cf. Rogers et al., 2018).

Potential causes of drought-induced tree mortality

Global change-type drought-induced tree mortality is a complex syndrome with several interdependent processes involved (McDowell et al., 2011; Meir, Mencuccini, & Dewar, 2015). Various factors, both biotic and abiotic, might ultimately and species-specifically contribute to the death of an individual tree (Waring, 1986; Anderegg et al., 2015; Wang, Peng, Kneeshaw, Larocque, & Luo, 2012).

Trees often have a legacy of reduced vigour triggered by past events evoked up to several decades in the past, increasing the individual mortality risk (Buras et al., 2018; Cailleret et al., 2017; Hauck, Leuschner, & Homeier, 2019; Timofeeva et al., 2017; Trugman et al., 2018). According to our current understanding, two tightly inter-related physiological mechanisms are involved in drought-induced mortality that may also predispose trees to subsequent pest attacks (Hartmann et al., 2018b; McDowell et al., 2008). These are assumed to be hydraulic failure through tissue dehydration and partial or complete loss of xylem functionality, and carbon starvation due to drought impacts on photosynthesis and mobilization of non-structural carbohydrates (Sevanto et al., 2014; Adams et al., 2017). In conifers, the lethal level of hydraulic failure is thought to correspond to the xylem pressure at 50% loss of hydraulic conductance, while in angiosperms the water potential at 88% loss of hydraulic conductance is believed to represent the point of no return (Barigah et al., 2013; Brodribb & Cochard, 2009; Brodribb, Bowman, Nichols, Delzon, & Burlett, 2010; Urli et al., 2013). Given a tree's demand in conduit capacity under severe drought drops below a few percent after stomatal closure, an alternative explanation is the interruption of the soil-root capillary continuum, with tissue dehydration and xylem embolism as the consequences (Körner, 2019). The fatal consequences of embolized xylem conduits only come into play when soil moisture returns and the conduits remain blocked.

Current global change-type droughts act in different ways on the physiological integrity of a plant than hydrologically comparable but cooler drought events (Adams et al., 2009; Leuzinger, Bigler, Wolf, & Körner, 2009; Williams et al., 2013). During drought, higher temperatures further increase the atmospheric vapour pressure deficit (Yuan et al., 2019), which has a larger negative effect on transpiration and net primary production than elevated temperatures or drought alone (Eamus, Boulain, Cleverly, & Breshears, 2013; RUEHR, Gast, Weber, Daub, & Arneith, 2016). During low soil moisture and high evaporative demand, leaf water potentials will reach species-specific minimal threshold values that trigger stomatal closure (Birmi et al., 2018; Brodribb, Holbrook, Edwards, & Gutierrez M, 2003; Cruziat, Cochard, & Ameglio, 2002; Li et al., 2016; Martin-StPaul, Delzon, & Cochard, 2017). After stomatal closure, residual water loss continues through the cuticle (g_{\min}), via incompletely closed stomata or through other tissues such as bark (Choat et al., 2018; Cochard, 2019; Duursma et al., 2019). When this residual loss of water is not replenished from soil sources this will cause a critical dehydration of living tissue and can lead to a collapse of the hydraulic system, with fatal consequences when the conduits cannot be refilled when the moisture regime improves (Choat et al., 2018; Körner, 2019). Under normal climatic conditions, g_{\min} is approximately 100-times smaller than the maximum stomatal conductance (Kerstiens, 1996; Körner, 1994; Matyssek & Herrpich, 2017), but it may

increase steeply at temperatures above 40°C (Billon et al., 2020; Riederer & Schreiber, 2001; Schuster et al., 2016).

Physiological integrity of trees during the 2018 drought event

It is likely that the exceptional climatic conditions experienced in 2018 in the DACH region directly impaired the physiological integrity of trees (Adams et al., 2009; Leuzinger, Bigler, Wolf, Körner, 2009; Williams et al., 2013). During the 2018 heat wave, leaf temperatures above 40°C were measured in four urban broad-leaved tree species in Würzburg, Germany (Böll et al., unpublished) and up to 40°C in four forest broad-leaved tree species at the Swiss Canopy Crane II site in Hölstein, Switzerland (Hoch et al., unpublished). This might have resulted in substantial residual water loss as g_{\min} increases dramatically at such high leaf temperatures as mentioned above.

To assess the water status of trees during the 2018 drought event, midday leaf water potentials (P_{\min}) were assessed for 20 coniferous and broad-leaved tree species at several sites in the DACH region (Table 1). For many of the investigated tree species, observed P_{\min} were in the range of the most negative values ever reported under field conditions. In eight of the twenty species studied, P_{\min} values indicate that the air entry point of xylem embolism formation had been reached by mid-August 2018. These data confirm that during the 2018 drought event many of the observed trees in the DACH region must have reached their physiological limits, beyond which fatal tissue dehydration takes place, accompanied by a loss of the hydraulic integrity of the trees (Choat et al., 2018; Delzon & Cochard, 2014; Tyree & Sperry, 1989). Direct measurements of xylem hydraulic conductivity loss in sun-exposed branches in early September at the Swiss Canopy Crane II site in Hölstein, Switzerland, showed that European beech trees at this site were embolized on average by $56.7 \pm 3.2\%$ (mean \pm SE; $n = 32$ branches, 12 trees). Most of these trees showed partial to complete canopy dieback but no obvious signs of mortality. Yet, mortality of European beech trees was reported from other locations in the DACH region as mentioned above. In contrast to European beech, some Norway spruce trees showed complete loss of hydraulic conductivity in upper-canopy branches at the Swiss Canopy Crane II site; these individuals all died off in the following weeks. Our data suggest that drought-induced hydraulic failure is a strong indicator of severe damage observed in temperate forests as a consequence of the 2018 drought event. Because the degree of drought-induced embolism formation was not explored in temperate tree species for the drought events in 2003 or 2015 (e.g. Breda, Huc, Granier, & Dreyer, 2006; Dietrich, Delzon, Hoch, Kahmen, 2019; Leuzinger, Zotz, Asshoff, & Körner, 2005; Tomasella et al., 2018), the physiological data collected in 2018 are unique for temperate European forests. They

Table 1. Minimum leaf water potential (P_{\min} , MPa) measured in mid-August 2018, xylem pressure at 12% loss of hydraulic conductance (P_{12} , MPa) and the P_{12} hydraulic safety margin (HSM $P_{\min}-P_{12}$) for 18–20 temperate tree species at four sites in Germany (from North to South: Unterlüß, Göttingen, Kranzberg, Freiburg) and one site in Switzerland (Hölstein). A negative HSM $P_{\min}-P_{12}$ (in bold) indicates that the air-entry point of embolism formation has been crossed. At all sites, leaf samples were collected from the uppermost canopy of mature trees with the exception of the site in Freiburg, which was only established in 2011. For the P_{\min} measurements, one to eight leaves were measured and averaged per individual tree. The xylem vulnerability curves were constructed according to common protocols with the flow centrifuge technique (Delzon, Douthe, Sala, & Choat 2010; Schuldt et al., 2016); missing data were taken from the literature except for the two ring-porous species *F. excelsior* and *Q. robur* that were excluded (¹ Choat et al., 2012; ² Lübke et al. unpublished; ³ Dietrich, Delzon, Hoch, Kahmen, 2019; ⁴ Tomasella et al., 2018; ⁵ Schuldt et al. unpublished). Values are mean \pm SE. Further given are sampling date for P_{\min} measurements, average tree height per species and site (H), and number of trees (n) and branches (in parentheses) for P_{\min} and P_{12} measurements.

