

Tamm review: Drought-induced Scots pine mortality – trends, contributing factors, and mechanisms

Review Article

Author(s):

Bose, Arun K.; [Gessler, Arthur](#) ; Büntgen, Ulf; [Rigling, Andreas](#) 

Publication date:

2024-06-01

Permanent link:

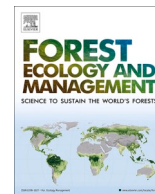
<https://doi.org/10.3929/ethz-b-000668678>

Rights / license:

[Creative Commons Attribution 4.0 International](#)

Originally published in:

Forest Ecology and Management 561, <https://doi.org/10.1016/j.foreco.2024.121873>



Tamm review: Drought-induced Scots pine mortality – trends, contributing factors, and mechanisms

Arun K. Bose^{a,b,c,*}, Arthur Gessler^{a,d}, Ulf Büntgen^{a,e,f,g}, Andreas Rigling^{a,b}

^a Swiss Federal Research Institute WSL, Zürcherstrasse 111, Birmensdorf CH-8903, Switzerland

^b Forest Ecology, Department of Environmental Systems Science, ETH Zurich, Zurich 8092, Switzerland

^c Forestry and Wood Technology Discipline, Khulna University, Khulna- 9208, Bangladesh

^d Institute of Terrestrial Ecosystems, ETH Zurich, Zurich 8092, Switzerland

^e Department of Geography, University of Cambridge, Downing Place, Cambridge CB2 3EN, UK

^f Global Change Research Institute (CzechGlobe), Czech Academy of Sciences, Brno 603 00, Czech Republic

^g Department of Geography, Faculty of Science, Masaryk University, Brno 611 37, Czech Republic

ARTICLE INFO

Keywords:

Climate change
Global warming
Drought extremes
Forest dieback
Pinus sylvestris

ABSTRACT

A recent increase in the intensity and frequency of climate extremes under global warming is likely to continue to cause unprecedented rates of forest dieback in different habitats around the world. As one of the most widely distributed tree species, Scots pine (*Pinus sylvestris* L.) has experienced widespread mortality over the past two decades and many of those forests transitioned to broadleaved dominance inducing massive changes in ecosystem functioning and services. Here, we synthesize the factors and processes underlying drought-induced Scots pine mortality. Our review identifies agreement across studies on the impact of drought, prevalence of crown defoliation prior to mortality, influence of stand density and ecological growth memory, as well as the presence of biotic agents, such as insects and mistletoes. Studies generally agree that drought triggered self-thinning plays an important role. The post-mortality stand density seems far below the comparable pre-drought numbers of trees per hectare, which indicates a significant reduction in the productivity of forest stands. Most surprisingly, we show while Scots pine mortality in the early-2000 s occurred at the species' arid distribution limits, high mortality rates are now also reported from the species' climatic optimum where growth conditions used to be more beneficial. Extreme droughts such as 2003, 2015 and 2018 are causing this observed pattern, which may indicate that an increase in frequency of extreme drought could challenge Scots pine trees growing in climatically favorable areas. Our review indicates that tree level acclimation strategies such as lowering leaf area and enhancing water-use efficiency as well as stand-level adjustments including self-thinning are apparently not sufficient to prevent Scots pine mortality induced by frequent extreme droughts and associated impact of biotic agents (insects and mistletoes). However, we still lack clear understanding in linking functional strategies of the species to local climatic variation to fully understand the capabilities of the species to grow and survive in the future climate.

1. Introduction

Tree mortality is a key ecological process that affects the dynamics of forest stand development, impacts the availability of substrates, and provides new habitats for biodiversity (Franklin et al., 1987). Any elevated level of tree mortality can alter forest dynamics, causing shifts in vegetation composition and impacting the functioning and productivity of forest ecosystems at different spatiotemporal scales (Allen et al., 2010; Anderegg et al., 2013; Batllori et al., 2020). In recent decades,

several studies conducted in temperate and Mediterranean Europe reported that drought-induced mortality of Scots pine (*Pinus sylvestris* L.) is causing shifts in vegetation composition and ecosystem function (e.g., Galiano et al., 2010; Rigling et al., 2013; Vacchiano et al., 2012; Vilà-Cabrera et al., 2013; Vilà-Cabrera et al., 2011). These studies identified that many populations of Scots pine across Europe are declining together with a substantial reduction of their regeneration, which might be a concern as the species is considered relatively drought resistant (Irvine et al., 1998; Jiang et al., 2023). Moreover, a recent

* Correspondence to: Swiss Federal Institute for Forest, Snow and Landscape Research, Zürcherstrasse 111, Birmensdorf CH-8903, Switzerland.
E-mail address: arun.bose@wsl.ch (A.K. Bose).

Europe-wide analysis showed that although the growth of Scots pine increased towards the boreal biome the growth has been decreased across the Mediterranean region because of rising temperature and precipitation reduction (Pretzsch et al., 2023).

Scots pine is one of the most widely distributed tree species covering a range of 10,000 km longitudinally (8°W in Spain to 141°E in Russia) and 3,700 km latitudinally (70°N in Scandinavia to the mountains of the Sierra Nevada in Spain at 37°N – order from south to north) (Kraakau et al., 2013). Scots pine is a boreal tree species but shows acclimation and adaptation capacities to vastly different climatic and edaphic conditions (Bose et al., 2020a; Poyatos et al., 2007). The species can display conservative growth strategies during droughts by adjusting its stomatal conductance (Irvine et al., 1998), crown transparency (Dobbertin et al., 2010), intrinsic water-use efficiency (Timofeeva et al., 2017), and leaf-to-sapwood area ratio (Martínez-Vilalta et al., 2009). In semi-arid conditions such as the Mediterranean region and the inner-Alpine valleys, Scots pines usually maintain small height and crown stature and show low radial growth rates over decades to centuries (Bigler et al., 2006; Sánchez-Salguero et al., 2015). This acclimation strategy is consistent to the growth differentiation balance hypothesis (GDBH) proposed by Herms and Mattson (1992). The GDBH assumes that scarcity of resources constrains growth more than photosynthesis, which leads to greater allocation of assimilated C to the secondary metabolism and, thus, to defense, but when resources are plentiful growth gains priority over defense (Lerdau et al., 1994). However, long, frequent, and severe soil and atmospheric droughts adversely impact such conservative growth strategy and may cause mortality after persistent declines in crown transparency and radial growth (Hunziker et al., 2022; Sánchez-Salguero et al., 2012).

Scots pine has also a tendency for investing relatively low amount of the assimilated carbon for root growth but a high proportion for crown development when water availability is high (Bose et al., 2022), which is not consistently observed among plant species (Poorter et al., 2012). The resulting large above-ground structure (crown and leaf area) then increases the water demand and that may expose trees to crown dieback or even mortality under warm and dry periods (Feichtinger et al., 2014; Rigling et al., 2003; Zweifel et al., 2020). As an early successional pioneer species, Scots pine can form homogenous and dense monocultural stands which can increase demand for resources due to low niche complementarity and therefore high competition between trees (Steckel et al., 2020). Drought has been reported as a central factor for Scots pine tree mortality by triggering increased competition among trees (Galiano et al., 2010). In addition, rising temperatures stimulate population dynamics of potentially harmful insect populations and hemi-parasitic mistletoes indirectly contributing to mortality of drought-stressed Scots pines (Dobbertin & Rigling, 2006; Sangüesa-Barreda et al., 2013; Vacchiano et al., 2012; Wermelinger et al., 2008). In addition, the legacy of past climatic and stand structural conditions can affect the current responses of trees via epigenetic changes (Bose et al., 2020b; Lamelas et al., 2024) and through ecological memory of growth, morphological and physiological structure (Peltier et al., 2022; Pretzsch, 2021). For example, the water transport system characterized by xylem structure and crown morphology may represent an ecological memory and determine a tree's growth and vitality in the future (Zweifel et al., 2020). In mesic and highly productive growing conditions, the memory of faster growth during the early phase of life could predispose a tree to dieback or mortality when they become exposed to persistent dry events at maturity (Pretzsch, 2021).

The drought-induced mortality of Scots pines is particularly well studied compared to that of other tree species. The rich body of scientific literature allowed us to review agreement and disagreement on how tree, stand, site, climatic and biotic variables are associated with the drought-induced mortality of this species. This is relevant because synthesized knowledge is required to disentangle the direct and indirect effects of site-specific processes against general drivers of Scots pine mortality. This understanding is crucial for predicting the vulnerability

of Scots pine forests to and resilience in future climate changes. The purpose of this review is to summarize current knowledge and to examine links between extreme droughts and associated impacts of biotic factors on Scots pine mortality. We first reviewed observed drought-induced mortality patterns and how they vary along the geographical gradient and whether the sites where mortality occurs are located across and along the arid distribution limit or also towards the climatically more favourable areas of the species distribution. We then synthesized abiotic and biotic drivers and mechanisms responsible for tree mortality. We also examined whether growth-climate relationships along the geographical gradient in Europe provide additional insights to tree mortality patterns of Scots pine.

