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Are Scots pine forest edges particularly prone to drought-induced mortality?

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Supplementary material for this article is available [online](#)

Abstract

Climate change is expected to exacerbate the frequency of drought-induced tree mortality world-wide. To better predict the associated change of species composition and forest dynamics on various scales and develop adequate adaptation strategies, more information on the mechanisms driving the often observed patchiness of tree die-back is needed. Although forest-edge effects may play an important role within the given context, only few corresponding studies exist. Here, we investigate the regional die-back of Scots pine in Franconia, Germany, after a hot and dry summer in 2015, thereby emphasizing possible differences in mortality between forest edge and interior. By means of dendroecological investigations and close-range remote sensing, we assess long-term growth performance and current tree vitality along five different forest-edge distance gradients. Our results clearly indicate a differing growth performance between edge and interior trees, associated with a higher vulnerability to drought, increased mortality rates, and lower tree vitality at the forest edge. Prior long-lasting growth decline of dead trees compared to live trees suggests depletion of carbon reserves in course of a long-term drought persisting since the 1990s to be the cause of regional Scots pine die-back. These findings highlight the forest edge as a potential focal point of forest management adaptation strategies in the context of drought-induced mortality.

1. Introduction

In the course of climate change and associated ‘hotter droughts’, an increased frequency of drought-induced forest die-back seems likely (Adams *et al* 2009, 2015, Allen *et al* 2010, 2015, Bennett *et al* 2015, Bonan 2008, Breshears *et al* 2005, Cailleret *et al* 2017, Martínez-Vilalta *et al* 2012, McDowell *et al* 2008). Since forests cover around 30 percent of the land surface, store roughly 45 percent of terrestrial carbon, and contribute about 50 percent of terrestrial net primary productivity, it is crucial to understand the mechanisms governing tree mortality, particularly due to several possible

feedback loops between forest die-back and climate change but also to increase the reliability of dynamic global vegetation models (Allen *et al* 2015, Bonan 2008, Cailleret *et al* 2017, McDowell *et al* 2008).

Despite an increasing number of studies addressing forest mortality world-wide, we yet lack a detailed understanding of the frequently observed patchiness of forest die-back, i.e. the occurrence of neighboring dead and live trees (Allen *et al* 2010, Bennett *et al* 2015, Cailleret *et al* 2017, Pellizzari *et al* 2016, Petrucco *et al* 2017). Possible inciting factors triggering individual die-back are a differing competition for water, light, and nutrients among trees (Allen *et al* 2010,

Bigler *et al* 2006, Cailleret *et al* 2017, Chen *et al* 1993), differences regarding soil conditions and thus plant available water capacity (Lévesque *et al* 2013, Oberhuber 2017, Oberhuber and Kofler 2000, Rehschuh *et al* 2017), allometric tree features such as height, canopy volume, and leaf-area index (Adams *et al* 2015, Bennett *et al* 2015, Dobbertin *et al* 2010, Seidel *et al* 2016, Seidel and Menzel 2016), genetic variability (Allen *et al* 2010, Petrucco *et al* 2017, Seidel *et al* 2016, Seidel and Menzel 2016), and the selective influence of biotic pathogens such as bark beetles, fungi, and mistletoe (Dobbertin and Rigling 2006, Galiano *et al* 2011, Wermelinger *et al* 2008). Moreover, hydraulic properties play an important role regarding the impact of different types of drought on particular tree species: while isohydric species often are considered to suffer from carbon depletion caused by excessive stomatal closure in course of multi-annual droughts resulting in a long-lasting growth decline and finally tree death, anisohydric species are prone to hydraulic failure which may trigger abrupt die-back under intense short-term droughts (Allen *et al* 2010, Cailleret *et al* 2017, Galiano *et al* 2010, McDowell *et al* 2008, Pellizzari *et al* 2016, Rigling *et al* 2013).

In this context, the forest edge may be of particular importance. A couple of case studies have reported more incoming photosynthetic active radiation, higher soil- and air temperatures, a lower plant available water capacity and relative humidity, and in some cases an increased tree mortality at the forest edge—particularly at south-facing edges—if compared to the forest interior (Cadenasso *et al* 1997, Chen *et al* 1993, Cienciala *et al* 2002, Laurance *et al* 2001, 2011, Laurance and Williamson 2001, Matlack 1993, Young and Mitchell 1994). Nevertheless, forest-edge effects are yet hardly considered in large-scale investigations on tree mortality nor are they implemented in dynamic global vegetation models.

Under this framework, the relatively isohydric Scots pine (*Pinus sylvestris* L.) is of particular interest since it is (i) one of the most widely distributed tree species on Earth, (ii) one of the most frequently studied tree species in environmental sciences, (iii) of high economic importance for forestry, and (iv) increasingly affected by drought-induced die-back (Bigler *et al* 2006, Cienciala *et al* 2002, Dobbertin *et al* 2005, 2007, 2010, Dobbertin and Rigling 2006, Eilmann *et al* 2010, 2011, 2013, Galiano *et al* 2010, 2011, Giuggiola *et al* 2013, Gruber *et al* 2012, Lebourgeois *et al* 2010, Lévesque *et al* 2013, Martínez-Vilalta *et al* 2009, 2012, Oberhuber *et al* 1998, Oberhuber 2017, Oberhuber and Gruber 2010, Oberhuber and Kofler 2000, Pellizzari *et al* 2016, Pichler and Oberhuber 2007, Rebetez and Dobbertin 2004, Rigling *et al* 2013, Sánchez-Salguero *et al* 2015, Seidel *et al* 2016, Seidel and Menzel 2016, Swidrak *et al* 2011, Zweifel *et al* 2009). Scots pine die-back following extreme drought events has been reported from the Mediterranean and the dry inner-Alpine valleys (e.g. Dobbertin *et al* 2005, Galiano *et al* 2010,

Martínez-Vilalta *et al* 2012, 2009, Pichler and Oberhuber 2007) and although its physiological response as well as possible underlying mechanisms have been studied in detail (Eilmann *et al* 2011, Galiano *et al* 2011, Rigling *et al* 2013), Scots pine forest-edge effects are yet only marginally investigated (Cienciala *et al* 2002).