Species	Location	Date	H (m)	P_{\min} (MPa)	$n P_{\min}$	P_{12} (MPa)	$n P_{12}$	HSM $P_{\min}-P_{12}$
<i>Abies alba</i>	Hölstein, CH	8/8/2018	34.0	-1.82 to -2.63	10	$-3.02 \pm 0.15^{1)}$	5	1.20
<i>Acer campestre</i>	Göttingen, DE	8/23/2018	13.3	-2.25 to -3.00	3	-3.69 ± 0.55	5	0.69
<i>Acer platanoides</i>	Göttingen, DE	8/23/2018	17.5	-2.63 to -3.38	2	-2.87 ± 0.63	5	-0.41
	Freiburg, DE	8/14/2018	3.7	-2.20 to -2.68	4	-3.71 ± 0.05	18	1.03
<i>Acer pseudoplatanus</i>	Göttingen, DE	8/23/2018	15.0	-1.24 to -1.88	2	-2.26 ± 0.34	6	0.38
	Hölstein, CH	8/7/2018	31.0	-1.98 to -2.30	5	$-2.53 \pm 0.43^{2)}$	5	0.23
<i>Alnus glutinosa</i>	Göttingen, DE	8/23/2018	9.3	-1.19 to -1.28	3	-1.37 ± 0.04	5	0.09
<i>Betula pendula</i>	Freiburg, DE	8/14/2018	4.2	-0.87 to -2.45	4	-2.18 ± 0.05	16	-0.27
<i>Carpinus betulus</i>	Göttingen, DE	8/23/2018	13.3	-1.83 to -2.38	5	-3.47 ± 0.26	5	1.09
	Hölstein, CH	8/8/2018	20.0	-1.70 to -2.30	5	$-3.61 \pm 0.14^{3)}$	4	1.82
	Unterlüß, DE	8/19/2018	32.4	-2.01 to -2.66	3	-2.67 ± 0.10	3 (11)	0.01
<i>Fagus sylvatica</i>	Göttingen, DE	8/22/2018	20.0	-1.17 to -2.39	3	-2.37 ± 0.11	7	-0.02
	Kranzberg, DE	7/29/2018	28.0	-1.60 to -2.20	8	$-2.64 \pm 0.14^{4)}$	7-8	0.44
	Hölstein, CH	8/7/2018	31.0	-2.08 to -3.32	10	-2.74 ± 0.16	9	-0.58
<i>Fraxinus excelsior</i>	Göttingen, DE	8/21/2018	8.0	-3.68	1			
	Hölstein, CH	8/16/2018	33.0	-2.25 to -2.80	3			
<i>Juglans regia</i>	Göttingen, DE	8/23/2018	15.0	-1.29 to -1.54	3	-1.24 ± 0.33	3	-0.30
<i>Larix decidua</i>	Freiburg, DE	8/14/2018	3.1	-1.71 to -2.53	4	-2.98 ± 0.10	16	0.45
	Unterlüß, DE	8/23/2018	28.6	-1.96 to -2.03	3	-2.89 ± 0.04	3 (7)	0.86
<i>Picea abies</i>	Freiburg, DE	8/14/2018	2.0	-0.91 to -3.65	4	-3.02 ± 0.04	15	-0.63
	Kranzberg, DE	7/29/2018	32.0	-1.67 to -2.07	6	$-3.15 \pm 0.09^{4)}$	7-8	1.08
	Hölstein, CH	8/16/2018	36.0	-1.67 to -4.20	10	-3.08 ± 0.05	9 (22)	-1.12
<i>Pinus sylvestris</i>	Freiburg, DE	8/14/2018	2.7	-1.37 to -2.43	4	-2.43 ± 0.06	19	0.00
	Hölstein, CH	8/7/2018	37.0	-1.72 to -2.10	10	$-2.36 \pm 0.27^{3)}$	3	0.64
<i>Populus alba</i>	Göttingen, DE	8/22/2018	12.5	-1.33 to -1.60	2	-0.87 ± 0.26	4	-0.73
<i>Pseudotsuga menziesii</i>	Unterlüß, DE	8/21/2018	40.7	-2.41 to -2.50	3	-2.70 ± 0.10	3 (8)	0.20
<i>Quercus petraea</i>	Hölstein, CH	8/17/2018	33.0	-1.77 to -2.77	10	$-3.52 \pm 0.52^{3)}$	2	1.75
<i>Quercus robur</i>	Freiburg, DE	8/14/2018	1.8	-2.88 to -3.16	4			
<i>Salix caprea</i>	Göttingen, DE	8/22/2018	15.0	-1.31 to -1.47	2	-1.22 ± 0.23	4	-0.25
<i>Sorbus torminalis</i>	Hölstein, CH	8/16/2018	20.0	-3.30 to -4.53	3	$-4.79 \pm 0.14^{5)}$	2	0.26
<i>Tilia cordata</i>	Göttingen, DE	8/23/2018	16.0	-1.67 to -1.80	3	-2.50 ± 0.06	5	0.70

demonstrate the severity by which the 2018 drought impaired the water supply status of dominant temperate tree species.

The widely observed premature leaf senescence in July and August 2018, particularly for European beech, could have been a response to reduce leaf area in the attempt to protect the hydraulic system from severe and lethal dehydration. This phenomenon is indeed well described for temperate broad-leaved tree species (Breda, Huc, Granier, & Dreyer, 2006; Marchin, Zeng, Hoffmann, 2010; Munne-Bosch & Alegre, 2004). Early leaf senescence might either

be induced by hydraulic failure of the petiole (Hochberg et al., 2017; Wolfe, Sperry, & Kursar, 2016), or by metabolic dysfunctions in foliar cells as a result of high tissue temperatures or photo-oxidative stress (Juvany, Müller, & Munné-Bosch, 2013; Lange, 1959; Martinez-Vilalta, Anderegg, Sapes, & Sala, 2019; Oliver & Bewley, 1997; Pflug et al., 2018). Investigations at the Swiss Canopy Crane II site in Hölstein, Switzerland, revealed that discoloured European beech leaves showing signs of early senescence in early August had foliar nitrogen (N) contents of $1.1 \pm 0.1\%$ ($n = 10$ trees), which is similar to the N concentration of

leaf-litter collected in autumn 2017 ($1.0 \pm 0.1\%$, $n = 10$ litter traps). This indicates that early senescence in European beech leaves most likely resulted from a controlled physiological process, initiated to reduce the risk of lethal tissue dehydration (cf. Breda, Huc, Granier, & Dreyer, 2006; Marchin, Zeng, & Hoffmann, 2010; Ruehr, Gast, Weber, Daub, & Arneth, 2016). Despite the protective measure of early senescence, we observed that trees - in particular European beech - suffered from substantial loss of hydraulic conductivity and massive canopy dieback (Fig. 2; Fig. 6). Either premature leaf senescence occurred too late, or it did not guarantee sufficient protection from lethal tissue dehydration caused by residual water loss through the bark (e.g. Oren & Pataki, 2001).

To assess the recovery potential of canopy dieback observed in European beech canopies, 795 trees presenting signs of early leaf coloration during August and September

2018 were monitored and compared with 138 ‘healthy’ nearby control trees displaying regular leaf senescence at three sites near Basel, Zurich and Schaffhausen in Switzerland. A survey in April 2019 revealed that leaf flushing of individuals, especially from stands with good soil water holding capacity, was often unaffected despite extraordinary dry winter and spring climatic conditions. However, one fourth of the drought-affected trees showed partial crown dieback in 2019, and in one third of these trees more than 50% of the tree crown was dead in April 2019 (Table 2). In contrast, almost all of the less affected control trees had an intact crown at that time. Preliminary data confirm that the water transport capacity of branches with legacy effects had not been restored in the following spring 2019 (Fig. 6). Extremely low precipitation rates during winter and spring might have aggravated this situation. Further investigations will reveal whether the recovery from xylem embolism is