2. Methods

The literature review was conducted based on peer-reviewed publications. Pertinent scientific publications were identified using online search engines Google Scholar and Web of Science and combinations of the following factorial keywords: “Scots pine AND mortality”, “dieback, “factors AND affecting AND mortality”, “mechanisms AND associated AND Scots pine AND mortality”. We used both the local name “Scots pine” and Scientific name “*Pinus sylvestris*” for literature search. We first identified studies that reported the mortality events of adult trees (Supplementary Table SM1). For each of those studies, we extracted geographical location/s (latitude and longitude) of the mortality and identified drivers and mechanisms that were tested as causes for mortality. It is important to consider that the analysed drivers and mechanisms of tree mortality differed between the studies. For understanding the role of ecological memory of past growth on tree mortality, we considered studies that reported tree-ring width data of still living and dead trees of the same site (Supplementary Table SM2). To understand how the role of ecological memory of past radial growth trajectories in determining mortality varies across species, we considered Scots pine, “angiosperms”, “other gymnosperms”. We recognize that such comparison is rather qualitative as the studies are conducted in different regions (even in different continents) and not all studies examined “Scots pine”, “other gymnosperms”, and “angiosperms” together. We found 7 studies and 12 sites for Scots pine, 7 studies and 15 sites for “other gymnosperms” and 8 studies and 9 sites for angiosperms (see Supplementary Table SM2 for more details). For each site, we visually examined the growth trajectory of live and dead trees and developed three categories based on the growth onset of live and dead trees. These categories are superior, inferior, and similar growth onset indicating higher, lower, and similar radial growth, respectively in dead trees compared to present live trees. The “growth onset” characterises the radial growth at the initial phase (first 20–30 years) of life. We then quantified the percentage of total sites had superior, inferior and similar growth onset in present dead trees compared to present live trees.

For understanding the role of intrinsic water-use efficiency and tree mortality, we considered studies that examined $\delta^{13}\text{C}$ in tree ring of live and dead trees of the same site (Supplementary Table SM3). We also synthesized literature for examining potential linkages between growth-climate sensitivity and tree mortality (Supplementary Table SM4). For this objective, we used the search terms “Scots pine AND growth sensitivity”, “Scots pine AND climate-growth AND relationship”, and “Scots pine AND climate-growth AND correlation”. For that, we only considered studies that reported radial growth sensitivity (i.e. correlation coefficient and respective *p*-value) to monthly temperature and precipitation from previous year June to current year September. For the consistency, we did not consider studies that reported correlation coefficient to minimum or maximum temperature/precipitation (e.g., Sánchez-Salguero et al., 2015; Sensuła et al., 2015), or used non-detrended ring-width indices or basal area increment (e.g., Sidor et al., 2018), or used earlywood/latewood instead of whole ring-width (e.g., Lebourgeois et al., 2010). We also excluded studies that examined growth responses of trees growing under special habitat conditions

such as the treeline (e.g., Franke et al., 2017; Linderholm, 2002), dunes (e.g., Cedro et al., 2022), or peatlands (e.g., Linderholm et al., 2002; Moir et al., 2011). However, from both Linderholm et al. (2002) and Moir et al. (2011), we considered non-peatland sites.

3. Drought induced Scots pine mortality

A review of the literature revealed that 37 published studies, including sites from temperate and Mediterranean Europe (Supplementary Table SM1), have investigated drought-induced tree mortality of Scots pine. These studies covered a latitudinal gradient from 35° N to 52° N (Fig. 1) and an elevational gradient from 200 m to 1700 m. The earliest study was published in 1998, but 30% of the studies were published from 2020 to 2022. This may indicate that the occurrence of Scots pine mortality has been increased in recent years which may result from more frequent extreme drought events including the droughts in 2003, 2015 and 2018. A high percentage of these studies were conducted in the moisture- and high-temperature limited edge of the Scots pine distribution; 91% of the studies were conducted at sites that received less than 1000 mm of annual precipitation (Fig. 2). Studies from the warm and dry edge of distribution especially dominated until 2012 (Fig. 2) indicating (as one would expect) that drought-induced mortality occurred mostly at naturally dry and warm sites. However, the results from Fig. 2 showed that compared to earlier years a higher percentage of studies report drought-induced mortality towards the climatic core areas of Scots pine distribution. This indicates that dieback presently also occurs at sites which are not necessarily extreme for Scots pine from a long-term precipitation and temperature point of view, but may be limited by soils of low water holding capacities where a reduction in precipitation might become critical (unfortunately, the available literature does not allow to test this hypothesis).

Our review identified drought-induced crown defoliation and tree mortality in semi-arid environments of Austria (Oberhuber, 2001), France (Archambeau et al., 2020; Lemaire et al., 2022), Germany (e.g.,

Buras et al., 2018; Haberstroh et al., 2022; Hartmann et al., 2022), Italy (Vacchiano et al., 2012; Vertui & Tagliaferro, 1998), Poland (Tyminska-Czabańska et al., 2022), Romania (Hereş et al., 2021), Spain (e.g., Galiano et al., 2010; Hereş et al., 2012; Sánchez-Salguero et al., 2012), and Switzerland (e.g., Dobbertin et al., 2005; Rigling et al., 2013). Drought-induced Scots pine mortality has been episodic, which constrained us in drawing temporal dynamics. Hartmann et al. (2022) showed that the mortality rates of Scots pine increased tenfold (from <0.1% in 2018 to 1% in 2020) following the 2018 drought in Germany, while Vilà-Cabrera et al. (2011) reported a 11-fold increase in standing tree mortality over a 10-year period while studying inventory plots in the Iberian Peninsula of Spain covering a region from 10° W to 3° E longitude and from 43° to 35° N latitude. In the Rhone valley of Switzerland, Rigling et al. (2013) showed that the percentage of Scots pine mortality was 60% higher than that of the companion species pubescent oak (*Quercus pubescens*) over a period of 20 years. They showed that the Rhone valley has been exposed to persistent warm and dry periods and that persistent dry conditions were associated with the mortality of Scots pine. They found that the stand density of trees larger than 12 cm (DBH) was 200 trees per hectare, which is extremely low compared to other natural non-drought exposed Scots pine stands of similar age (50–100 years). This may indicate that the drought impact was not just capturing the natural self-thinning process but significantly reducing the tree density of the forest stands. Increase growth rates at the population level through fertilization (Pretzsch & Biber, 2022), precipitation and temperature may also trigger self-thinning-induced tree mortality in Scots pine stands (Toraño Caicoya et al., 2024). In such cases self-thinning induced mortality mainly eliminated small sized trees rather trees from all size classes (Pretzsch et al., 2022). However, in the context of our synthesis while examining 37 studies, we found that 30 of those studies were conducted at sites receiving annual precipitation from 320 to 775 mm. The self-thinning related mortality that we synthesized is more likely triggered by frequently occurred extreme drought events than by increased growth rates (e.g., Galiano et al., 2010;