In Franconia, Germany, Scots pine is projected to reach its climatic limit in course of the anticipated climate change (Walentowski *et al* 2017). In this context, the regionally pronounced Scots pine die-back after the hot and dry summer in 2015 may be considered an early-warning signal (Gößwein *et al* 2017). Several stands were affected, showing mortality rates ranging from single trees up to about 90% of local Scots pine die-back (personal observation). From field impressions it appeared that forest-edges were particularly affected, thereby rendering this extreme event an ideal case for studying forest-edge effects on Scots pine mortality.

Here, we investigate Scots pine growth performance and vitality along five different forest-edge distance gradients in Franconia combining dendrochronological means with close-range remote sensing techniques. We hypothesize that (i) Scots pine vulnerability to drought and mortality rates after the 2015 drought are more pronounced at the forest edge and in particular at south-facing forest edges when compared to the forest interior and (ii) being a relatively isohydric species, dead Scots pine trees are characterized by preceding growth decline, possibly indicating a long-term depletion of carbon reserves as the main cause of tree death.

2. Material and methods

2.1. Study sites

In 2016 and 2017, we investigated five different Scots pine stands in close proximity to Nuremberg in Franconia, Germany (figure 1). For each site we acquired dendrochronological samples from the forest edge and interior and obtained multispectral images derived from close-range remote sensing. The sites were selected to represent stands being significantly affected by Scots pine die-back (as derived from visual interpretation) and rather similar conditions across sites. We chose stands with mature, dominant Scots pine specimens and a presumably low influence of other vegetation. Due to several restrictions (sampling permissions, flight-allowances for the UAV, degree of affectedness) the finally selected stands varied with respect to co-occurring species composition and stand size (table 1).

2.2. Dendroecology

Altogether, 152 trees were analyzed using dendrochronological means. At each site we sampled two different ‘micro-sites’, i.e. trees growing directly at the forest edge and trees growing in the forest

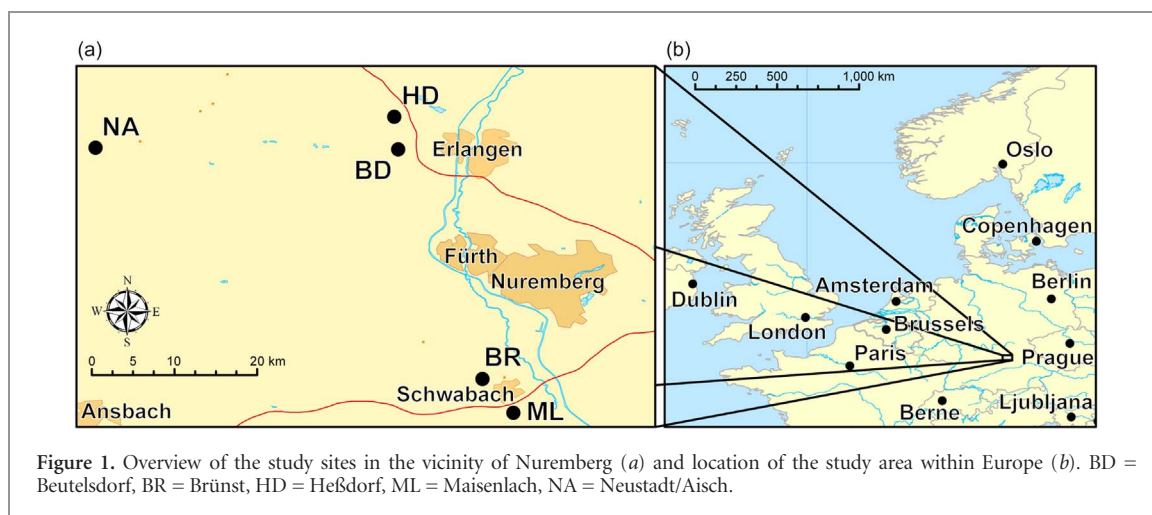


Table 1. Main characteristics of the investigated stands. From left to right: site ID, size class (see discussion and also Young and Mitchell 1994), edge orientation, co-occurring vegetation, and the number of sampled trees (n) at the edge and interior, respectively.

| ID ^a (latitude, longitude) | Size class | Edge | Understory | n (edge/interior) |
|---------------------------------------|----------------|------|-----------------|---------------------|
| BD (49.59 N, 10.91 E) | small (< 4 ha) | W | none | 30 (15/15) |
| BR (49.34 N, 11.00 E) | large (> 9 ha) | W | broadleaf trees | 30 (15/15) |
| HD (49.63 N, 10.90 E) | large (> 9 ha) | S | none | 30 (15/15) |
| ML (49.30 N, 11.03 E) | large (> 9 ha) | S | broadleaf trees | 40 (20/20) |
| NA (49.59 N, 10.58 E) | small (< 2 ha) | S | broadleaf trees | 22 (12/10) |

^a BD = Beutelsdorf, BR = Brünst, HD = Heßdorf, ML = Maisenlach, NA = Neustadt/Aisch.

interior. Depending on the availability of Scots pine trees and specific site conditions, sample size (at least ten specimens per micro-site) and distance of interior trees to the forest edge (at least 50 m) varied among stands (table 1).