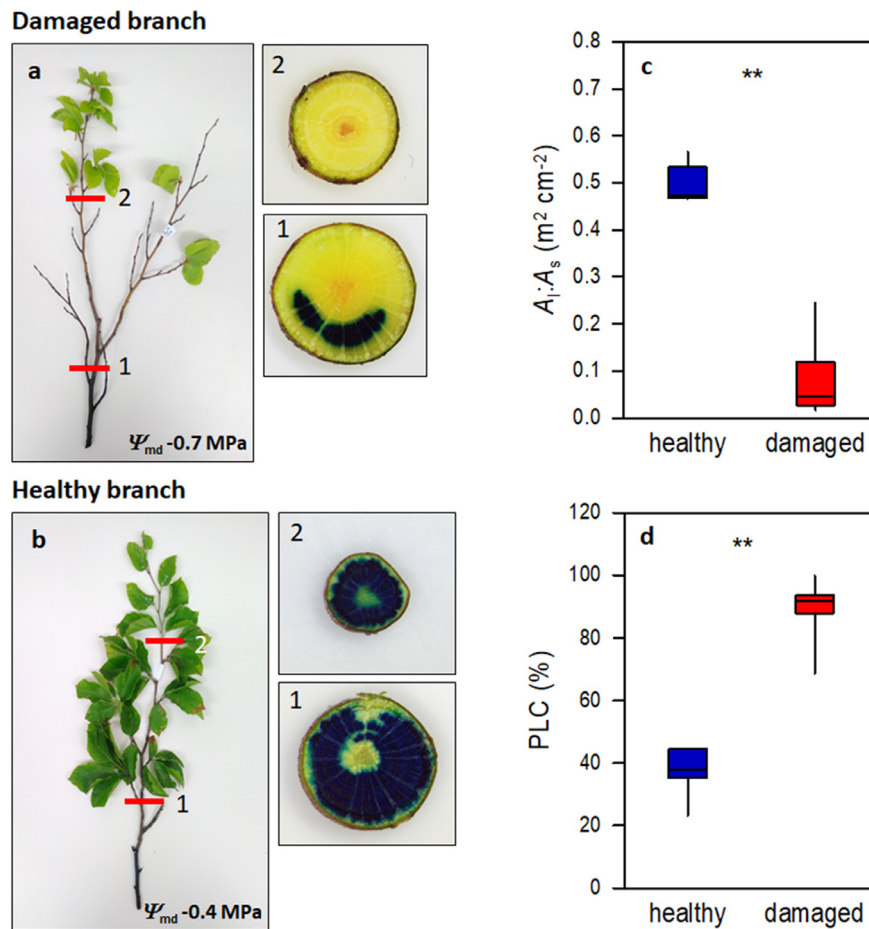


Fig. 6. Visualisation of the conductive xylem (a, b), the leaf-to-sapwood area ratio ($A_l:A_s$, c) and percentage loss of hydraulic conductance (PLC, d) of healthy and damaged sun-exposed upper-canopy branches of mature *F. sylvatica* trees at the Swiss Canopy Crane II site in Hölstein, Switzerland. For the visualization of the conductive xylem area, branches were collected in spring 2019 and subsequently placed in a 2% methylene blue solution for 24 h in the greenhouse allowing for transpiration-driven water uptake of the staining solution. For determining the supported leaf area per cross-section and the native degree of embolism, branches were collected from 5 healthy and 6 damaged trees in early summer 2019; the percentage loss of conductance (PLC) was measured according to standard protocols (Torres-Ruiz et al., 2015). Both $A_l:A_s$ ($\chi^2=7.67$, $df=1$, $P<0.01$) and PLC ($\chi^2=7.50$, $df=1$, $P<0.01$) differed significantly between healthy and damaged branches (Kruskal–Wallis test).

Table 2. Legacy effects for *Fagus sylvatica* at three sites near Basel, Zurich and Schaffhausen in Switzerland. In 2018, a total of 933 tree individuals were selected. Of these, 138 trees were categorized as healthy, while 795 showed signs of premature leaf senescence or partial canopy dieback. In April 2019, the same individuals were surveyed once more and the bark and crown condition documented. Given are tree individuals from both groups (healthy and damaged trees, in numbers or percentage) that show signs of bark damage, bark exudation, and/or crown mortality between 20% and 100%.

State of the trees	Healthy trees (n=138)		Damaged trees (n=795)	
	number	%	number	%
Bark damaged	5	3.6	65	8.2
Bark exudation	8	5.8	147	18.5
Crown mortality > 20%	1	0.7	131	16.5
Crown mortality > 50%	0	0	45	5.7
Crown mortality = 100%	0	0	10	1.3

possible in the season after a drought, or if it requires the formation of new woody tissue to fully restore hydraulic functionality (McDowell, Brodribb, & Nardini, 2019; Ruehr, Grote, Mayr, & Arneht, 2019).

Expected mid- and long-term effects

Trees suffering from drought-induced mortality often have a legacy of reduced vigour (cf. Cailleret et al., 2017; Kannenberg et al., 2019). In addition to the immediate climatic conditions experienced in 2018, preceding drought events could thus have triggered the high mortality rates observed. Long-term effects of the 2018 drought might well extend beyond the currently observed damages, especially as the summer in 2019 was again particularly dry and hot in many areas across the DACH region, aggravating stress on already weakened trees. Impaired carbon dynamics can limit regrowth of new woody tissue and may be responsible for patterns of delayed tree mortality after drought exposure (Trugman et al., 2018).

Because the defence metabolism can be impaired after a drought event, trees are vulnerable to insect or pathogen infestation in the following growing season (Bigler, Bräker, Bugmann, Dobbertin, & Rigling, 2006; Huang et al., 2020). Consequently, drought is reportedly the major cause of massive bark beetle outbreak in the actual and the following years (Christiansen, Waring, & Berryman, 1987; Hart, Veblen, Eisenhart, Jarvis, & Kulakowski, 2014). In Norway spruce, resin exudation and thus defence capability declines with a reduction in relative tissue water content (Netherer et al., 2015). This makes this economically important tree species highly susceptible to successive infestations by Eurasian spruce bark beetle (*Ips typographus*) during and after drought-exposure, especially at lower elevations (Biedermann et al., 2019; Hentschel et al., 2014; Kazda & Pichler, 1998; Lévesque et al., 2013; Seidl, Schelhaas, & Lexer, 2011; Seidling, 2007; Vitali, Büntgen, & Bauhus, 2017). Aggravating this situation, warmer winters are expected to increase bark beetle annual population levels and distribution (Goodsman et al., 2018). As a consequence, increased

Norway spruce mortality will most likely continue in the coming years, especially at lower or mid-range elevations outside its natural range. In 2019, for example, the level of bark beetle-infested wood has for the first time reached over one million cubic metres since 2005 in Switzerland (Stroheker, Forster, & Queloz, 2020).

Weakened and damaged European beech trees, on the other hand, are vulnerable to pathogen attacks by microfungus infections, a phenomenon well-described for this species after severe drought (Jung, 2009; Lonsdale, 1980; Schindler, 1951), as well as to insect attacks by beech splendour beetle (*Agrilus viridis*; Gößwein & Lemme, 2017; von Vietinghoff-Riesch & Vité, 1952). Although European beech would naturally cover more than 60% of the area of Germany (Bohn et al., 2003), the impact of the 2018 drought event suggests that a future hotter and drier climate could severely affect the vitality of European beech, particularly at lower elevations and even in the centre of its distribution (cf. Buras & Menzel, 2019; Knutzen, Dulamsuren, Meier, & Leuschner, 2017; Zimmermann, Hauck, Dulamsuren, & Leuschner, 2015).

Conclusion and outlook

The 2018 drought and heatwave has set a new benchmark for future drought events, and has marked a change in Central European forest dynamics. Current reports on drought-induced tree mortality are reminiscent of the internationally acknowledged and historical discussions on the European beech decline ('Buchensterben') of the late 1940s and forest decline ('Waldsterben') of the early 1980s. In the late 1940s, several exceptionally dry years resulted in large-scale die-off of European beech that was explained by repeated extreme events of drought and late frost (Brück-Dyckhoff, Petercord, & Schopf, 2019; Schindler, 1951). In the 1980s, the apparent widespread forest dieback across large areas of Central and Eastern Europe was associated with air pollution, both dry and wet deposition by acid rain, sulphur oxide, heavy metals, oxidized and reduced N compounds and high ozone levels (Schulze, 1989; Schütt & Cowling,

1985; Ulrich, 1990). Remarkably, the symptoms of dieback became epidemic after the centennial 1976 drought. In the following years, air pollution was reduced by desulfurizing emissions from industrial installations and the mandatory introduction of automobile catalysers. Because current damages to trees are also ubiquitous, media and stakeholders have meanwhile introduced the term ‘Waldsterben 2.0’. We do not recommend using such terminology because today and back in the 1980s trees were dying, not forests. Today, selected species may be massively affected by climate change such as Norway spruce, which has extensively been planted outside its natural range. However, tree species showing very high mortality rates will be replaced by others over time. As a consequence, we will most likely experience tremendous forest changes but not a complete dieback. Such a conversion will nonetheless be harsh for the forestry sector and for the general population as the forests we have appreciated for generations will change, at least in given areas.

The high mortality rates observed in 2018 illustrate that climate change is acting on the structure and composition of forests in the DACH region, even if quantification of the direct and indirect effects remains challenging. At the stand level, species-specific differences in drought sensitivity might further alter tree species dominance and species composition (Cavin, Mountford, Peterken, & Jump, 2013; Weber, Bugmann, Fonti, & Rigling, 2008), especially if it likewise affects tree regeneration (Wohlgemuth, Gallien, & Zimmermann, 2016). In this context, it is important to consider how the resilience of forests to disturbance in Central Europe can be enhanced by management practices. Changes in forestry practices initiated by singular or repeated drought events might have even stronger impacts on the future composition of Central European forests than the drought events themselves. The likelihood that such shifts in forest policy will be implemented also highlights the need for intensified research on the consequences of drought events on individual tree species, different site conditions and forest ecosystems. For instance, various sources advocate a paradigm shift from monocultures towards mixed forest stands in order to compensate for the potential loss of individual species. Although tree diversity is not systematically related to increased drought resistance of forests (Forrester et al., 2016; Grossiord, 2019), mixing appropriate species to increase the likelihood of complementary effects might indeed be able to mitigate drought impacts (Ammer, 2017; Gonzalez de Andres et al., 2018; Anderegg et al., 2018). In addition, non-native temperate tree species from Northern America, Eastern Europe or Central Asia are frequently referred to as an all-in-one solution. Given the longevity of trees, however, it remains questionable if such species should be introduced to our forests; they would not only need to be economically profitable and resistant against local pathogens but also need to be non-invasive and able to provide ecological functions including host-insect interactions.