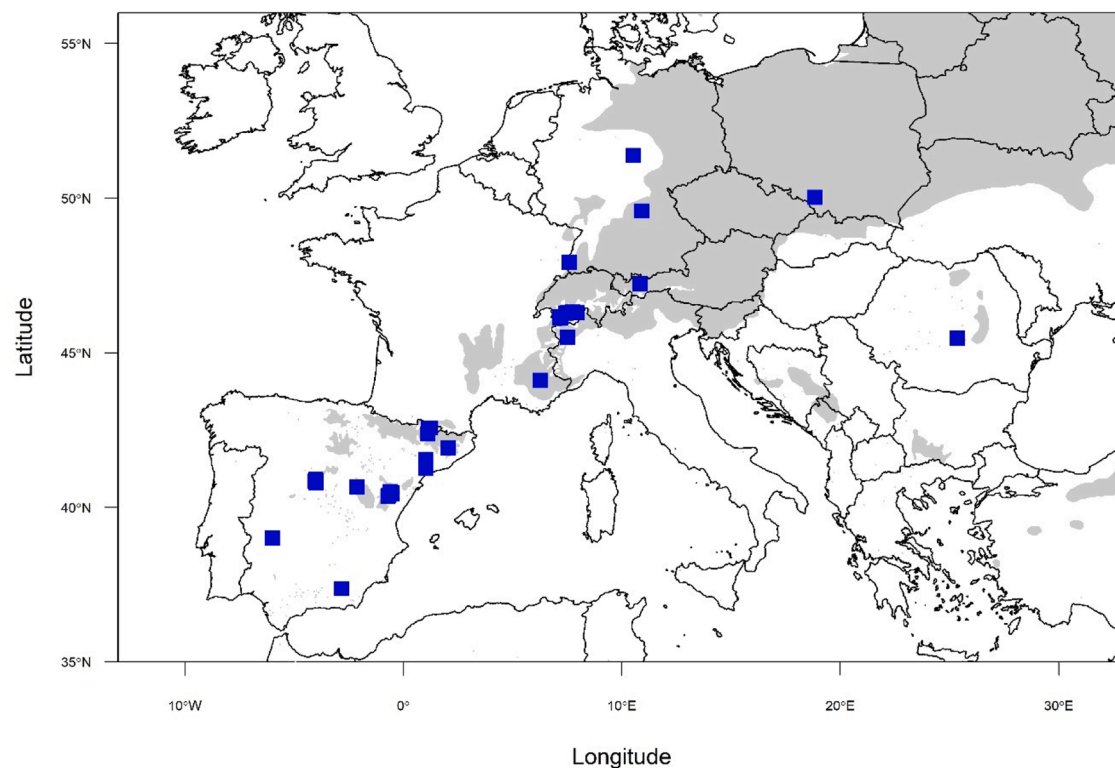


Fig. 1. Blue rectangles indicate locations of Scots pine mortality identified by different studies (N=37). Shaded areas in the figure indicates the distribution of Scots pine according to Máttyás et al. (2004).

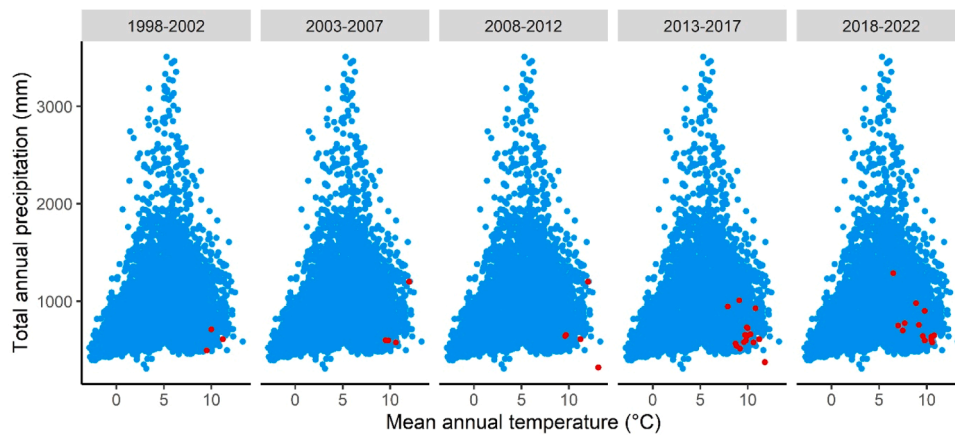


Fig. 2. Climate space of Scots pine distribution (light blue circles) and locations identified where Scots pine mortality occurred (red circles) over the past 25 years (1998–2022). The first study that reported Scots pine mortality was published in 1998. The climate data was downloaded from World Clim: <http://worldclim.org>. It represents average monthly climate data for 1970–2000. The data were created by Steve Fick and Robert Hijmans.

Rigling et al., 2013; Vilà-Cabrera et al., 2013).

Although the analysed drivers and mechanisms of tree mortality differed between the considered studies (Fig. 3), our review identified the direct or indirect effect of drought and/or heat as primary driver of Scots pine mortality in 89% of the studies. The second most important climatic variable contributing to pine mortality was vapor pressure deficit (VPD) (Fig. 3). However, very few studies considered and measured VPD as the potential drivers of mortality. VPD has been identified as a dominant environmental growth constraint for European tree species in recent years (Trotsiuk et al., 2021) and induced plausible changes in forest dynamics and species distribution (Grossiord et al., 2020). In addition to environmental factors, 25% of the studies showed that tree size was an important factor in explaining drought-induced

mortality of Scots pine. These studies demonstrate that smaller trees showed a higher mortality compared to larger trees. Dense forest structures may act as intrinsic continuous stress on small and suppressed trees and that stress intensifies under drought, when soil water and nutrient resources get limiting, and could, thus, indirectly contribute to mortality (Archambeau et al., 2020). Scots pine trees that are weakened by continuous competition and droughts (Rigling et al., 2013; Weber et al., 2008) become more susceptible to additional biotic contributing factors such as insects and pathogens (Heiniger et al., 2011; Jaime et al., 2019; Wermelinger et al., 2008), and hemiparasitic mistletoes (Rigling et al., 2010; Sangüesa-Barreda et al., 2013; Wang et al., 2023) resulting in a higher risk of mortality. In our review, 22% and 19% of the studies identified insects/pathogens and mistletoes, respectively as drivers of

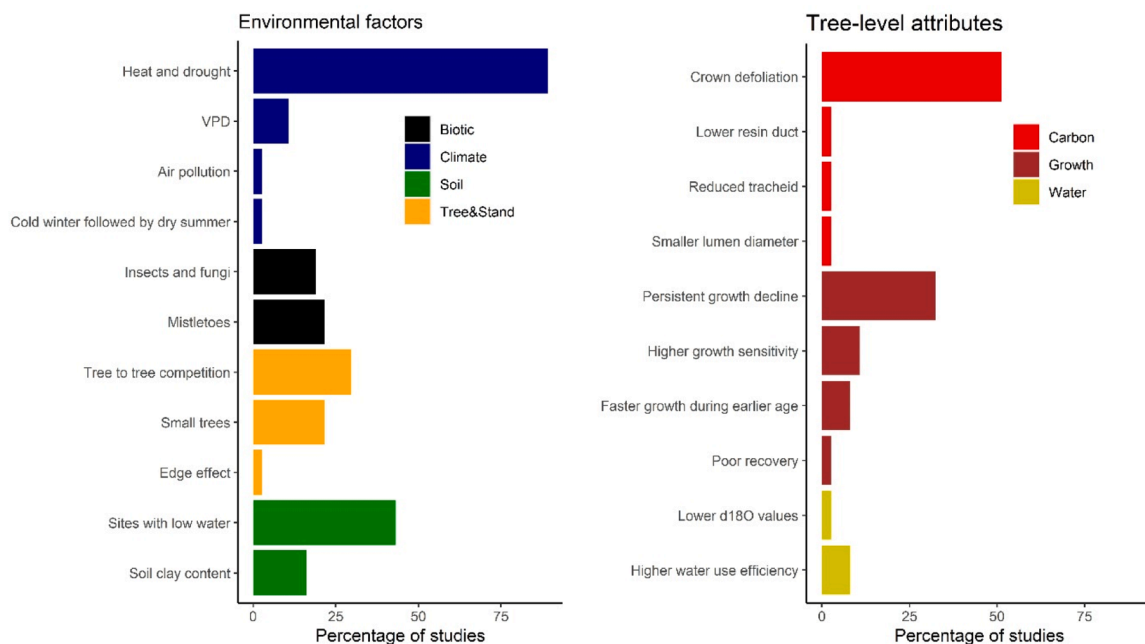


Fig. 3. Percentage of studies (N=37) that identified the factors and underlying processes driving Scots pine mortality. Environmental factors and tree-level attributes are grouped by four and three categories, respectively. Note. All environmental factors and tree-level attributes listed above were not considered by all studies. Therefore, the percentage values are biased to some factors which were often examined (e.g., heat and drought and crown defoliation). However, this summary figure provides the list of factors and processes which were found responsible for Scots pine mortality. Note. small trees: smaller trees of the tree size classes within a plot had higher mortality compared to larger trees; lower number of resin duct: dead trees had a lower resin duct compared to live trees; smaller lumen diameter: dead trees had smaller lumen diameter compared to live trees; higher growth sensitivity: dead trees were more sensitive to climate prior to dead compared to present live trees; lower $d^{18}O$ values: dead trees were associated with lower $d^{18}O$ value in tree-ring compared to live trees.

Scots pine mortality (Fig. 3). Scots pine is a host for a large number of harmful insect species (Wermelinger et al., 2008), and increased temperature together with drought not only trigger water-stress for Scots pine it also makes the trees vulnerable to insect attack (Jaime et al., 2019). Beetle species are known to contribute to tree mortality by their larval feeding, and adult beetles often colonize suppressed and weak Scots pine trees (Bose et al., 2022; Wermelinger et al., 2008).

4. Mechanisms underlying drought-induced Scots pine mortality

McDowell et al. (2008) introduced a framework with three interactive and non-exclusive mechanisms for explaining drought-induced mortality in trees: (i) carbon starvation, (ii) hydraulic failure and (iii) biotic agents. Carbon starvation describes the situation when the carbon demand for metabolism and defense is not met due to reduced photosynthesis and associated low carbohydrate supply (McDowell & Sevanto, 2010), while hydraulic failure occurs when water transport from roots to leaves disrupts through xylem embolism (Mantova et al., 2022). Synthesizing data of 19 experimental and observational studies covering 26 species, Adams et al. (2017) showed that while xylem hydraulic failure often appears to be a necessary condition for drought-induced mortality, carbon starvation was not universal across species but more common in conifers (Galiano et al., 2011).