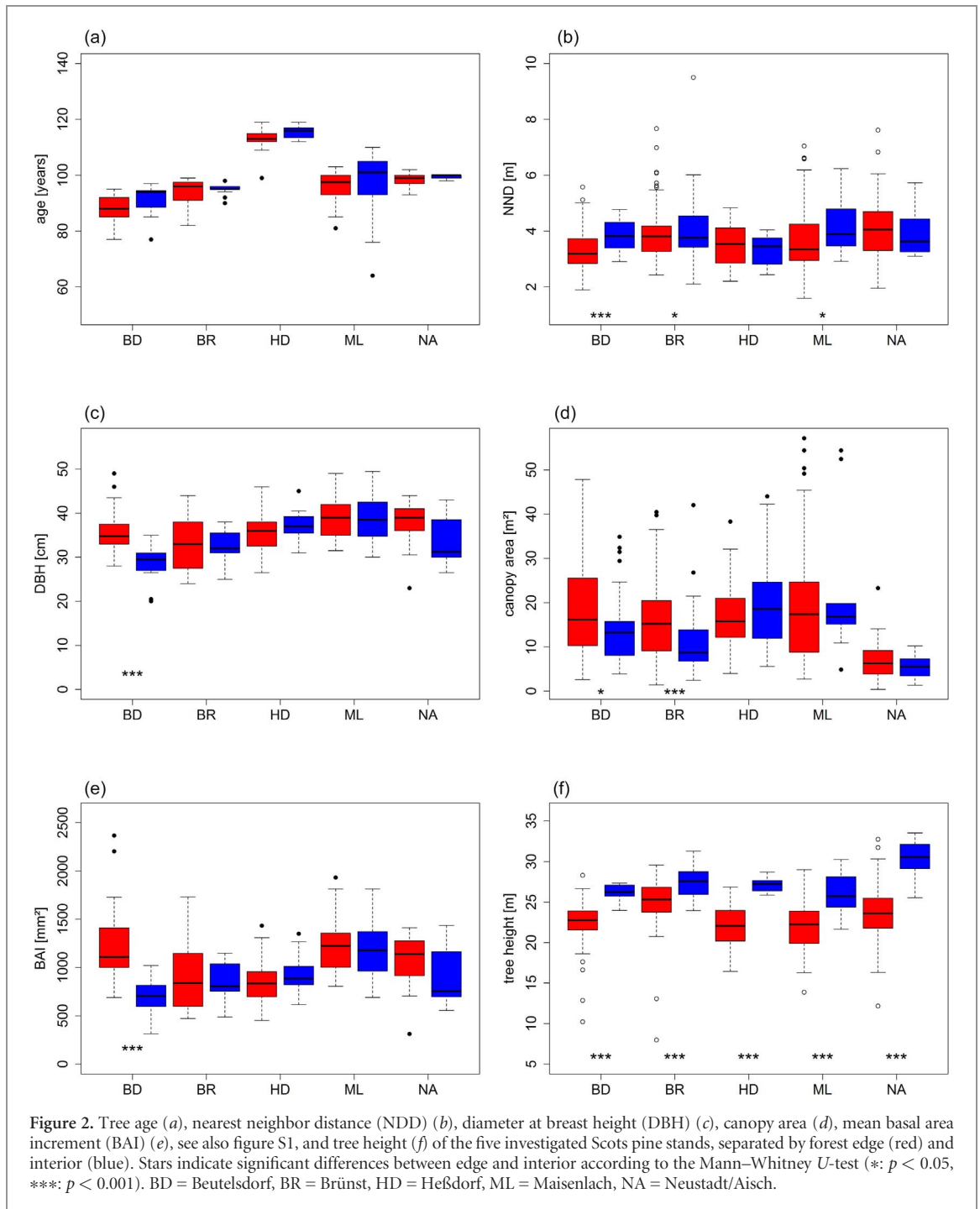
Our dendroecological survey was based on measurements of ring-widths (RW), earlywood- and latewood widths (EW and LW, respectively), and meaningful tree features, from which basal area increments (BAI) and a resulting earlywood-latewood width ratio (LER) were derived. Our computations and analyses comprise a detrending of ring-width related variables (resulting in the indices RWI, EWI and LWI), computation of measurement's coherence using Gleichläufigkeit (glk aka coefficient of coherence, Buras and Wilmking 2015, Eckstein and Bauch 1969) and expressed population signal (EPS, Buras 2017, Wigley *et al* 1984), the comparison of BAI-chronologies derived from dead and live trees, principal component gradient analysis (PCGA) (Buras *et al* 2016) to explore for systematically differing climatic responses between edge and interior trees, as well as the computation of climate growth relationships with various climate parameters. Although we performed various climate correlation analyses, we particularly emphasize the relationship between EWI (early-wood index) and early summer water availability since other studies on Scots pine reported highest growth rates and strongest correlations with water availability for the early growing season (Oberhuber 2017, Oberhuber and Gruber 2010). A detailed description of data handling, statistical analyses, and data sources is given in

part A of the supplementary information, available at stacks.iop.org/ERL/13/025001/mmedia (Akaike 2011, Beguería *et al* 2014).

2.3. Close-range remote sensing

Close-range remote sensing images were acquired using an Ascending Technologies Falcon 8 octocopter (Intel Drone Team, Krailling, Germany) equipped with a MicaSense RedEdge[®] multispectral camera (Seattle, WA). The final resolution of the obtained images ranged from 6.59–8.02 cm per pixel. From those images we derived the normalized difference vegetation index (NDVI) as a proxy for vegetation vitality (Breshears *et al* 2005, Lausch *et al* 2016, Lillesand *et al* 2014). Using GIS software, we digitized altogether 6649 Scots pine canopies and extracted for each of those tree height, canopy area, the distance to the nearest neighbor (NDD), the minimum distance to the forest edge, and the corresponding mean NDVI. Mean NDVI values were used to classify significantly devitalized Scots pine individuals and investigated for forest edge distance effects using regression models. A detailed description of the image acquisition and post-processing using Pix4DMapper Pro Educational (version 3.1.18, Pix4D SA, Lausanne, Switzerland), data handling, and subsequent statistical analyses is given in part B of the supplementary information.

All statistical analyses were performed in 'R' (version 3.2.2; R foundation for statistical computing, Vienna) extended for the packages 'dplr' (Bunn *et al* 2012), 'rgdal' (Keitt *et al* 2011), 'lattice' (Sarkar 2008), and 'SPEI' (Beguería and Vicente-Serrano 2013).