The current controversial discussions on the suitability of Douglas fir (*Pseudotsuga menziesii*), a tree species imported from Northern America a century ago as supplement or substitute for Norway spruce, shows the difficulty of such suitability assessments (cf. Spiecker, Lindner, & Schuler, 2019). Nevertheless, the first evidence of the impact of the 2018 drought event on forests in the DACH region highlights the need to adapt current silvicultural measures in order to prepare Central European forests for future climatic conditions.

Finally, our assessment revealed the limitation of current European ground-based measures for spatially continuously monitoring drought impacts on forest growth and mortality, which is vital for the mechanistic and ecological interpretation of the consequences of extreme climatic events. A core aim of the ICP Forests Level II plot network, for example, is the monitoring of atmospheric deposition as a response to the above mentioned air pollution in the 1980s (Michel et al. 2018). Although these plots continuously monitor relevant parameters for the assessment of drought impacts, their number is unfortunately limited. However, in order to understand how site characteristics, management practices, species identity and community composition interact in determining the drought vulnerability of trees or forest stands, physiologically meaningful stress variables are needed at high spatial and temporal resolution. Novel remote sensing-based techniques suited to assess the water status of trees as a cross-scale indicator of mortality risk are promising in this regard (cf. Damm et al., 2018; Hunt, Ustin, & Riaño, 2013; Martínez-Vilalta et al., 2019). These techniques include microwave systems (Konings, Rao, & Steele-Dunne, 2019; Rao, Anderegg, Sala, Martínez-Vilalta, & Konings, 2019) or optical indices based on infrared reflectance (Marusig et al., 2020; Sun et al., 2019). Although current spatial and spectral resolution often limit their applicability, future space-born remote sensing missions providing data free of charge will allow to monitor forest health at high resolution.

Acknowledgements

This assessment evolved from a meeting of the working group ‘Ecosystem Research’ of the Ecological Society of Germany, Austria and Switzerland, held at the University of Basel in June 2019. We thank Tanja Sanders for helpful discussions, Miriam Fischer for provision of leaf water potential data from Unterlüß, Silvan Pfefferkorn for constructing the xylem vulnerability curves for all trees at the site in Göttingen, Celine Aymon and Martin Kistler for field data on beech trees in Switzerland, Charles Nock for tree height data from Freiburg, and Roman Link for data on the native degree of embolism in spruce and beech. The authors thank one anonymous reviewer, Kris Verheyen and the editor for comments that helped improving the manuscript. Peter Hajek was funded by DFG grant number 384026712. Allan

Buras, Anja Rammig and Christian Zang acknowledge funding by the Bavarian Ministry of Science and the Arts in the context of the Bavarian Climate Research Network (Bay-KliF), Mana Gharun acknowledges funding by the Swiss National Science Foundation project ICOS-CH Phase 2 (20FI20_173691), and Ansgar Kahmen financial support by the Swiss Federal Office for the Environment for the Swiss Canopy Crane II site.

References

- Adams, H. D., Guardiola-Claramonte, M., Barron-Gafford, G. A., Villegas, J. C., Breshears, D. D., Zou, C. B., Troch, P. A., & Huxman, T. E. (2009). Temperature sensitivity of drought-induced tree mortality portends increased regional die-off under global-change-type drought. *Proceedings of the National Academy of Sciences of the United States of America*, *106*, 7063–7066.
- Adams, H. D., Zeppel, M. J. B., Anderegg, W. R. L., Hartmann, H., Landhäusser, S. M., Tissue, D. T., et al. (2017). A multi-species synthesis of physiological mechanisms in drought-induced tree mortality. *Nature Ecology & Evolution*, *1*, 1285–1291.
- Allen, C. D., Breshears, D. D., & McDowell, N. G. (2015). On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere*, *6* Art129.
- Ammer, C. (2017). Unravelling the importance of inter- and intraspecific competition for the adaptation of forests to climate change. In F. M. Canovas, U. Lüttge, R. Matyssek (Eds.), *Progress in botany*. Switzerland: Springer.
- Ammer, C., Albrecht, L., Borchert, H., Brosinger, F., Dittmar, C., Elling, W., et al. (2005). Zur Zukunft der Buche (*Fagus sylvatica* L.) in Mitteleuropa. *Allgemeine Forst und Jagdzeitung*, *176*, 60–67.
- Anderegg, W. R. L., Anderegg, L. D. L., & Huang, C.-Y. (2019). Testing early warning metrics for drought-induced tree physiological stress and mortality. *Global Change Biology*, *25*, 2459–2469.
- Anderegg, W. R. L., Hicke, J. A., Fisher, R. A., Allen, C. D., Aukema, J., Bentz, B., et al. (2015). Tree mortality from drought, insects, and their interactions in a changing climate. *New Phytologist*, *208*, 674–683.
- Anderegg, W. R. L., Konings, A. G., Trugman, A. T., Yu, K., Bowling, D. R., Gabbitas, R., Karp, D. S., et al. (2018). Hydraulic diversity of forests regulates ecosystem resilience during drought. *Nature*, *561*, 538–541.
- Anyamba, A., & Tucker, C. J. (2012). Historical perspectives on AVHRR NDVI and vegetation drought monitoring. In B. D. Wardlow, M. C. Anderson, J. P. Verdin (Eds.), *Remote sensing of drought: Innovative monitoring approaches* (pp. 23–44). CRC Press.
- Barigah, T. S., Charrier, O., Douris, M., Bonhomme, M., Herbet, S., Améglio, T., et al. (2013). Water stress-induced xylem hydraulic failure is a causal factor of tree mortality in beech and poplar. *Annals of Botany*, *112*, 1431–1437.
- BDF (Bund Deutscher Forstleute). (2019). *Der Wald ist in Gefahr - Die Politik muss handeln*. Pressemitteilung: Marshallplan für den Wald. 29.03.2019 https://www.bdf-online.de/fileadmin/user_upload/www_bdf-online_de/pdf/2019/19-05_Wald_in_Gefahr_-_Marshallplan_fuer_den_Wald_noetig.pdf.
- Biedermann, P. H. W., Müller, J., Grégoire, J.-C., Gruppe, A., Hage, J., Hammerbacher, A., Hofstetter, R. W., Kandasamy, D., Kolarik, M., Kostovcik, M., et al. (2019). Bark beetle population dynamics in the Anthropocene: Challenges and solutions. *Trends in Ecology & Evolution*, *34*, 914–924.
- Bigler, C., Bräker, O. U., Bugmann, H., Dobbertin, M., & Rigling, A. (2006). Drought as an inciting mortality factor in Scots pine stands of the Valais, Switzerland. *Ecosystems*, *9*, 330–343.
- Billon, L.-M., Blackmann, C., Cochard, H., Adnane, H., Cartailleur, J., Souchal, R., & Torres-Ruiz, J. M. The DroughtBox: A new standard tool for phenotyping plant residual transpiration. *Plant, Cell & Environment*, in press. <https://doi.org/10.1111/pce.13750>
- Birami, B., Gattmann, M., Heyer, A. G., Grote, R., Arneth, A., & Ruehr, N. K. (2018). Heat waves alter carbon allocation and increase mortality of Aleppo pine under dry conditions. *Frontiers in Forests and Global Change*, *1*, 1–17.
- BMEL (Bundesministerium für Ernährung und Landwirtschaft). (2019a). Ergebnisse der Waldzustandserhebung 2018. (https://www.bmel.de/DE/Wald-Fischerei/Waelder/_texte/Waldzustandserhebung.html).
- BMEL (Bundesministerium für Ernährung und Landwirtschaft). (2019b). Deutschlands Wald im Klimawandel - Eckpunkte und Maßnahmen Diskussionspapier zum Nationalen Waldgipfel, 25.09.2019. (https://www.bmel.de/SharedDocs/Downloads/Landwirtschaft/Wald-Jagd/Wald_Diskussionspapier.html).
- BMEL (Bundesministerium für Ernährung und Landwirtschaft). (2020). Waldschäden: Bundesministerium veröffentlicht aktuelle Zahlen, Pressemitteilung Nr 40/2020. (<https://www.bmel.de/SharedDocs/Pressemitteilungen/DE/2020/040-wald-schaeden.html>).
- Bohn, U., Neuhäusl, R., Gollub, G., Hettwer, C., Neuhäuslová, Z., Raus, T., Schlüter, H., & Weber, H. (2003). Bonn, Germany: Bundesamt für Naturschutz (BfN)/Federal Agency for Nature Conservation.
- Bolte, A. (2005). Zur Zukunft der Buche in Mitteleuropa. *AFZ-Der Wald* 20–21.
- Breda, N., Huc, R., Granier, A., & Dreyer, E. (2006). Temperate forest trees and stands under severe drought: A review of eco-physiological responses, adaptation processes and long-term consequences. *Annals of Forest Science*, *63*, 625–644.
- Brinkmann, N., Eugster, W., Buchmann, N., & Kahmen, A. (2019). Species-specific differences in water uptake depth of mature temperate trees vary with water availability in the soil. *Plant Biology*, *21*, 71–81.
- Brinkmann, N., Eugster, W., Zweifel, R., Buchmann, N., & Kahmen, A. (2016). Temperate tree species show identical response in tree water deficit but different sensitivities in sap flow to summer soil drying. *Tree Physiology*, *36*, 1508–1519.
- Brodribb, T. J., Bowman, D. J. M. S., Nichols, S., Delzon, S., & Burtlett, R. (2010). Xylem function and growth rate interact to determine recovery rates after exposure to extreme water deficit. *New Phytologist*, *188*, 533–542.
- Brodribb, T. J., & Cochard, H. (2009). Hydraulic failure defines the recovery and point of death in water-stressed conifers. *Plant Physiology*, *149*, 575–584.
- Brodribb, T. J., Holbrook, N. M., Edwards, E. J., & Gutierrez M, V. (2003). Relations between stomatal closure, leaf turgor and xylem vulnerability in eight tropical dry forest trees. *Plant, Cell & Environment*, *26*, 443–450.
- Brück-Dyckhoff, C., Petercord, R., & Schopf, R. (2019). Vitality loss of European beech (*Fagus sylvatica* L.) and infestation by the European beech splendour beetle (*Agrilus viridis*