Trees can avoid water stress under droughts through efficient stomatal control (Salmon et al., 2020) and increasing root:shoot ratio (Bose et al., 2020b) or can tolerate drought through osmotic adjustment or increasing resistance to embolism (Urli et al., 2013). However, stomatal closure over a long period can be unsustainable as it will reduce carbon assimilation and associated carbon balance in trees (Galiano et al., 2011; Poyatos et al., 2013), while structural adjustments (i.e., leaf area and sapwood) during droughts strongly depends on the legacy of pre-drought structural conditions (Zweifel et al., 2020) and acclimation of the xylem structure occurs over the longer term only (Eilmann et al., 2009). At the stand level, water availability per individual tree will depend on the overall water demand of the vegetation, input of water (precipitation, lateral inflow in the soil), soil water storage capacity, and root systems of the competing trees (Grossiord, 2019).

Overall, the responses to drought depend on a range of factors and processes including tree size (Bennett et al., 2015; Colangelo et al., 2017), species-specific functional traits (Anderegg et al., 2016; Greenwood et al., 2017), stand structure (Clark et al., 2016; Venturas et al., 2021), species composition (Hajek et al., 2022; Thrippleton et al., 2018; Weber et al., 2008), biotic agents (Jonas et al., 2014; Wermelinger et al., 2008; Williams et al., 2012), and legacy effects of past climate and forest management (Gimmi et al., 2010; Lloret et al., 2022; Senf et al., 2018). The magnitude of the interactions among multiple inciting and exacerbating factors associated with diverse forest mortality processes highlights the complexity in understanding tree mortality dynamics (Allen et al., 2015). Based on our literature review, we discussed below four biological and community-level mechanisms that were found relevant in explaining the mortality of Scots pine. Among the four mechanisms, (i) water vs carbon depletion and (ii) the ecological memory of the past tree development deals with tree-level processes while (iii) soil predisposing factors and (iv) legacy effects of past forest management deals with stand-level processes.

4.1. Water vs carbon depletion in Scots pine

Several studies indicated that Scots pine trees growing under semi-arid conditions such as in Swiss Rhone valley and northeastern Spain are subjected to carbon availability limitations and their mortality may be related to carbon starvation (e.g., Galiano et al., 2011; Hereş et al., 2014; Timofeeva et al., 2017; Voltas et al., 2013). However, a study that measured changes in NSC (non-structural carbohydrates: soluble sugars and starch) after a winter drought did not reveal any evidence of depleted carbon reserves in stems of dying trees compared with healthy

trees (Voltas et al., 2013). However, a tendency of carbon starvation in Scots pine trees has been identified by Aguadé et al. (2015b) in northeastern Spain. When studying defoliated and non-defoliated trees in northeastern Spain, Aguadé et al. (2015a) showed that total NSC significantly decreased during drought in needles. In addition, *Omnia* P. Karst infection was detected in defoliated trees and was associated with depleted root starch reserves during and after drought (Aguadé et al., 2015a). Moreover, Galiano et al. (2011) showed that trees that failed to recover leaf area contained very low levels of carbon reserves. This depletion of carbon reserves was strongly related to the probability of tree mortality. However, Schönbeck et al. (2018) showed a constant soluble sugar and starch values in needles across different soil water availability and along a gradient of defoliation. However, strongly defoliated trees, which have a high probability to die within the next few years (Hunziker et al., 2022) displayed decreased C reserves. While studying Scots pine trees in northeastern Spain and Switzerland, respectively Hereş et al. (2014) and Timofeeva et al. (2017) showed that dying Scots pine trees exerted stronger stomatal control and a more conservative water-use strategy compared to surviving trees. Reduced stomatal conductance for more than three decades reduced the production of new carbohydrates in those trees, and they probably died due to carbon starvation.

Our review did not find any study that quantitatively identified hydraulic failure as an underlying mechanism for Scots pine mortality, although few studies tested that experimentally (e.g., Aguadé et al., 2015a; Aguadé et al., 2015b). However, Salmon et al. (2015) showed that defoliated Scots pine trees had lower needle water potentials and smaller hydraulic safety margins compared to non-defoliated trees in Prades mountain of northeastern Spain. Meanwhile, Poyatos et al. (2013) showed that, at the same site, sap flow per unit leaf area was actually higher in defoliated trees indicating an increased water transport efficiency determined by higher water use per unit leaf area. These structural and physiological adjustments indicate continuous stress in defoliated trees and its vulnerability to water-stress. Moreover, Voltas et al. (2013) observed higher growth rates in later dying Scots pine trees compared to surviving ones and fast growth decline and mortality after a drought and late frost event indicating hydraulic failure as mortality mechanism (see also Gessler et al., 2018). Our review identified that physiological mechanisms underlying Scots pine mortality are not well understood, however, several studies provided hypothetical frameworks on whether tree mortality was related to depletion in carbon or water in trees (e.g., Haberstroh et al., 2022; Hereş et al., 2014; Timofeeva et al., 2017).

4.2. Ecological memory of the past tree development

A classical approach for understanding and modelling tree mortality responses to environmental stresses or management treatments is based on trees current size, age, environmental conditions, and competitive status (Burkhardt & Tomé, 2012; Weiskittel et al., 2011). However, recent research into the growth and mortality response to environmental stress provides increasing evidence that current reactions of trees to environmental conditions can be determined by conditions that trees experienced in the past (Bose et al., 2020b; Ogle et al., 2015; Ovenden et al., 2021; Pretzsch, 2021; Zweifel et al., 2020). While reviewing global-scale tree mortality data, Jump et al. (2017) demonstrated that periods of favorable climate that promoted abundant tree growth can lead to structural overshoot or an unbalanced aboveground tree biomass relative to below-ground root biomass and can lead to water stress in trees when droughts inevitably return.

The results of our review showed that current-dead Scots pine trees from 50% of the sites ($N=12$) had faster growth during their early phases of life ("superior growth onset") compared to current-living trees (Fig. 4). This result suggests that the memory of superior growth onset is closely associated with mortality of Scots pine. However, for "other gymnosperms" the "superior growth onset" was related to mortality in

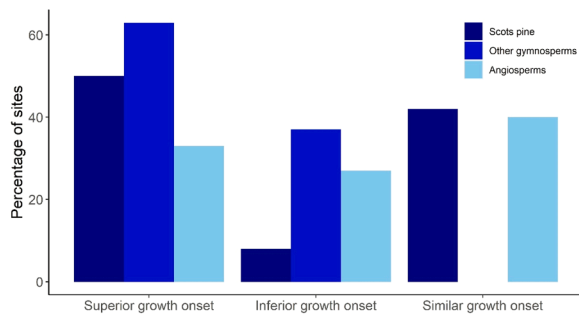


Fig. 4. Initial growth trajectories of dead trees relative to live trees of Scots pine, other gymnosperms and angiosperms species. The results are based on 7 studies and 12 sites for Scots pine, 7 studies and 15 sites for other gymnosperms and 8 studies and 9 sites for angiosperms (see [Supplementary Table SM2](#) for more details). Superior, inferior, and similar growth onset indicate higher, lower, and similar radial growth, respectively in dead trees compared to present live trees during the initial years of life.

higher percentage of sites compared to Scots pine (Fig. 4). Our synthesis also shows that at 45% of the sites, the growth trajectory during the earlier phases of life of current-dead Scots pine trees was similar to current-living Scots pine trees. This group of dead trees had experienced a long and persistent growth decline over a period of 30 or more years prior to death (e.g., [Hereş et al., 2012](#); [Oberhuber, 2001](#); [Timofeeva et al., 2017](#)), which may indicate their persistent struggle for survival under water limiting conditions. These trees might have died through persistent water stress and competition from neighbouring trees ([Voltas et al., 2013](#)), and the ones currently living but also showing persistent growth decline and low growth rate would probably die in near future ([Cailleret et al., 2017](#); [Weber et al., 2008](#)). This particular growth trajectory of maintaining low-growth rate over a long-period prior to death was not common in other gymnosperms but was visible in angiosperm species (e.g., [Bigler & Bugmann, 2004](#); [Colangelo et al., 2018](#)).