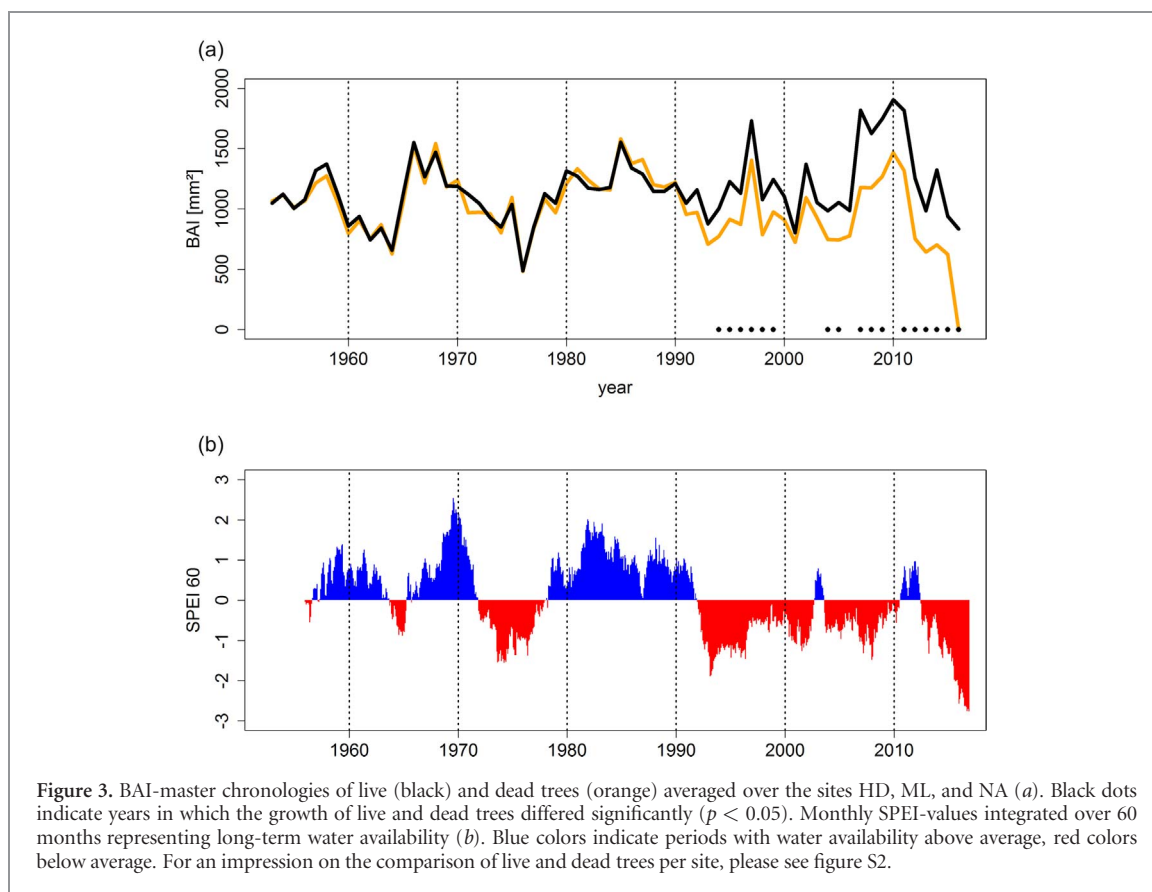
3. Results

3.1. Tree-rings revealed a stronger response to drought at the forest-edge

Tree-height was the only parameter which expressed a systematic difference between micro-sites with edge trees being significantly smaller than interior trees at all sites (figures 2(a)–(f)) whereas growth did not vary systematically (figure S1). Detrended tree-rings (RWI) expressed a strong common signal with an average glk of 0.64 and an EPS of 0.98. Negative correlations of the regional RWI master chronology with July and August temperatures ($r = -0.31, -0.28$, respectively, $p < 0.05$) and positive correlations with spring and

summer water availability (e.g. $r = 0.65, p < 0.001$ for SPEI6 of August) indicated growing season drought to be the main growth limiting factor of Scots pine in the study area.

Seventeen percent of all trees investigated (26 out of 152) died after 2015 and 73 percent of those (19 out of 26) were located at the forest edge. Interestingly, dead trees were only found in stands with south-facing forest edges, i.e. in HD, ML, and NA with 5, 13, and 8 trees, respectively. At these sites 80, 100, and 25 percent of dead trees originated from the forest edge, respectively. The corresponding BAI master chronologies of dead and surviving trees from these sites differed significantly ($p < 0.05$; figures 3(a) and S2 from the



1990s onwards in course of a long-lasting drought (figure 3(b)).

Regarding site-specific analyses, PCGA revealed a clear separation site between edge and interior RWI-series in all sites (figure 4(a)). Moreover, forest-edge trees expressed significantly lower latewood–earlywood ratios (LER) in comparison to forest-interior trees ($p < 0.001$; figures 4(b) and S3). At all sites, edge trees indicated a higher drought susceptibility compared to the interior. The most prominent differences were observed for correlations between early-summer precipitation (i.e. SPI2 values for May and June) and EWI-series ($p < 0.05$ at all sites; figures 5 and S4). These results were supported by the comparison of climate correlations with regional forest-edge and -interior master chronologies. For instance, the May SPI2 correlation of the regional edge-EWI master chronology was 0.43 ($p < 0.001$) compared to 0.21 ($p = 0.10$) for the regional interior-EWI master chronology (figure S5).

3.2. NDVI revealed lower vitality towards the forest edge

In all investigated stands we found Scots pine canopy NDVI to significantly increase with distance to the forest edge ($p < 0.001$ for all models), indicating higher photosynthetic activity and thus presumably higher vitality towards the forest interior (figure 6). The explained variance of corresponding best-fit models ranged from 0.18 (HD) to 0.76 (BR) across sites, whereas a global model expressed an explained

variance of 0.38 (figure 7). The forest edge effect appeared to be most pronounced over the first 50 m of forest–edge distance and to diminish after 100 m distance.