- L., Buprestidae, Coleoptera). *Forest Ecology and Management*, 432, 150–156.
- Buras, A., & Menzel, A. (2019). Projecting tree species composition changes of European forests for 2061–2090 under RCP 4.5 and RCP 8.5 scenarios. *Frontiers in Plant Science*, 9, 1–13.
- Buras, A., Rammig, A., & Zang, C. (2020). Quantifying impacts of the drought 2018 on European ecosystems in comparison to 2003. *Biogeosciences*, 17, 1655–1672.
- Buras, A., Schunk, C., Zeiträg, C., Herrmann, C., Kaiser, L., Lemme, H., Straub, C., Taeger, S., Gößwein, S., Klemmt, H.-J., et al. (2018). Are Scots pine forest edges particularly prone to drought-induced mortality. *Environmental Research Letters*, 13, 025001.
- Cailleret, M., Jansen, S., Robert, E. M. R., Desoto, L., Aakala, T., Antos, J. A., Beikircher, B., Bigler, C., Bugmann, H., Caccianiga, M., et al. (2017). A synthesis of radial growth patterns preceding tree mortality. *Global Change Biology*, 23, 1675–1690.
- Camenisch, C., Brázdil, R., Kiss, A., Pfister, C., Wetter, O., Rohr, C., Contino, A., & Retsö, D. (2020). Extreme heat and drought in 1473 and their impacts in Europe in the context of the early 1470s. *Regional Environmental Change*, 20, 19.
- Cavin, L., Mountford, E. P., Peterken, G. F., & Jump, A. S. (2013). Extreme drought alters competitive dominance within and between tree species in a mixed forest stand. *Functional Ecology*, 27, 1424–1435.
- Choat, B., Brodribb, T. J., Brodersen, C. R., Duursma, R. A., López, R., & Medlyn, B. E. (2018). Triggers of tree mortality under drought. *Nature*, 558, 531–539.
- Choat, B., Jansen, S., Brodribb, T. J., Cochard, H., Delzon, S., Bhaskar, R., Bucci, S. J., Feild, T. S., Gleason, S. M., Hacke, U. G., et al. (2012). Global convergence in the vulnerability of forests to drought. *Nature*, 491, 752–755.
- Christiansen, E., Waring, R. H., & Berryman, A. A. (1987). Resistance of conifers to bark beetle attack: Searching for general relationships. *Forest Ecology and Management*, 22, 89–106.
- Cochard, H. (2019). A new mechanism for tree mortality due to drought and heatwaves. bioRxiv, Feb. 3, 2019. <https://doi.org/10.1101/531632>
- Cruziat, P., Cochard, H., & Ameglio, T. (2002). Hydraulic architecture of trees: Main concepts and results. *Annals of Forest Science*, 59, 723–752.
- Damm, A., Paul-Limoges, E., Haghghi, E., Simmer, C., Morsdorf, F., Schneider, F. D., van der Tol, C., Migliavacca, M., & Rascher, U. (2018). Remote sensing of plant-water relations: An overview and future perspectives. *Journal of Plant Physiology*, 227, 3–19.
- Delzon, S., & Cochard, H. (2014). Recent advances in tree hydraulics highlight the ecological significance of the hydraulic safety margin. *New Phytologist*, 203, 355–358.
- Delzon, S., Douthe, C., Sala, A., & Cochard, H. (2010). Mechanism of water-stress induced cavitation in conifers: Bordered pit structure and function support the hypothesis of seal capillary-seeding. *Plant, Cell and Environment*, 33, 2101–2111.
- Deshayes, M., Guyon, D., Jeanjean, H., Stach, N., Jolly, A., & Hagolle, O. (2006). The contribution of remote sensing to the assessment of drought effects in forest ecosystems. *Annals of Forest Science*, 63, 579–595.
- Dietrich, L., Delzon, S., Hoch, G., & Kahmen, A. (2019). No role for xylem embolism or carbohydrate shortage in temperate trees during the severe 2015 drought (G Battipaglia, Ed.). *Journal of Ecology*, 107, 334–349.
- Dobbertin, M., Mayer, P., Wohlgemuth, T., Feldmeyer-Christe, E., Graf, U., Zimmermann, N. E., & Rigling, A. (2005). The decline of *Pinus sylvestris* L. forests in the Swiss Rhone valley - A result of drought stress. *Phyton - Annales Rei Botanicae*, 45, 153–156.
- Duursma, R. A., Blackman, C. J., López, R., Martin-StPaul, N. K., Cochard, H., & Medlyn, B. E. (2019). On the minimum leaf conductance: Its role in models of plant water use, and ecological and environmental controls. *New Phytologist*, 221, 693–705.
- Eamus, D., Boulain, N., Cleverly, J., & Breshears, D. D. (2013). Global change-type drought-induced tree mortality: Vapor pressure deficit is more important than temperature per se in causing decline in tree health. *Ecology and Evolution*, 3, 2711–2729.
- Etzold, S., Ziemińska, K., Rohner, B., Bottero, A., Bose, A. K., Ruehr, N. K., Zingg, A., & Rigling, A. (2019). One century of forest monitoring data in Switzerland reveals species- and site-specific trends of climate-induced tree mortality. *Frontiers in Plant Science*, 10. doi:10.3389/fpls.2019.00307.
- Fischer, E. M., Sedláček, J., Hawkins, E., & Knutti, R. (2014). Models agree on forced response pattern of precipitation and temperature extremes. *Geophysical Research Letters*, 41, 8554–8562.
- Forrester, D. I., Bonal, D., Dawud, S., Gessler, A., Granier, A., Pollastrini, M., & Grossiord, C. (2016). Drought responses by individual tree species are not often correlated with tree species diversity in European forests (J Finn, Ed.). *Journal of Applied Ecology*, 53, 1725–1734.
- ForstBW (Forstliche Versuchs- und Forschungsanstalt Baden-Württemberg). (2018). Waldzustandsbericht 2018 (<https://mlr.baden-wuerttemberg.de/fileadmin/redaktion/m-mlr/intern/dateien/publikationen/Wald/Waldzustandsbericht2018.pdf>).
- García-Herrera, R., Garrido-Perez, J. M., Barriopedro, D., Ordóñez, C., Vicente-Serrano, S. M., Nieto, R., Gimeno, L., Sorí, R., & Yiou, P. (2019). The European 2016/17 drought. *Journal of Climate*, 32, 3169–3187.
- González de Andrés, E., Camarero, J. J., Blanco, J. A., Imbert, J. B., Lo, Y.-H., Sangüesa-Barreda, G., & Castillo, F. J. (2018). Tree-to-tree competition in mixed European beech-Scots pine forests has different impacts on growth and water-use efficiency depending on site conditions (M Turnbull, Ed.). *Journal of Ecology*, 106, 59–75.
- Goodsman, D. W., Groszklos, G., Aukema, B. H., Whitehouse, C., Bleiker, K. P., McDowell, N. G., Middleton, R. S., & Xu, C. (2018). The effect of warmer winters on the demography of an outbreak insect is hidden by intraspecific competition. *Global Change Biology*, 24, 3620–3628.
- Gößwein, S., & Lemme, H. (2017). Prachtkäfer profitieren vom Trockensommer 2015. *LWF aktuell*, 1/2017, 14–17.
- Grossiord, C. (2019). Having the right neighbors: How tree species diversity modulates drought impacts on forests. *New Phytologist*, in press <https://doi.org/10.1111/nph.1566>.
- Hanel, M., Rakovec, O., Markonis, Y., Máca, P., Samaniego, L., Kyselý, J., & Kumar, R. (2018). Revisiting the recent European droughts from a long-term perspective. *Scientific Reports*, 8, 1–11.
- Hargreaves, G. H. (1994). Defining and using reference evapotranspiration. *Journal of Irrigation and Drainage Engineering*, 120, 1132–1139.
- Harris, I., Jones, P. D., Osborn, T. J., & Lister, D. H. (2014). Updated high-resolution grids of monthly climatic observations - the CRU TS3.10 Dataset. *International Journal of Climatology*, 34, 623–642.