4.3. Soil predisposing factors

Studying across a latitudinal gradient from southern Spain to northern Germany, [Bose et al. \(2020a\)](#) showed that the resilience to extreme droughts have decreased over the recent decades in Scots pine trees from low-productivity sites. This continuous decrease in resilience to extreme droughts can lead to crown defoliation and dying of the whole tree ([Cabon et al., 2023](#); [DeSoto et al., 2020](#)). These low-productivity sites reported by [Bose et al. \(2020a\)](#) are located towards the drier edge of Scots pine distribution where the annual growth has been affected by frequent drought events over the past 30 years. Scots pine growing on stony soils, which are common across alpine regions, can be extremely sensitive to short-term fluctuations of water availability ([Oberhuber et al., 1998](#)). Soil depth may act as a long-term predisposing factor ([Oberhuber, 2001](#)), as Scots pine strongly relies on soil water stored at the top soil layer to meet summer evaporative demand ([Bose et al., 2022](#)). Among soil properties, stoniness, clay content and soil depth influence the soil water holding capacity, and a persistent decline in soil water can trigger crown defoliation rates in Scots pine ([Galiano et al., 2010](#)), and can lead to mortality ([Hunziker et al., 2022](#)).

Although many of our identified sites where drought-induced mortality of Scots pine occurs are located at the drier edge of the Scots pine distribution, [Madrigal-González et al. \(2020\)](#) and [Vilà-Cabrera et al. \(2013\)](#) showed that the species can also be sensitive to drought-induced mortality when growing under less dry conditions. [Lévesque et al. \(2013\)](#) demonstrated that tree growth in mesic sites with deeper soils is strongly controlled by the water availability in current summer, and hence, an increased warming or drought in summer will threaten such fast growing trees from mesic sites as well. In mesic environmental conditions, Scots pine shows a tendency of growing relatively faster and

developing higher above-ground biomass (e.g., longer xylem and higher leaf area) compared to trees growing in drier conditions and on shallower soils ([Rigling et al., 2002](#); [Timofeeva et al., 2017](#)). Those trees from mesic sites could become vulnerable when they face a persistent exposure to dry climatic conditions ([Bose et al., 2022](#); [Jump et al., 2017](#)). In the mesic environment, when the conditions change from moist to dry, the reaction of trees could either be maintaining the growth and physiological activities using the accumulated carbon reserves ([Zweifel et al., 2020](#)) or adjusting traits and functions according to the changes in the new environment ([Grossiord et al., 2018](#)). For example, in the Swiss Rhone valley, Scots pine trees were irrigated over a nine-years period, and when the irrigation was stopped in 2013, the trees' initial reaction was to maintain the leaf area and radial growth possibly using their carbon reserves ([Schönbeck et al., 2018](#); [von Arx et al., 2017](#)). However, these trees returned quickly to the level of growth and leaf area of stressed control trees (which were never irrigated) ([Bose et al., 2022](#); [Zweifel et al., 2020](#)). This indicates that Scots pine trees currently growing under less dry conditions such as at higher elevation sites or on deeper soils in central and Mediterranean Europe could also be vulnerable to extreme droughts if the frequency of the drought events increased in future ([Camarero et al., 2011](#); [Sánchez-Salguero et al., 2015](#)).

4.4. Legacy effects of past forest management

Forest management options such as reductions of stand density and/or increase in species mixing are often proposed to increase resistance of individual trees and forests against extreme droughts ([Ammer, 2019](#); [Bose et al., 2018](#); [Sohn et al., 2016b](#)). Stand density reductions by thinning have been found to be effective across conifers in decreasing inter-tree competition and mortality since the available resources were shared among less trees ([Bottero et al., 2021](#); [Giuggiola et al., 2013](#); [Giuggiola et al., 2015](#); [Sohn et al., 2016b](#)). However, opposite results have also been found where thinning can increase water stress and tree dieback ([Camarero et al., 2011](#)). This could happen due to sudden changes in stand microclimate conditions such as increases in wind penetration into the residual stand and increases in evaporative demand ([Bladon et al., 2007](#)) and superficial soil water depletion as a result of higher soil evaporation ([Simon et al., 2017](#)). Increases in evaporative demand could cause cavitation in xylem even though less trees are competing for the soil water resources ([Brodrribb et al., 2021](#)). An increase in VPD alone in the absence of soil drought can lead to hydraulic damages but also to a reduction of photosynthesis due to stomatal closure. VPD induced cavitation will also constrain water supply to leaves, eventually additionally reducing the rates of photosynthesis. In addition, thinning-associated faster growth and crown development can predispose trees to water stress under extreme drought events as observed for silver fir (*Abies alba*) in Spain ([Camarero et al., 2011](#)).

Our literature review revealed that 8 published studies have investigated the impact of stand density on drought-induced tree mortality of Scots pine (Table 1). These studies were conducted in temperate and Mediterranean Europe. Overall, these studies agree that densification resulted from the lack of thinning interventions may act as an intrinsic continuous stress factor on Scots pine trees through increased competition for resources, and that densification stress could intensify under extreme climatic dryness. The current structure and composition of many Scots pine forests in Spain, Switzerland, Romania and elsewhere in Europe is associated with relatively young (younger than 100 years), homogenous, and dense stands that resulted from abandonment of traditional agricultural and forest uses during the 20th century ([Hereş et al., 2021](#); [Rigling et al., 2013](#); [Vilà-Cabrera et al., 2011](#)). The mortality was primarily associated with smaller and suppressed trees (Table 1), which may indicate that self-thinning was probably the main driving process of this mortality, and that self-thinning processes might have been triggered by extreme climatic conditions ([Bigler et al., 2006](#); [Rigling et al., 2013](#); [Vilà-Cabrera et al., 2013](#)). In addition, the

Table 1

List of studies investigating how the legacy of forest densification (i.e., lack of forest management) modulates drought impacts on mortality of Scots pine.

Location	Legacy of forest densification effects				Scale of observation	References
	Direct effect of densification	Interactive effect with drought	Interactive effects with tree size	Interactive effects with site aridity		
Central Pyrenees, Spain	Increased mortality	NC	Higher mortality of smaller trees	NC	Tree/Plot	Galiano et al., 2010
Iberian Peninsula, Spain	Increased mortality	Drought effect was intensified by the stand density	Higher mortality of smaller trees	Dry and wet sites were equally vulnerable to mortality	Plot	Vila` Cabrera et al., 2011
Catalonia, Spain	Effect of stand density was dependent upon soil depth and summer aridity	Low density stands associated with low summer water balance had higher mortality	Higher mortality of smaller trees	In dry sites, intensive thinning increased tree mortality, but low soil depth had no effect on mortality	Plot	Vila` Cabrera et al., 2013
Rhone valley, Switzerland	Increased mortality	Stand densification effect was intensified by droughts	Higher mortality of smaller trees	Higher mortality in drier sites	Plot	Rigling et al., 2013
NFI data of Switzerland	Increased mortality	NC	Higher mortality of smaller trees	Higher mortality across dry-low elevation sites	Plot	Etzold et al., 2019
NFI data of Finland, France, Germany, Spain, and Sweden	Increased mortality	Stand densification effect was intensified by droughts	NC	Effect of conspecific basal area increasing mortality was higher in dry sites	Plot	Archambeau et al., 2020
Valsain pinewood, Spain	Increased mortality	Stand densification contributed to drought-induced tree mortality	NC	Effect of stand densification was similar across dry and wet sites	Plot	Madrigal-Gonzalez et al., 2020
Carpathians, Romania	Increased mortality	Stand densification contributed to drought-induced tree mortality	NC	NC	Plot	Heres et al., 2021

NC: not considered in the analysis.

probability of Scots pines being infested by bark beetles was higher with high Scots pine density and basal area (Jaime et al., 2019).

Species mixing aims to promote the efficient uptake and utilization of the available resources by reducing the functional redundancy and through niche complementarity among trees (Ammer, 2019). However, studies on potential roles of species mixing showed that species richness is not always positively related to drought resistance (Grossiord, 2019; Ovenden et al., 2022) and can even increase tree mortality (Searle et al., 2022) in forest ecosystems, therefore, should be dependent upon site-specific biotic and abiotic factors (Forrester et al., 2016). Scots pine has often shown higher biomass growth when mixed with other species including *Quercus petraea* and *Q. robur* (Pretzsch et al., 2020), *Fagus sylvatica* (Pretzsch et al., 2016), *Picea abies* (Ruiz-Peinado et al., 2021) and *Pinus pinaster* (Riofrío et al., 2017). Using a large latitudinal and longitudinal gradient in Europe, Steckel et al. (2020) showed that Scots pine in mixed stands with *Quercus* species exhibited a higher drought resistance (i.e., the ability to maintain growth during drought) compared to homogenous Scots pine forests. Similar to that finding of Steckel et al. (2020), Scots pine displayed higher resistance to extreme drought when it was growing with Norway spruce across sites located in temperate, hemiboreal and boreal Europe (Aldea et al., 2022). However, tree ring isotopes, which are highly sensitive indicators of gas exchange responses to drought (Supplementary Table SM3 and Jucker et al., 2017), indicated that drought events more strongly affected intrinsic water use efficiency of Scots pine when growing in mixtures compared to monoculture, both in boreal and Mediterranean ecosystems (Forrester et al., 2016). Our review indicates that mixing Scots pine with other tree species will increase the growth and survival of Scots pine as well as of associated tree species under extreme drought conditions (e.g., De Cáceres et al., 2021; Gea-Izquierdo et al., 2014; Martínez-Vilalta et al., 2012), but the response of intrinsic water use efficiency might indicate that longer or more intensive droughts might negatively affect Scots pine in mixed stands in future (González de Andrés et al., 2018).