Significantly devitalized trees were observed in all stands and their percentage decreased significantly with increasing forest-edge distance (Spearman's rho = -0.94 , $p < 0.001$; figure 8). As for canopy-based NDVI (figure 7), the change of percentage of devitalized trees was most pronounced over the first 100 m of forest–edge distance, decreasing from on average 17 percent to values below four percent above a distance of 100 m (figure 8).

4. Discussion

4.1. The forest-edge: a focal point of Scots pine mortality?

Our results highlight the importance of the forest-edge for Scots pine growth performance. First of all, PCGA-loadings clearly separated edge- from interior-trees, thereby indicating differing growth-performance on the long-term which was also reflected in lower latewood–earlywood ratios at the forest edge. Secondly, climate-growth relationships revealed a significantly higher drought sensitivity of edge-trees compared to the interior. Thirdly, canopy-based NDVI—a proxy for tree productivity and vitality—decreased significantly towards the forest edge and fourthly, the frequency of dead trees (as derived from dendrochronological

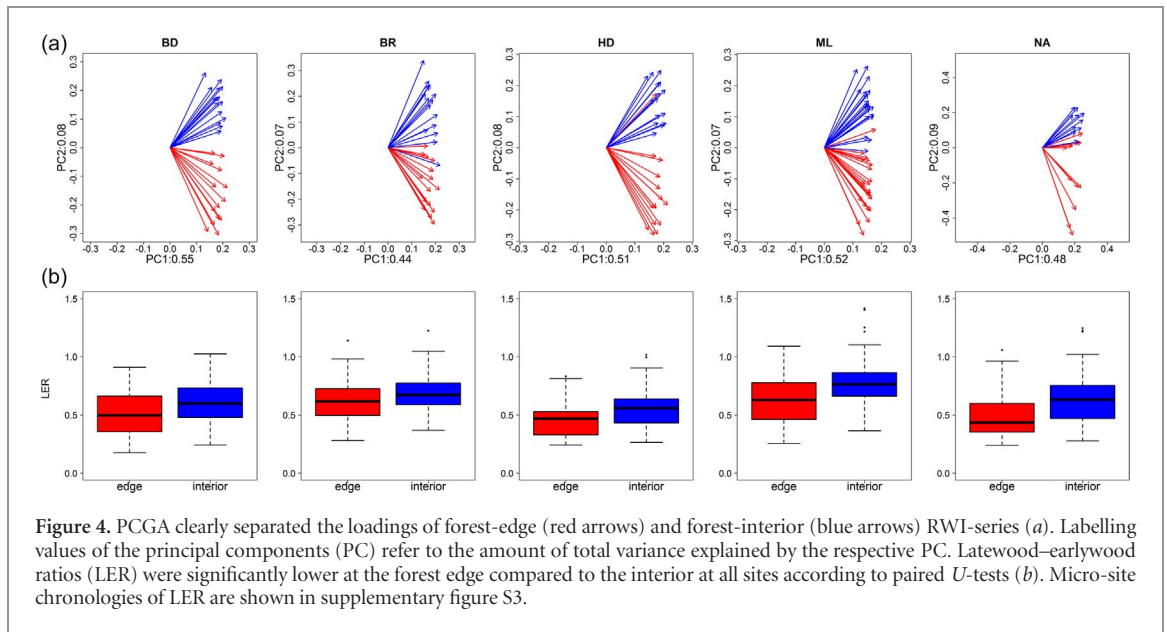


Figure 4. PCGA clearly separated the loadings of forest-edge (red arrows) and forest-interior (blue arrows) RWI-series (a). Labelling values of the principal components (PC) refer to the amount of total variance explained by the respective PC. Latewood–earlywood ratios (LER) were significantly lower at the forest edge compared to the interior at all sites according to paired *U*-tests (b). Micro-site chronologies of LER are shown in supplementary figure S3.