- Hart, S. J., Veblen, T. T., Eisenhart, K. S., Jarvis, D., & Kulakowski, D. (2014). Drought induces spruce beetle (*Dendroctonus rufipennis*) outbreaks across northwestern Colorado. *Ecology*, *95*, 930–939.
- Hartmann, H., Moura, C. F., Anderegg, W. R. L., Ruehr, N. K., Salmon, Y., Allen, C. D., Arndt, S. K., Breshears, D. D., Davi, H., Galbraith, D., et al. (2018b). Research frontiers for improving our understanding of drought-induced tree and forest mortality. *New Phytologist*, *218*, 15–28.
- Hartmann, H., Schuldt, B., Sanders, T. G. M., Macinnis-Ng, C., Boehmer, H. J., Allen, C. D., Bolte, A., Crowther, T. W., Hansen, M. C., Medlyn, B. E., et al. (2018a). Monitoring global tree mortality patterns and trends. Report from the VW symposium 'Crossing scales and disciplines to identify global trends of tree mortality as indicators of forest health'. *New Phytologist*, *217*, 984–987.
- Hauck, M., Leuschner, C., & Homeier, J. (2019). Klimawandel und Vegetation. *Eine globale Übersicht*. Berlin/Heidelberg: Springer Spektrum.
- Hentschel, R., Rosner, S., Kayler, Z. E., Andreassen, K., Børja, I., Solberg, S., Tveito, O. E., Priesack, E., & Gessler, A. (2014). Norway spruce physiological and anatomical predisposition to dieback. *Forest Ecology and Management*, *322*, 27–36.
- Hochberg, U., Windt, C. W., Ponomarenko, A., Zhang, Y.-J., Gersony, J., Rockwell, F. E., & Holbrook, N. M. (2017). Stomatal closure, basal leaf embolism, and shedding protect the hydraulic integrity of grape stems. *Plant Physiology*, *174*, 764–775.
- Huang, J., Kautz, M., Trowbridge, A. M., Hammerbacher, A., Raffa, K. F., Adams, H. D., Goodson, D. W., Xu, C., Meddens, A. J. H., Kandasamy, D., et al. (2020). Tree defence and bark beetles in a drying world: Carbon partitioning, functioning and modelling. *New Phytologist*, *225*, 26–36. doi:10.1111/nph.16173.
- Hunt, E. R., Ustin, S. L., & Riaño, D. (2013). Remote sensing of leaf, canopy, and vegetation water contents for satellite environmental data records. In J. Qu, A. Powell, M. V. K. Sivakumar (Eds.), *Satellite-based applications on climate change* (pp. 335–357). Dordrecht/Netherlands: Springer.
- Ionita, M., Tallaksen, L. M., Kingston, D. G., Stage, J. H., Laaha, G., Van Lanen, H. A. J., Scholz, P., Chelcea, S. M., & Haslinger, K. (2017). The European 2015 drought from a climatological perspective. *Hydrology and Earth System Sciences*, *21*, 1397–1419.
- Jung, T. (2009). Beech decline in Central Europe driven by the interaction between Phytophthora infections and climatic extremes. *Forest Pathology*, *39*, 73–94.
- Juvany, M., Müller, M., & Munné-Bosch, S. (2013). Photo-oxidative stress in emerging and senescing leaves: A mirror image. *Journal of Experimental Botany*, *64*, 3087–3098.
- Kannenber, S. A., Maxwell, J. T., Pederson, N., D'Orangeville, L., Ficklin, D. L., & Phillips, R. P. (2019). Drought legacies are dependent on water table depth, wood anatomy and drought timing across the eastern US (J Williams, Ed.). *Ecology Letters*, *22*, 119–127.
- Kazda, M., & Pichler, M. (1998). Priority assessment for conversion of Norway spruce forests through introduction of broadleaf species. *Forest Ecology and Management*, *102*, 245–258.
- Kerstiens, G. (1996). Cuticular water permeability and its physiological significance. *Journal of Experimental Botany*, *47*, 1813–1832.
- Knutzen, F., Dulamsuren, C., Meier, I. C., & Leuschner, C. (2017). Recent climate warming-related growth decline impairs European beech in the center of its distribution range. *Ecosystems*, *20*, 1494–1511.
- Konings, A. G., Rao, K., & Steele-Dunne, S. C. (2019). Macro to micro: Microwave remote sensing of plant water content for physiology and ecology. *New Phytologist*, *223*, 1166–1172.
- Körner, C. (1994). Leaf diffusive conductances in the major vegetation types of the globe. In Schulze ED, Caldwell MM (eds) *Ecophysiology of photosynthesis*. *Ecol Studies*, *100*, 463–490 Springer, Berlin.
- Körner, C. (2019). No need for pipes when the well is dry—a comment on hydraulic failure in trees. *Tree Physiology*, *39*, 695–700.
- Lange, O. L. (1959). Untersuchungen über Wärmehaushalt und Hitzeresistenz mauretanischer Wüsten- und Savannenpflanzen. *Flora oder Allgemeine Botanische Zeitung*, *147*, 595–651.
- Leuschner, C. (2009). *Die Trockenheitsempfindlichkeit der Rotbuche vor dem Hintergrund des prognostizierten Klimawandels*. *Jahrbuch der Akademie der Wissenschaften zu Göttingen*. Berlin, Germany: Walter de Gruyter.
- Leuzinger, S., Bigler, C., Wolf, A., & Körner, C. (2009). Poor methodology for predicting large-scale tree die-off. *Proceedings of the National Academy of Sciences of the United States of America*, *106*, E106 author reply E107.
- Leuzinger, S., Zotz, G., Asshoff, R., & Körner, C. (2005). Responses of deciduous forest trees to severe drought in Central Europe. *Tree physiology*, *25*, 641–650.
- Lévesque, M., Siegwolf, R., Eilmann, B., Brang, P., Bugmann, H., & Rigling, A. (2013). Drought response of five conifer species under contrasting water availability suggests high vulnerability of Norway spruce and European larch. *Global Change Biology*, *19*, 3184–3199.
- LF-RP (Landesforsten Rheinland-Pfalz). (2018). Waldzustandsbericht (2018). (https://mueef.rlp.de/fileadmin/mulewf/Publikationen/Waldzustandsbericht_2018.pdf)
- Li, S., Feifel, M., Karimi, Z., Schuldt, B., Choat, B., & Jansen, S. (2016). Leaf gas exchange performance and the lethal water potential of five European species during drought (R Tognetti, Ed.). *Tree Physiology*, *36*, 179–192.
- Lonsdale, D. (1980). Nectria coccinea infection of beech bark: Variations in disease in relation to predisposing factors. *Annales des Sciences Forestières*, *37*, 307–317.
- Luterbacher, J., Dietrich, D., Xoplaki, E., Grosjean, M., & Wanner, H. (2004). European seasonal and annual temperature variability, trends, and extremes since 1500. *Science*, *303*, 1499–1503.
- Marchin, R., Zeng, H., & Hoffmann, W. (2010). Drought-deciduous behavior reduces nutrient losses from temperate deciduous trees under severe drought. *Oecologia*, *163*, 845–854.
- Martinez-Vilalta, J., Anderegg, W. R. L., Sapes, G., & Sala, A. (2019). Greater focus on water pools may improve our ability to understand and anticipate drought-induced mortality in plants. *New Phytologist*, *223*, 22–32.
- Martin-StPaul, N., Delzon, S., & Cochard, H. (2017). Plant resistance to drought depends on timely stomatal closure (H Maherali, Ed.). *Ecology Letters*, *20*, 1437–1447.
- Marusig, D., Petruzzellis, F., Tomasella, M., Napolitano, R., Altobelli, A., & Nardini, A. (2020). Correlation of field-measured and remotely sensed plant water status as a tool to monitor the risk of drought-induced forest decline. *Forests*, *11*, 77.