5. Ecological factors of growth-climate sensitivity

Tree radial growth is a particularly sensitive indicator of drought stress and associated mortality and can be followed for decades to centuries back in time (Cailleret et al., 2017). Environmental factors that significantly influence radial growth for decades prior to mortality can provide valuable signals on which factors are constraining tree growth and inducing persistent stress in trees (Cailleret et al., 2019). Tree growth sensitivity to climatic factors (e.g., precipitation or temperature) refers to the responsiveness of trees' biological processes to climate (Peltier & Ogle, 2020). The magnitude of growth sensitivity to a climatic variable indicates the importance of that climatic variable for growth at a given site (Wilmking et al., 2020). Therefore, the patterns of growth sensitivity may serve as early warning signs for mortality in the face of drought.

A review of the literature revealed that 29 studies, including 140 sampling sites (Supplementary Table SM4) from boreal, temperate and Mediterranean Europe, have investigated the growth sensitivity of Scots pine in relation to monthly temperature and precipitation of the current and previous year. Significant relationships of Scots pine tree-ring widths were more commonly found with precipitation compared to temperature and more with current-year climate than previous-year climate (Fig. 5 and Supplementary Fig. SM1). The percentage of sites that had significant relationships between tree-ring widths and monthly climatic variables varied across geographical gradient (latitudes and longitudes). The precipitation in May and June of the current year was found to be the most important variable and was positively related to tree-ring width. However, the percentage of sites that had positive relationship with June precipitation decreased with increasing latitude indicating higher dependency of southern European sites on precipitation occurring in early summer. February and March temperature of the current year were more often positively related to tree-ring width than the temperature in summer, autumn, or previous-year winter. The importance of current-year spring temperature for tree growth was more common towards the northern latitude in Europe. The temperature in current-year June or in July was negatively associated with tree-ring

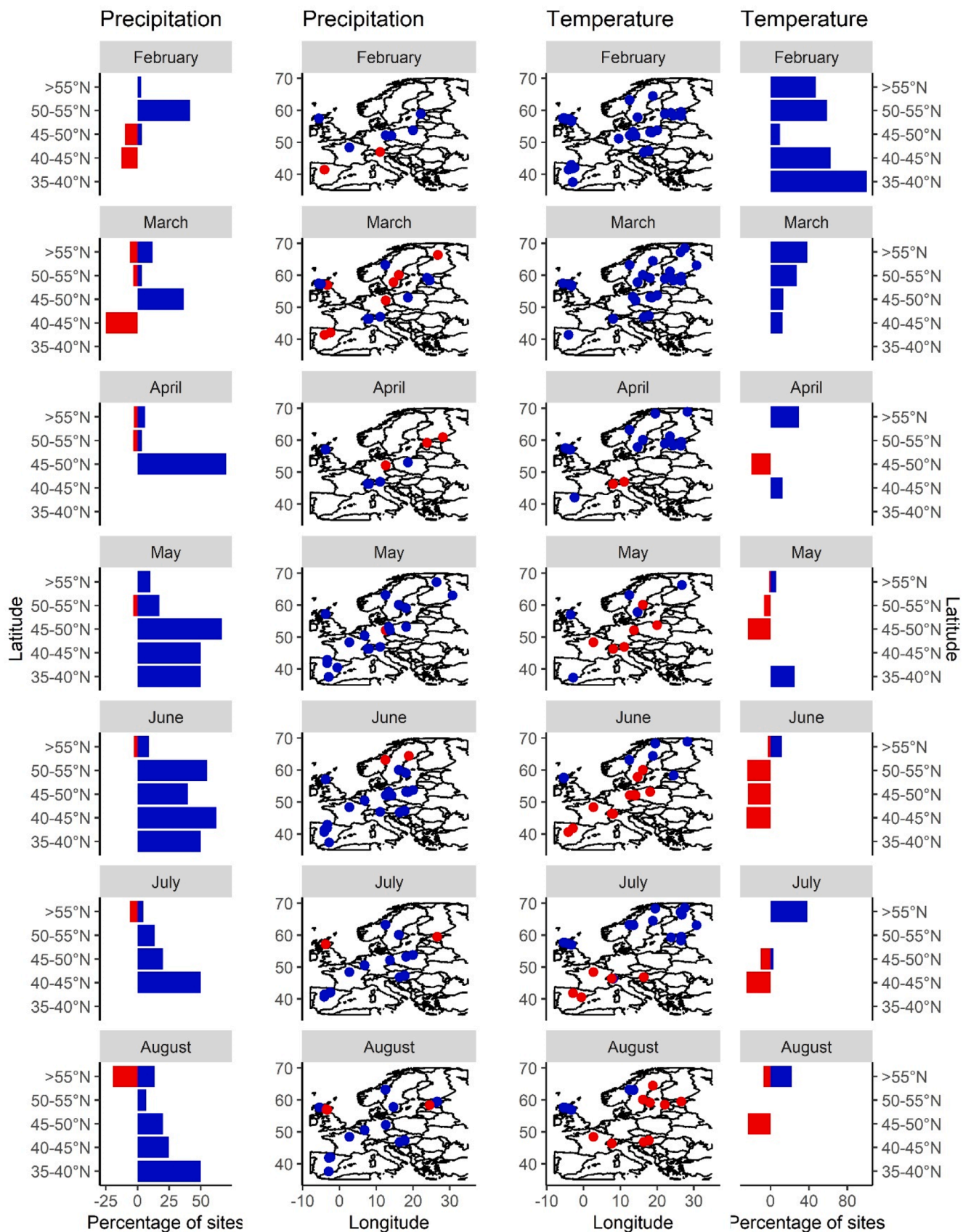


Fig. 5. Growth response of Scots pine to monthly climatic conditions based on the results of 29 studies and 140 sampling sites (Supplementary Table SM4). Each row corresponds to a month (most important months are included which are all from the current year). Left and right panels refer to growth response to monthly total precipitation (mm) and mean temperature (°C), respectively. The two outermost columns present the proportion of sites showing significant ($\alpha = 0.05$) negative and positive responses as a function of latitude. Negative responses are shown in red and positive in blue.

width of sites located in central Europe but not of sites located above 55° latitude (Fig. 5). This may imply that warmer temperatures can reduce growth across a wide range of forests in central Europe. However, warmer temperature can increase tree growth of Scots pine towards northern Europe as indicated by Pretzsch et al. (2023). Scots pine trees growing across southern Spain (35° - 40° N) were mostly unrelated with our climatic variables except current year June and previous year September precipitation (Fig. 5 and Supplementary Fig. SM1).

An important finding of our synthesis is that growth of Scots pine trees located below 55° N, which is more than half of its distribution area in Europe, is positively associated with summer precipitation. This higher dependency of precipitation over temperature is contributing to the observed high vulnerability to drought as shown by recent studies examining the response of Scots pine to the 2018 European drought (e.g., Haberstroh et al., 2022; Hartmann et al., 2022; Tyminińska-Czabańska et al., 2022). The two findings that (1) growth sensitivity of Scots pine is depending on summer precipitation in warm and dry sites and (2) mortality is also driven by precipitation reduction in summer shows how relevant growth-climate sensitivity studies are for predicting the risk for Scots pine mortality in a changing climate. Several studies conducted on pine species in Europe and north America reported a higher growth-sensitivity to climatic factors of current-dead trees compared to live ones (e.g., Ogle et al., 2000; Timofeeva et al., 2017). However, it is important to consider that the effect of growth sensitivity on the likelihood of mortality can be modified by endogenous factors such as tree age (Ogle et al., 2000), tree size (Campbell et al., 2021) and phylogeny (Herguido et al., 2016).