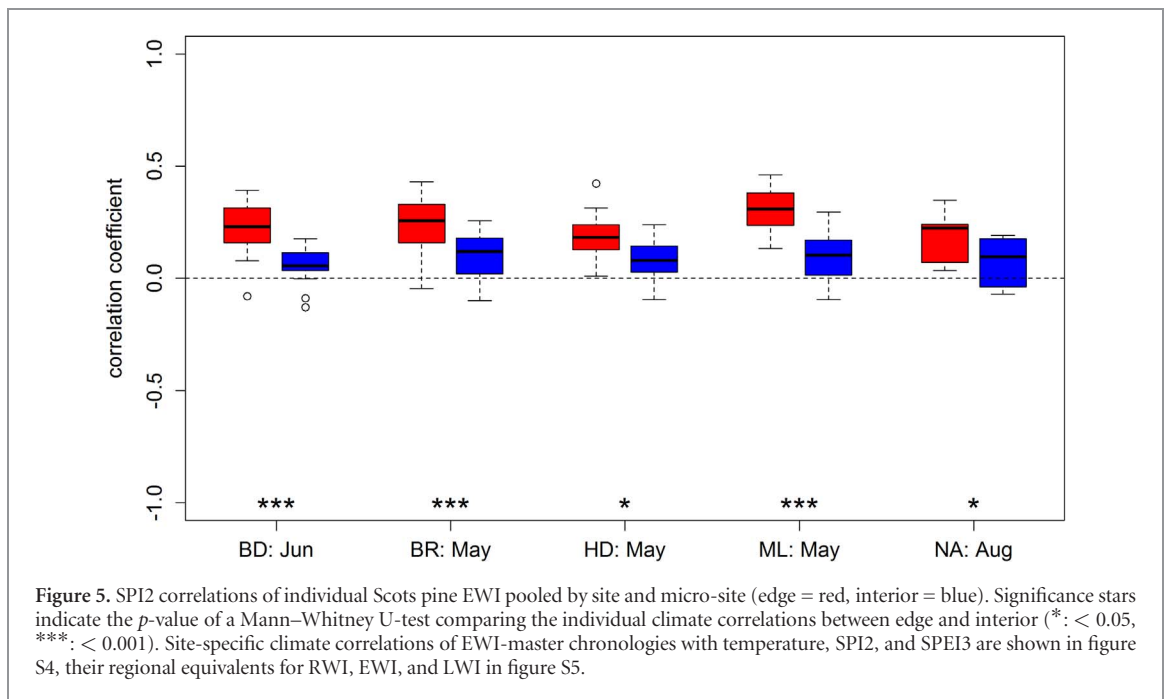


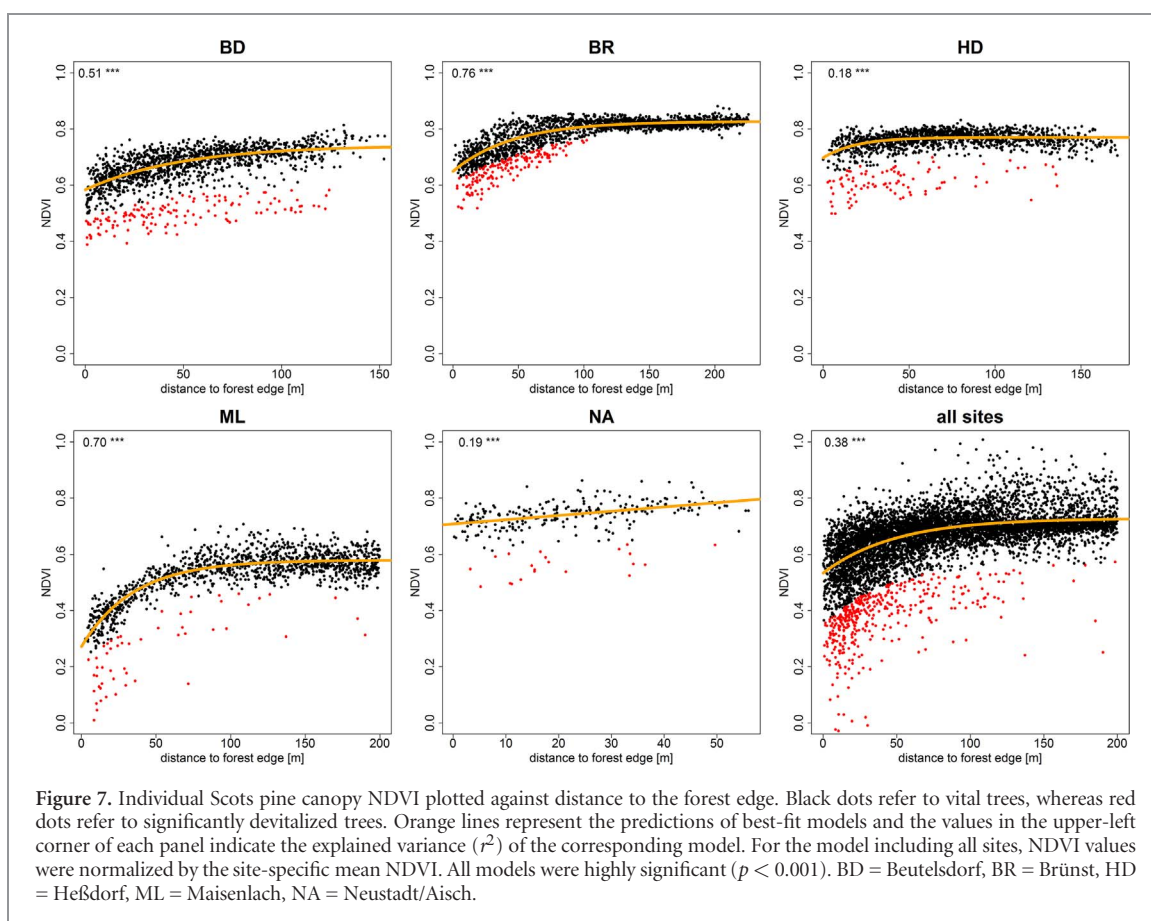
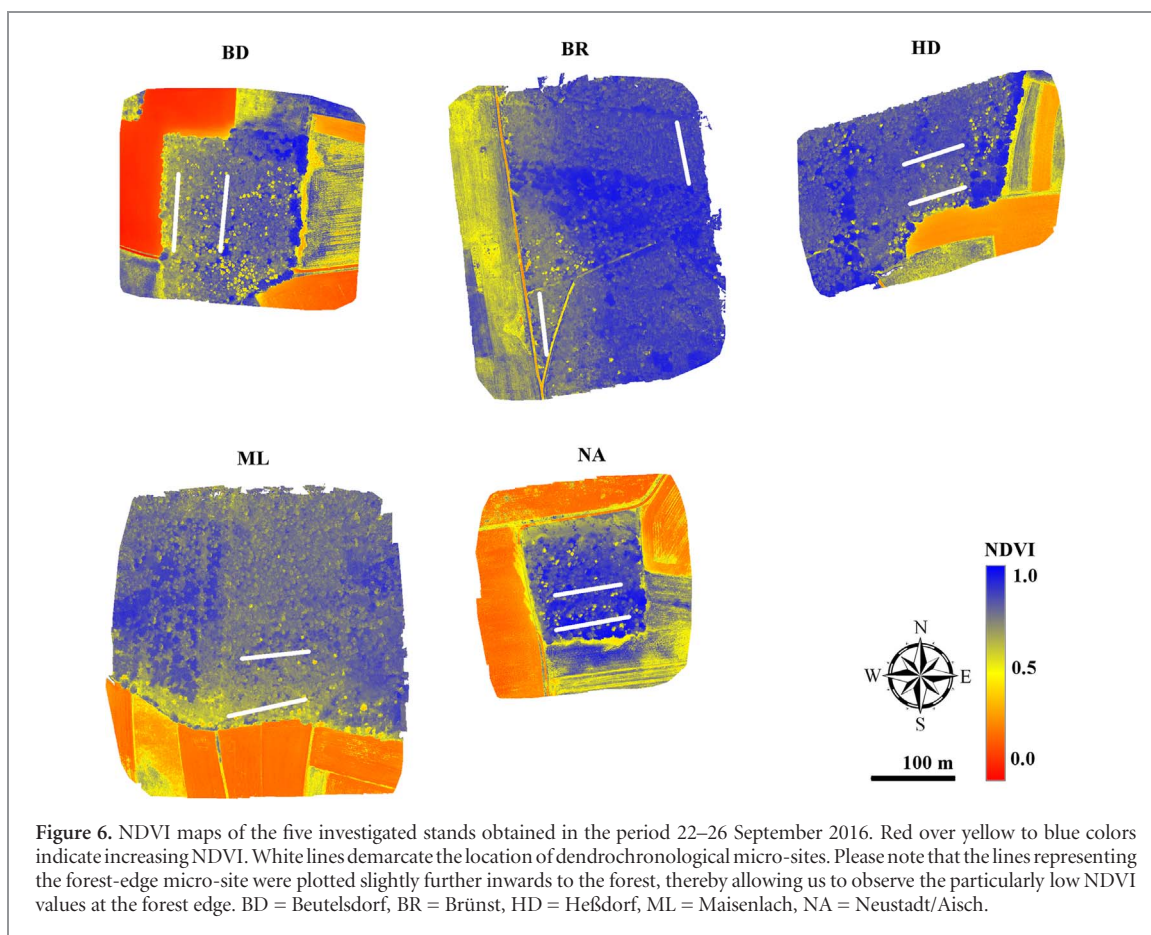
Figure 5. SPI2 correlations of individual Scots pine EWI pooled by site and micro-site (edge = red, interior = blue). Significance stars indicate the *p*-value of a Mann–Whitney *U*-test comparing the individual climate correlations between edge and interior (*: < 0.05 , ***: < 0.001). Site-specific climate correlations of EWI–master chronologies with temperature, SPI2, and SPEI3 are shown in figure S4, their regional equivalents for RWI, EWI, and LWI in figure S5.