- Matyssek, R., & Herppich W, B. (2017). Experimentelle Pflanzenökologie: Physikalische Grundlagen von Transpiration, CO₂-Aufnahme, Gasleitfähigkeiten und deren Bestimmungen. *Experimentelle Pflanzenökologie*. Berlin Heidelberg: Springer Spektrum.
- Mayer, J. (2004). Deutliche Blattverluste bei Eiche und Buche – Der Kronenzustand des Laubholzes verschlechtert sich deutlich. *LWF Aktuell* 43/2004.
- McDowell, N. G., Beerling, D. J., Breshears, D. D., Fisher, R. A., Raffa, K. F., & Stitt, M. (2011). The interdependence of mechanisms underlying climate-driven vegetation mortality. *Trends in Ecology and Evolution*, 26, 523–532.
- McDowell, N. G., Brodrribb, T. J., & Nardini, A. (2019). Hydraulics in the 21 st century. *New Phytologist*, 224, 537–542.
- McDowell, N. G., Coops, N. C., Beck, P. S. A., Chambers, J. Q., Gangodagamage, C., Hicke, J. A., Huang, C.-Y., Kennedy, R., Krofcheck, D. J., Litvak, M., et al. (2015). Global satellite monitoring of climate-induced vegetation disturbances. *Trends in Plant Science*, 20, 114–123.
- McDowell, N., Pockman, W. T., Allen, C. D., Breshears, D. D., Cobb, N., Kolb, T., Plaut, J., Sperry, J., West, A., Williams, D. G., et al. (2008). Mechanisms of plant survival and mortality during drought: Why do some plants survive while others succumb to drought. *New Phytologist*, 178, 719–739.
- Meir, P., Mencuccini, M., & Dewar, R. C. (2015). Drought-related tree mortality: Addressing the gaps in understanding and prediction. *New Phytologist*, 207, 28–33.
- Meteo Schweiz. (2012). *Klimabulletin Jahr 2011. Bundesamt für Meteorologie und Klimatologie*. Switzerland: Zurich.
- Michel, A., Seidling, W., & Prescher, A.-K. (2018). Forest condition in Europe: 2018 technical report of ICP forests. Report under the UNECE convention on long-range transboundary air pollution (CLRTAP). BFW -Dokumentation 25/2018. Vienna: BFW Austrian Research Centre for Forests.
- Munné-Bosch, S., & Alegre, L. (2004). Die and let live: Leaf senescence contributes to plant survival under drought stress. *Functional Plant Biology*, 31, 203.
- Murray, F. W. (1967). On the computation of saturation vapor pressure. *Journal of Applied Meteorology*, 6, 203–204.
- Netherer, S., Matthews, B., Katzensteiner, K., Blackwell, E., Henschke, P., Hietz, P., Pennerstorfer, J., Rosner, S., Kikuta, S., Schume, H., et al. (2015). Do water-limiting conditions predispose Norway spruce to bark beetle attack. *New Phytologist*, 205, 1128–1141.
- NW-FVA (Nordwestdeutsche Forstliche Versuchsanstalt). (2019). Waldschutzinfo Nr. 06 / 2019. (https://www.nw-fva.de/fileadmin/user_upload/Abteilung/Waldschutz/Waldschutz-Infos_2019/Waldschutzinfo_06-2019_Komplexe_Schaeden_an_Buche.pdf).
- Oliver, M. J., & Bewley, J. D. (1997). Desiccation-tolerance of plant tissues: A mechanistic overview. *Horticultural reviews* (pp. 171–213). Oxford, UK: John Wiley & Sons, Inc.
- Oren, R., & Pataki, D. E. (2001). Transpiration in response to variation in microclimate and soil moisture in southeastern deciduous forests. *Oecologia*, 127, 549–559.
- Orth, R., Vogel, M. M., Luterbacher, J., Pfister, C., & Seneviratne, S. I. (2016). Did European temperatures in 1540 exceed present-day records. *Environmental Research Letters*, 11, 1–10.
- Orth, R., Zscheischler, J., & Seneviratne, S. I. (2016). Record dry summer in 2015 challenges precipitation projections in Central Europe. *Scientific Reports*, 6, 28334.
- Peng, J., Wu, C., Zhang, X., Wang, X., & Gonsamo, A. (2019). Satellite detection of cumulative and lagged effects of drought on autumn leaf senescence over the Northern Hemisphere. *Global Change Biology*, 25, 2174–2188.
- Pflug, E. E., Buchmann, N., Siegwolf, R. T. W., Schaub, M., Rigling, A., & Arend, M. (2018). Resilient leaf physiological response of European beech (*Fagus sylvatica* L.) to summer drought and drought release. *Frontiers in Plant Science*, 9, 1–11.
- Rao, K., Anderegg, W. R. L., Sala, A., Martínez-Vilalta, J., & Konings, A. G. (2019). Satellite-based vegetation optical depth as an indicator of drought-driven tree mortality. *Remote Sensing of Environment*, 227, 125–136.
- Raspe, S., Grimmeisen, W., & Schulze, B. (2004). Der Sommer 2003 grub dem Wald das Wasser ab – Modell- und Messergebnisse aus bayerischen Wäldern. *LWF Aktuell* 43/2004.
- Raspe, S., Schulz, C., & Kroll, F. (2004). Wenn schon im Sommer tonnenweise Blätter fallen – Baumentwicklung und Streufall. *LWF Aktuell*, 43/2004.
- Rebetez, M., & Dobbertin, M. (2004). Climate change may already threaten Scots pine stands in the Swiss Alps. *Theoretical and Applied Climatology*, 79, 1–9.
- Rebetez, M., Mayer, H., Dupont, O., Schindler, D., Gartner, K., Kropp, J. P., & Menzel, A. (2006). Heat and drought 2003 in Europe: A climate synthesis. *Annals of Forest Science*, 63, 569–577.
- Rennenberg, H., Seiler, W., Matyssek, R., Gessler, A., & Kreuzwieser, J. (2004). Die Buche (*Fagus sylvatica* L.) – ein Waldbaum ohne Zukunft im südlichen Mitteleuropa. *Allgemeine Forst und Jagdzeitung*, 175, 210–224.
- Riederer, M., & Schreiber, L. (2001). Protecting against water loss: Analysis of the barrier properties of plant cuticles. *Journal of Experimental Botany*, 52, 2023–2032.
- Rigling, A., Bigler, C., Eilmann, B., Feldmeyer-Christe, E., Gimmi, U., Ginzler, C., Graf, U., Mayer, P., Vacchiano, G., Weber, P., et al. (2013). Driving factors of a vegetation shift from Scots pine to pubescent oak in dry Alpine forests. *Global Change Biology*, 19, 229–240.
- Rigling, A., Etzold, S., Bebi, P., Brang, P., Ferretti, M., Forrester, D., Gärtner, H., Gessler, A., Ginzler, C., Moser, B., Schaub, M., Stroheker, S., Trotsiuk, V., Walthert, L., Zweifel, R., & Wohlgemuth, T. (2019). Wie viel Trockenheit ertragen unsere Wälder? Lehren aus extremen Trockenjahren. 2019, In M. Bründl & J. Schweizer (Eds.), *Lernen aus Extremereignissen. Forum für Wissen 2019* 2019. (pp. 39–51). Davos: Lernen aus Extremereignissen.
- Rogers, B. M., Solvik, K., Hogg, E. H., Ju, J., Masek, J. G., Michaelian, M., Berner, L. T., & Goetz, S. J. (2018). Detecting early warning signals of tree mortality in boreal North America using multiscale satellite data. *Global Change Biology*, 24, 2284–2304.
- Rouse J, W., Haas R, W., Schell J, A., Deering D, W., & Harlan J.C. (1974). Monitoring the vernal advancement and retrogradation (Greenwave effect) of natural vegetation. NASA/GSFC Type III Final Report, Greenbelt, MD, USA.
- Ruehr, N. K., Gast, A., Weber, C., Daub, B., & Arneth, A. (2016). Water availability as dominant control of heat stress responses in two contrasting tree species (F Meinzer, Ed.). *Tree Physiology*, 36, 164–178.
- Ruehr, N. K., Grote, R., Mayr, S., & Arneth, A. (2019). Beyond the extreme: Recovery of carbon and water relations in woody plants following heat and drought stress. *Tree Physiology*, 39, 1285–1299.