6. Implications for forest management

Our review indicates that forest management interventions need to be based on site moisture legacies. Stand structures of Scots pine forests across Europe become more homogeneous with increasing site quality (Pretzsch et al., 2022). At dry sites, thinning interventions can reduce drought stress in Scots pine by reducing competition for soil water (Giuggiola et al., 2013; Sohn et al., 2016a). However, a reduction of stand density in moist sites could promote an unbalanced above-ground biomass relative to below ground root networks, and that could make the trees vulnerable when a drought event occurs after the intervention (Vilà-Cabrera et al., 2013). Heavy thinning in moist sites with taller trees could also make Scots pine trees vulnerable to windthrow as thinning usually increases wind penetration in post-thinned stands and trees in moist conditions are often associated with superficial root systems (Bladon et al., 2007). As a consequence, rather moderate thinning, which does not strongly change above ground space availability should be the preferred practice in normally well water-supplied stands, while stronger interventions are proposed at dry sites.

Mixing Scots pine with broadleaved species such as *Quercus* spp. on mesic to dry sites and with *Fagus sylvatica* in mesic sites could enhance complementarity and could benefit Scots pine trees as well as the companion trees under drought conditions (Pretzsch et al., 2016; Steckel et al., 2020). However, Condés and del Río (2015) showed that Scots pine mortality increased with the proportion of beech while beech benefited from the presence of Scots pine in semi-arid forests of Spain, probably due to unequal competitive strength for water. Our review also suggests that the response of trees to species mixture or drought may depend on the site conditions respective tree history (Hilmers et al., 2022). For example, as shown for *P. ponderosa* the initial growth trajectories such as wide tree ring and large xylem vessels resulted from wide initial spacing or repeated thinning could increase the risk of embolism under drought in the long term (McDowell et al., 2003). Forest management thus needs long-term strategies for establishing Scots pine in mixed stands and for adjusting the silvicultural regime comprising stand initiation as well as thinning intensity and frequency (Bolte et al., 2009).

7. Conclusion

How do changes in water stress interact with life history strategies of Scots pine to drive performance in changing environments? The answers to this question require understanding of the (i) nature of the variation of water stress in the past, at present, and in the future, (ii) the mean and the variation of the impact throughout the life cycle of the species, (iii) where in the life cycle the impact is most influential, and (iv) how coordinated functional strategies the species employ relate to the timescale and predictability of local climatic condition. Recent research has provided understanding on general patterns of drought-induced Scots pine mortality and tree- and forest-level acclimation strategies. Our synthesis indicates that the species has already been undergoing increases in crown transparency and decrease in radial growth leading to mortality at their dry distribution limits in the Mediterranean countries and semi-arid regions in central Europe. In addition, a significant number of studies identified increased mortality patterns in the climatic core areas of the distribution after the 2018 drought in central Europe. Our synthesis indicates that individual tree level acclimation strategies (e.g., lowering leaf area and enhancing water-use efficiency) and forest-level acclimation strategies (e.g., reduction in stand density) are not necessarily sufficient to cope with the challenges induced by the expected more frequent extreme droughts. However, we still lack clear understanding in linking functional strategies of the species to local climatic variation, local sites conditions (e.g., the water holding capacity of the soils) and combinations of biotic factors to fully understand the capabilities of the species to grow and survive in the future climate (Table 2).

In the context of global change, we currently face the following two uncertainties (i) how will the site conditions change in future, and (ii) how will the species perform under that changed growth conditions (Bolte et al., 2009). Future research should explore the adaptive potential of Scots pine under different climatic conditions and soil properties and examining the performance of different genotypes under variable growing conditions (e.g., Taeger et al., 2013). Our synthesis as well as current literature show a strong role of ecological memory in determining growth and mortality responses to present environmental conditions (Pretzsch, 2021; Zweifel et al., 2020). However, our current forest vegetation models do not incorporate the ecological memory of extreme events or the memory of past growth trajectories or stand structural conditions for predicting future growth or mortality behaviour (e.g., Forrester et al., 2021; Pretzsch et al., 2002). Future research should address these knowledge gaps for better predicting the future growth and/or mortality pattern of Scots pine and of other tree species.

Authors' contributions

A.K.B., A.R. and A.G. conceived the ideas, A.K.B. performed the review, analysed the data, and led the writing of the manuscript, UB contributed to the interpretation of the data and arguments. All authors contributed to the writing of the manuscript.

CRedit authorship contribution statement

Arun K. Bose: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Data curation, Conceptualization. **Arthur Gessler:** Writing – review & editing, Supervision, Conceptualization. **Ulf Buentgen:** Writing – review & editing, Conceptualization. **Andreas Rigling:** Writing – review & editing, Supervision, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Table 2
Summary of findings and possible interpretation of factors and processes responsible for Scots pine mortality.

Influence (Factors and processes)	Findings	Possible interpretation	References
Climate	Studies agree that drought in combination with heat and VPD increased tree mortality.	Drought reduces soil moisture, imposes stomatal closure, increases insect activities and vulnerability of trees to carbon and water limitation.	Galiano et al., 2011; Rigling et al., 2013; Poyatos et al., 2013; Lemaire et al., 2022
Tree size	Higher mortality of smaller trees.	Drought triggers self-thinning among trees.	Sanchez-Salguero et al., 2012; Vila-Cabrera et al., 2013; Etzold et al., 2019; Jaime et al., 2019
Stand density	Studies report competition among trees prevailed as continuous stress and contributed drought-induced mortality.	Land abandonment and lack of forest management may result densification of forest stands and increased vulnerability of weak and suppressed trees to drought.	Galiano et al., 2010; Vila-Cabrera et al., 2011, 2013; Etzold et al., 2019; Archambeau et al., 2020
Mistletoes	Reduced tree growth and increased mortality especially in semi-arid sites.	Mistletoes can take water and carbohydrates from host trees and can enhance crown defoliation prior declining in tree growth.	Dobbertin and Rigling, 2006; Gea-Izquierdo et al., 2014, Sanguesa-Barreda et al., 2013
Insects and diseases	Presence of bark beetles, diplovia shoot blight, root-rot infection and fungal infections were identified by some studies.	Drought associated with increased temperature can favour population growth of insect species such as bark beetles. Insect attacks were associated with suppressed and weak Scots pine trees.	Vertui and Tagliaferro, 1998; Dobbertin et al., 2007; Caballol et al., 2022; Lemaire et al., 2022
Soil depth	Inverse relationship between soil depth and number of dead trees was identified.	Soil depth measures the soil moisture availability for trees and can be determined by the soil clay content.	Oberhuber, 2001; Galiano et al., 2010; Haberstroh et al., 2022
Crown defoliation	Consistency across studies reporting crown defoliation prior tree death. Crown defoliation >75% is identified as the point of no-return.	Persistent decrease in leaf area may indicate stress in trees. Reduction in photosynthetic machineries can reduce carbon storage and induce mortality via carbon starvation.	Sanguesa-Barreda et al., 2013; Camarero et al., 2015; Buras et al., 2018; Hunziker et al., 2022
Growth trajectory	(a) Conservative strategies such as reduced growth and increased water-use efficiency could delay mortality event. (b) Superior growth onset during early phase of life could trigger mortality after drought.	(a) Present dead trees may show stronger isohydric behaviour with earlier stomatal closure compared to present live trees. This may lower photosynthesis and reduced production of new carbohydrates. (b) A faster growth in the earlier phase may indicate that trees that grow fast can build large xylem vessels and disproportionately higher above-ground biomass, which could make them more vulnerable to cavitation and hydraulic failure.	Heres et al., 2012; Voltas et al., 2013; Timofeeva et al., 2017; Buras et al., 2018
Growth sensitivity to climate	Current dead trees were more sensitive to climate compared to current live trees.	This may indicate a stronger coupling between climate and trees' biological activities, thus rendering them vulnerable with alternation of climate.	Heres et al., 2012; Voltas et al., 2013; Timofeeva et al., 2017

Data availability

Data will be made available on request.

Acknowledgement

We thank Swiss Federal Research Institute WSL for the financial support. Thanks also to Jordi Martinez-Vilalta for providing valuable feedback on an earlier version of the manuscript. We are thankful to Flurin Sutter and Andri Baltensweiler for extracting the climate data of Scots pine sites in Europe. We also thank to Sophia Etzold, Maxime Cailleret, Walter Oberhuber, Henrik Hartmann, Jaroslaw Socha and Giorgio Vacchiano for providing additional information and data related to the papers Etzold et al. (2019), Cailleret et al. (2017), Oberhuber (2001), Hartmann et al. (2022), Tymńska-Czabańska et al. (2022), and Vacchiano et al. (2012), respectively.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.foreco.2024.121873](https://doi.org/10.1016/j.foreco.2024.121873).