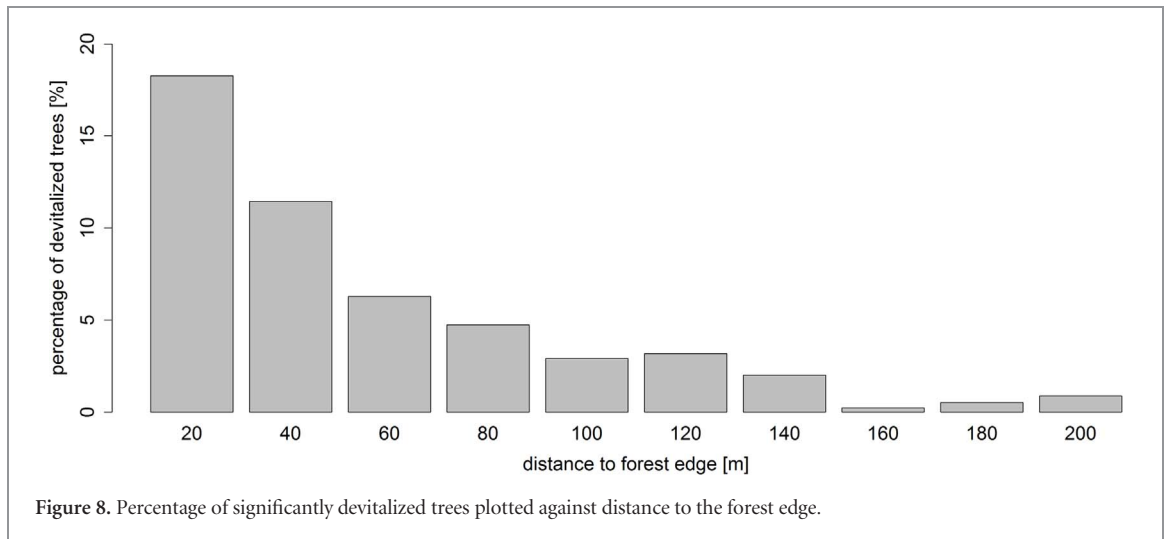
data) as well as the percentage of devitalized trees (as derived from close-range remote sensing) was on average higher at the forest edge. These findings strongly support our first initial hypothesis (i).

Regarding the underlying mechanisms causing higher drought-susceptibility, we hypothesize that mainly micro-climatic conditions, plant available soil water as well as a differing tree stature are of importance. That is, several investigations have reported higher air and soil temperatures as well as insolation rates and lower relative air humidity at the forest edge. In combination with higher wind speeds at the forest edge, these factors trigger a higher evapotranspirative demand of forest edge trees. This hypothesis is in line with studies reporting lower plant water availability and consequently an increased likelihood of

drought-induced tree mortality at the forest edge (Chen *et al* 1993, Laurance *et al* 2001, 2011, Matlack 1993, Young and Mitchell 1994).

We found tree height to be significantly lower at the forest edge which may indicate an adaptation of edge trees to drier conditions by increasing the root-shoot ratio (Seidel and Menzel 2016). Trees moreover showed a general tendency towards larger canopy areas at the edge but this difference was only significant in two out of five sites (figure 2(d)). However, canopy volume likely was higher at the forest edge since edge trees in general had more green branches at lower stem heights if compared to interior trees (personal observation). Higher canopy volumes result in higher leaf area indices and thus a higher evapotranspirative demand of corresponding trees (Seidel and Menzel 2016).





Given a possible mechanistic link, we also explored our data for effects of forest edge distance on tree height and tree height on NDVI, but found only few significant and altogether weak relationships revealing no consistent patterns (not shown).

Concluding, a drier micro climate and larger canopy volumes at the forest edge likely caused an earlier depletion of plant available soil water which in turn triggered an earlier seasonal closure of stomata of the isohydric Scots pine, thus resulting in an earlier seasonal growth cessation (Eilmann *et al* 2009, Pellizzari *et al* 2016). Further support of this assumption is given by the significantly lower latewood-earlywood ratios (LER) of forest-edge trees observed at all sites (figures 4 and S3) which may indicate a comparably earlier cessation of tree growth at the edge. Smaller LER as well as an earlier cessation of Scots pine growth under dry conditions have been reported in previous studies (Gruber *et al* 2010, Pichler and Oberhuber 2007). To further support our conclusions of an earlier growth cessation at the edge, we propose assessing cambial phenology of edge- and interior trees derived from micro-cores and/or dendrometers (Oberhuber 2017, Oberhuber and Gruber 2010, Swidrak *et al* 2011) as well as an air-borne thermal infrared monitoring of canopy temperatures as a proxy for transpirative cooling over the growing season (Lausch *et al* 2017, Seidel *et al* 2016).