- Samaniego, L., Thober, S., Kumar, R., Wanders, N., Rakovec, O., Pan, M., Zink, M., Sheffield, J., Wood, E. F., & Marx, A. (2018). Anthropogenic warming exacerbates European soil moisture droughts. *Nature Climate Change*, *8*, 421–426.
- Schär, C., Vidale, P. L., Lüthi, D., Frei, C., Häberli, C., Liniger, M. A., & Appenzeller, C. (2004). The role of increasing temperature variability in European summer heatwaves. *Nature*, *427*, 332–336.
- Schindler, U. (1951). Das Buchensterben; bisherige Veröffentlichungen und Auswertungen der staatlichen Unterlagen. *Forstarchiv*, *22*, 109–119.
- Schuldt, B., Knutzen, F., Delzon, S., Jansen, S., Müller-Haubold, H., Burlett, R., Clough, Y., & Leuschner, C. (2016). How adaptable is the hydraulic system of European beech in the face of climate change-related precipitation reduction. *New Phytologist*, *210*, 443–458.
- Schulze, E.-D. (1989). Air pollution and forest decline in a spruce (*Picea abies*) forest. *Science*, *244*, 776–783.
- Schuster, A.-C., Burghardt, M., Alfarhan, A., Bueno, A., Hedrich, R., Leide, J., Thomas, J., & Riederer, M. (2016). Effectiveness of cuticular transpiration barriers in a desert plant at controlling water loss at high temperatures. *AoB Plants*, *8* Plw027.
- Schütt, P., & Cowling, E. B. (1985). Waldsterben, a general decline of forests in central Europe: Symptoms, development, and possible causes. *Plant Disease*, *69*, 548–558.
- Seidl, R., Schelhaas, M.-J., & Lexer, M. J. (2011). Unraveling the drivers of intensifying forest disturbance regimes in Europe. *Global Change Biology*, *17*, 2842–2852.
- Seidling, W. (2007). Signals of summer drought in crown condition data from the German Level I network. *European Journal of Forest Research*, *126*, 529–544.
- Sevanto, S., McDowell, N. G., Dickman, L. T., Pangle, R., & Pockman, W. T. (2014). How do trees die? A test of the hydraulic failure and carbon starvation hypotheses. *Plant, Cell and Environment*, *37*, 153–161.
- Spiecker, H., Lindner, M., & Schuler, J. (2019). Douglas-fir – an option for Europe. *What Science Can Tell us*, *9*, 1–121.
- Stovall, A. E. L., Shugart, H., & Yang, X. (2019). Tree height explains mortality risk during an intense drought. *Nature Communications*, *10*, 4385.
- Stroheker, S., Forster, B., & Queloz, V. (2020). Zweithöchster je registrierter Buchdruckerbefall (*Ips typographus*) in der Schweiz. *Waldschutz Aktuell* *2*/2020.
- Sun, H., Feng, M., Xiao, L., Yang, W., Wang, C., Jia, X., Zhao, Y., Zhao, C., Muhammad, S. K., & Li, D. (2019). Assessment of plant water status in winter wheat (*Triticum aestivum* L.) based on canopy spectral indices (DA Lightfoot, Ed.). *PLOS ONE*, *14*, E0216890.
- Timofeeva, G., Treyde, K., Bugmann, H., Rigling, A., Schaub, M., Siegwolf, R., & Saurer, M. (2017). Long-term effects of drought on tree-ring growth and carbon isotope variability in Scots pine in a dry environment. *Tree Physiology*, *37*, 1028–1041.
- Tomasella, M., Beikircher, B., Häberle, K.-H., Hesse, B., Kallenbach, C., Matussek, R., & Mayr, S. (2018). Acclimation of branch and leaf hydraulics in adult *Fagus sylvatica* and *Picea abies* in a forest through-fall exclusion experiment. *Tree Physiology*, *38*, 198–211.
- Torres-Ruiz, J. M., Jansen, S., Choat, B., McElrone, A. J., Cochard, H., Brodrick, T. J., Badel, E., Burlett, R., Bouche, P. S., Brodersen, C. R., et al. (2015). Direct x-ray microtomography observation confirms the induction of embolism upon xylem cutting under tension. *Plant Physiology*, *167*, 40–43.
- Trenberth, K. E., Dai, A., van der Schrier, G., Jones, P. D., Barichivich, J., Briffa, K. R., & Sheffield, J. (2014). Global warming and changes in drought. *Nature Climate Change*, *4*, 17–22.
- Trugman, A. T., Detto, M., Bartlett, M. K., Medvigy, D., Anderegg, W. R. L., Schwalm, C., Schaffer, B., & Pacala, S. W. (2018). Tree carbon allocation explains forest drought-kill and recovery patterns (D Cameron, Ed.). *Ecology Letters*, *21*, 1552–1560.
- Tucker, C. J., & Choudhury, B. J. (1987). Satellite remote sensing of drought conditions. *Remote Sensing of Environment*, *23*, 243–251.
- Tyree, M. T., & Sperry, J. S. (1989). Vulnerability of xylem to cavitation and embolism. *Annual Review of Plant Physiology and Plant Molecular Biology*, *40*, 19–38.
- Ulrich, B. (1990). Waldsterben: Forest decline in West Germany. *Environmental Science & Technology*, *24*, 436–441.
- Urli, M., Porté, A. J., Cochard, H., Guengant, Y., Burlett, R., & Delzon, S. (2013). Xylem embolism threshold for catastrophic hydraulic failure in angiosperm trees. *Tree Physiology*, *33*, 672–683.
- Vitali, V., Büntgen, U., & Bauhus, J. (2017). Silver fir and Douglas fir are more tolerant to extreme droughts than Norway spruce in southwestern Germany. *Global Change Biology*, *23*, 5108–5119.
- Vitasse, Y., Bottero, A., Cailleret, M., Bigler, C., Fonti, P., Gessler, A., Lévesque, M., Rohner, B., Weber, P., Rigling, A., et al. (2019). Contrasting resistance and resilience to extreme drought and late spring frost in five major European tree species. *Global Change Biology*, *25*, 3781–3792.
- Von Vietinghoff-Riesch, A., & Vité, J. P. (1952). Zur Frage der Buchenprachtkäferschäden in Nordwestdeutschland. *Holz-Zentralblatt*, *78*, 845–847.
- Wang, W., Peng, C., Kneeshaw, D. D., Larocque, G. R., & Luo, Z. (2012). Drought-induced tree mortality: Ecological consequences, causes, and modeling. *Environmental Reviews*, *20*, 109–121.
- Waring, R. H. (1986). Characteristics of trees predisposed to die. *Studies in Environmental Science*, 117–123.
- Weber, P., Bugmann, H., Fonti, P., & Rigling, A. (2008). Using a retrospective dynamic competition index to reconstruct forest succession. *Forest Ecology and Management*, *254*, 96–106.
- West, H., Quinn, N., & Horswell, M. (2019). Remote sensing for drought monitoring & impact assessment: Progress, past challenges and future opportunities. *Remote Sensing of Environment*, *232*, 111291.
- Williams, A. P., Allen, C. D., Macalady, A. K., Griffin, D., Woodhouse, C. A., Meko, D. M., Swetnam, T. W., Rauscher, S. A., Seager, R., Grissino-Mayer, H. D., et al. (2013). Temperature as a potent driver of regional forest drought stress and tree mortality. *Nature Climate Change*, *3*, 292–297.
- Wohlgemuth, T., Gallien, L., & Zimmermann, N. E. (2016). Verjüngung von Buche und Fichte im Klimawandel. In A. R. Pluess, S. Augustin, P. Brang (Eds.), *Wald und Klimawandel* (pp. 115–135). Haupt, Bern: Grundlagen für Adaptationsstrategien.
- Wolfe, B. T., Sperry, J. S., & Kursar, T. A. (2016). Does leaf shedding protect stems from cavitation during seasonal droughts? A test of the hydraulic fuse hypothesis. *New Phytologist*, *212*, 1007–1018.
- Yuan, W., Zheng, Y., Piao, S., Ciais, P., Lombardozzi, D., Wang, Y., Ryu, Y., Chen, G., Dong, W., Hu, Z., et al. (2019). Increased atmospheric vapor pressure deficit reduces global vegetation growth. *Science Advances*, *5*, Eaax1396.

- Zang, C., Rothe, A., Weis, W., & Pretzsch, H. (2011). Zur Baumarteneignung bei Klimawandel: Ableitung der Trockenstress-Anfälligkeit wichtiger Waldbaumarten aus Jahringbreiten. *Allgemeine Forst- und Jagdzeitung*, 182(5/6), 98–112.
- Zhou, S., Zhang, Y., Park Williams, A., & Gentine, P. (2019). Projected increases in intensity, frequency, and terrestrial carbon costs of compound drought and aridity events. *Science Advances*, 5, Eaa5740.
- Zimmermann, J., Hauck, M., Dulamsuren, C., & Leuschner, C. (2015). Climate warming-related growth decline affects *Fagus sylvatica*, but not other broad-leaved tree species in Central European mixed forests. *Ecosystems*, 1, 560–572.
- Zscheischler, J., & Seneviratne, S. I. (2017). Dependence of drivers affects risks associated with compound events. *Science Advances*, 3, E1700263.

Available online at www.sciencedirect.com

ScienceDirect