In our study, forest-edge effects were most pronounced within the first 50 m and almost diminished after 100 m forest-edge distance which matches the existing literature well (Matlack 1993, Young and Mitchell 1994). The circumstance that we—based on dendrochronological data—only observed completely dead trees in stands with south-facing forest edges (i.e. HD, ML, and NA) is supported by studies which reported forest-edge effects to be most pronounced at southern expositions (Chen *et al* 1993, Matlack 1993, Young and Mitchell 1994). We want to stress that we also observed significantly affected Scots pine individuals at west-facing forest

edges, but our study indicates that south-facing edges may express enhanced drought vulnerability.

Interestingly, at the site NA the majority of dead trees were situated within the forest and not at the edge. Since NA represents a small forest less than 2 ha in size, it seems likely that different edge effects accumulated, thereby causing the comparably high mortality rates in the interior. This assumption is supported by a study from New Zealand which reported forests being less than 9 ha in size to be dominated by forest-edge effects (Young and Mitchell 1994) which may also explain why we found a relatively high number of devitalized trees in the interior of BD (figure 7)—a forest patch with less than 4 ha size (see table 1).

4.2. Drought and carbon depletion as likely drivers of Scots pine die-back

Our results suggest drought to be the main driver of recent Scots pine die-back in Franconia. Many dead trees did not even form latewood in 2015, likely indicating an early closure of stomata in 2015 before latewood formation had started. Such a long-lasting water stress may have resulted in carbon depletion and finally tree death. This assumption is supported by the comparison of master chronologies derived from dead and vital trees (figure 3) which indicated long-term carbon depletion in course of a long-lasting drought since 1990 (Cailleret *et al* 2017, Pellizzari *et al* 2016). As discussed in section 4.1, the observed significantly lower latewood-earlywood ratios at the forest edge also point into this direction, since relatively smaller latewood widths may indicate an earlier cessation of growth. The significant decrease of NDVI towards the forest edge further supports the carbon starvation hypothesis. That is, lower NDVI values represent a lower photosynthetic activity of forest edge trees, which may also indicate a lower stomatal aperture of forest-edge trees in September 2016 when the drought still was prevailing (Lausch *et al* 2017).

Altogether, our results also support our second initial hypothesis (ii). To back-up these conclusions additional analyses are desirable, focusing on the long-term hydraulic performance, possible differences regarding the discrimination against the stable isotope ^{13}C , and the closely related intrinsic water-use efficiency of dead and live trees (Eilmann *et al* 2010, Lévesque *et al* 2013, Pellizzari *et al* 2016, Petrucco *et al* 2017).

4.3. Open research questions

Yet, we are unable to explain why single trees at the forest edge died while some of their direct neighbors survived. This patchiness of tree die-back has been reported earlier but still lacks an explanation (Cailleret *et al* 2017, Pellizzari *et al* 2016, Petrucco *et al* 2017). As discussed for the comparison between edge and interior, differing crown sizes of edge trees may explain part of the observed patchiness of tree die-back. Since we did not explicitly measure the crown volume of single trees, this hypothesis needs to be tested further. In addition, other abiotic and biotic influencing factors—which may act to a different extent on individual trees—may govern the observed patterns. Possible other influencing factors may be a stronger competition for water resources (Giuggiola *et al* 2013) and a stronger infestation with mistletoe (Dobbertin and Rigling 2006, Galiano *et al* 2010), fungi such as *Diplodia pinea*, or bark-beetles such as *Tomicus piniperda* or *Phaenops cyanea* (Wermelinger *et al* 2008). However, most of those factors we ruled out as main influencing factor, since we observed that (i) literally all Scots pine individuals— independent of their current vitality— were infested with *D. pinea*, (ii) some of the dead trees were bare of mistletoe, and (iii) although *T. piniperda* and *P. cyanea* occurred in most of the observed stands, signs of their presence were not found on all dead trees (not shown). Finally, we want to mention the possibilities of hydraulic failure and phloem transport failure causing Scots pine die-back (Sevanto 2014, Sevanto *et al* 2014) but it is not clear how this could explain the observed long-lasting growth-decline of dying trees nor would it help to understand the occurrence of neighboring dead and live trees.

Consequently, more research is needed to extend our knowledge on possible mechanisms driving the patchiness of Scots pine die-back in Franconia. For this we recommend focusing on a comparison of wood anatomical properties and stable carbon isotopes, sap-flow measurements, spatial soil moisture patterns, predawn water potentials, canopy dimensions, and competitive status of neighboring dead and live trees and in relation to increasing forest edge distances.

5. Conclusions

Based on a dual approach combining dendrochronological means with close-range remote sensing

techniques, we were able to demonstrate that Scots pine in Franconia showed a high drought susceptibility which was significantly increased at the forest edge. As a consequence, mortality rates and the percentage of devitalized specimens after the hot and dry summer 2015 were higher at the edge compared to the interior—particularly at south-facing forest edges.

Our findings are especially important for forest management in terms of adapting local forests to climate change, particularly since Scots pine in Franconia has been predicted to suffer from drought in the 21st century (Walentowski *et al* 2017). Moreover, our study highlights potential positive feedback loops which may arise when drought-affected edges are deforested, thereby creating new vulnerable edges. Finally, since forest edges may express a significantly different productivity and climate change vulnerability in comparison to the forest interior, it is important to implement forest-edge effects in dynamic global vegetation models. Thereby potential biases of associated predictions can be minimized, particularly in managed environments where forest edges occur frequently. To back-up respective implementations, more research is needed assessing forest-edge effects across larger geographical gradients and including other widely distributed tree species.

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