References

- Adams, H.D., Zeppel, M.J.B., Anderegg, W.R.L., Hartmann, H., Landhäusser, S.M., Tissue, D.T., Huxman, T.E., Hudson, P.J., Franz, T.E., Allen, C.D., et al., 2017. A multi-species synthesis of physiological mechanisms in drought-induced tree mortality. *Nat. Ecol. Evol.* 1 (9), 1285–1291.
- Aguadé, D., Poyatos, R., Gómez, M., Oliva, J., Martínez-Vilalta, J., 2015a. The role of defoliation and root rot pathogen infection in driving the mode of drought-related physiological decline in Scots pine (*Pinus sylvestris* L.). *Tree Physiol.* 35 (3), 229–242.
- Aguadé, D., Poyatos, R., Rosas, T., Martínez-Vilalta, J., 2015b. Comparative drought responses of *Quercus ilex* L. and *Pinus sylvestris* L. in a montane forest undergoing a vegetation shift. *Forests* 6 (8), 2505–2529.
- Aldea, J., Ruiz-Peinado, R., del Río, M., Pretzsch, H., Heym, M., Brazaitis, G., Jansons, A., Metslaid, M., Barbeito, I., Bielak, K., et al., 2022. Timing and duration of drought modulate tree growth response in pure and mixed stands of Scots pine and Norway spruce. *J. Ecol.* 110 (11), 2673–2683.
- 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 (8), 1–55.
- Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H., et al., 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *For. Ecol. Manag.* 259 (4), 660–684.
- Ammer, C., 2019. Diversity and forest productivity in a changing climate. *N. Phytol.* 221 (1), 50–66.
- Anderegg, W.R.L., Kane, J.M., Anderegg, L.D.L., 2013. Consequences of widespread tree mortality triggered by drought and temperature stress. *Nat. Clim. Change* 3 (1), 30–36.
- Anderegg, W.R.L., Klein, T., Bartlett, M., Sack, L., Pellegrini, A.F.A., Choat, B., Jansen, S., 2016. Meta-analysis reveals that hydraulic traits explain cross-species patterns of drought-induced tree mortality across the globe. *Proc. Natl. Acad. Sci.* 113 (18), 5024.
- Archambeau, J., Ruiz-Benito, P., Ratcliffe, S., Fréjaville, T., Changenet, A., Muñoz Castañeda, J.M., Lehtonen, A., Dahlgren, J., Zavala, M.A., Benito Garzón, M., 2020. Similar patterns of background mortality across Europe are mostly driven by drought in European beech and a combination of drought and competition in Scots pine. *Agric. For. Meteorol.* 280, 107772.
- Battlori, E., Lloret, F., Aakala, T., Anderegg, W.R.L., Aynekulu, E., Bendixsen, D.P., Bentouati, A., Bigler, C., Burk, C.J., Camarero, J.J., et al., 2020. Forest and woodland replacement patterns following drought-related mortality. *Proc. Natl. Acad. Sci.* 117 (47), 29720–29729.
- Bennett, A.C., McDowell, N.G., Allen, C.D., Anderson-Teixeira, K.J., 2015. Larger trees suffer most during drought in forests worldwide. *Nat. Plants* 1 (10), 15139.
- 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 (3), 330–343.
- Bigler, C., Bugmann, H., 2004. Predicting the time of tree death using dendrochronological data. *Ecol. Appl.* 14 (3), 902–914.
- Bolte, A., Ammer, C., Löf, M., Madsen, P., Nabuurs, G.-J., Schall, P., Spathelf, P., Rock, J., 2009. Adaptive forest management in central Europe: climate change impacts, strategies and integrative concept. *Scand. J. For. Res.* 24 (6), 473–482.
- Bladon, K.D., Silins, U., Landhäusser, S.M., Messier, C., Liefers, V.J., 2007. Carbon isotope discrimination and water stress in trembling aspen following variable retention harvesting. *Tree Physiol.* 27 (7), 1065–1071.

- Bose, A.K., Gessler, A., Bolte, A., Bottero, A., Buras, A., Cailleret, M., Camarero, J.J., Haeni, M., Hereş, A.-M., Hevia, A., et al., 2020a. Growth and resilience responses of Scots pine to extreme droughts across Europe depend on predrought growth conditions. *Glob. Change Biol.* 26, 4521–4537.
- Bose, A.K., Moser, B., Rigling, A., Lehmann, M.M., Milcu, A., Peter, M., Rellstab, C., Wohlgemuth, T., Gessler, A., 2020b. Memory of environmental conditions across generations affects the acclimation potential of scots pine. *Plant Cell Environ.* 43 (5), 1288–1299.
- Bose, A.K., Nelson, A.S., Kane, M., Rigling, A., 2018. Density reduction in loblolly pine (*Pinus taeda* L.) stands to increase tree C assimilation: an approach with the dual $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ isotope signatures in needles. *Ann. For. Sci.* 75 (1), 8.
- Bose, A.K., Rigling, A., Gessler, A., Hagedorn, F., Brunner, I., Feichtinger, L., Bigler, C., Egli, S., Etzold, S., Gossner, M.M., et al., 2022. Lessons learned from a long-term irrigation experiment in a dry Scots pine forest: impacts on traits and functioning. *Ecol. Monogr.* 92 (2), e1507.
- Bottero, A., Forrester, D.I., Cailleret, M., Kohnle, U., Gessler, A., Michel, D., Bose, A.K., Bauhus, J., Bugmann, H., Cuntz, M., et al., 2021. Growth resistance and resilience of mixed silver fir and Norway spruce forests in central Europe – contrasting responses to mild and severe droughts. *Glob. Change Biol.* 27 (18), 4403–4419.
- Brodrribb, T., Brodersen, C.R., Carriqui, M., Tonet, V., Rodriguez Dominguez, C., McAdam, S., 2021. Linking xylem network failure with leaf tissue death. *N. Phytol.* 232 (1), 68–79.
- Buras, A., Schunk, C., Zeiträg, C., Herrmann, C., Kaiser, L., Lemme, H., Straub, C., Taeger, S., Gößwein, S., Klemm, H.-J., et al., 2018. Are Scots pine forest edges particularly prone to drought-induced mortality? *Environ. Res. Lett.* 13 (025001).
- Burkhardt, H.E., Tomé, M., 2012. *Modeling Forest Trees And Stands*. Springer Science & Business Media.
- Cabon, A., DeRose, R.J., Shaw, J.D., Anderegg, W.R.L., 2023. Declining tree growth resilience mediates subsequent forest mortality in the US Mountain West. *Glob. Change Biol.* 29 (17), 4826–4841.
- Cailleret, M., Dakos, V., Jansen, S., Robert, E.M.R., Aakala, T., Amoroso, M.M., Antos, J. A., Bigler, C., Bugmann, H., Caccianaga, M., et al., 2019. Early-warning signals of individual tree mortality based on annual radial growth. *Front. Plant Sci.* 9, 1964.
- Cailleret, M., Jansen, S., Robert, E.M.R., Desoto, L., Aakala, T., Antos, J.A., Beikircher, B., Bigler, C., Bugmann, H., Caccianaga, M., et al., 2017. A synthesis of radial growth patterns preceding tree mortality. *Glob. Change Biol.* 23 (4), 1675–1690.
- Camarero, J.J., Bigler, C., Linares, J.C., Gil-Pelegrín, E., 2011. Synergistic effects of past historical logging and drought on the decline of Pyrenean silver fir forests. *For. Ecol. Manag.* 262 (5), 759–769.
- Campbell, E.M., Magnussen, S., Antos, J.A., Parish, R., 2021. Size-, species-, and site-specific tree growth responses to climate variability in old-growth subalpine forests. *Ecosphere* 12 (5), e03529.
- Cedro, A., Cedro, B., Podlasiński, M., 2022. Differences in growth–climate relationships among scots pines growing on various dune generations on the Southern Baltic Coast. *Forests* 13 (3), 470.
- Clark, J.S., Iverson, L., Woodall, C.W., Allen, C.D., Bell, D.M., Bragg, D.C., D’Amato, A. W., Davis, F.W., Hersh, M.H., Ibanez, I., et al., 2016. The impacts of increasing drought on forest dynamics, structure, and biodiversity in the United States. *Glob. Change Biol.* 22 (7), 2329–2352.
- Colangelo, M., Camarero, J.J., Borghetti, M., Gazol, A., Gentilella, T., Ripullone, F., 2017. Size matters a lot: drought-affected Italian oaks are smaller and show lower growth prior to tree death. *Front. Plant Sci.* 8 (135).
- Colangelo, M., Camarero, J.J., Ripullone, F., Gazol, A., Sánchez-Salguero, R., Oliva, J., Redondo, M.A., 2018. Drought decreases growth and increases mortality of coexisting native and introduced tree species in a temperate floodplain forest. *Forests* 9 (4).
- Condés, S., del Río, M., 2015. Climate modifies tree interactions in terms of basal area growth and mortality in monospecific and mixed *Fagus sylvatica* and *Pinus sylvestris* forests. *Eur. J. For. Res.* 134 (6), 1095–1108.
- De Cáceres, M., Mencuccini, M., Martin-StPaul, N., Limousin, J.-M., Coll, L., Poyatos, R., Cabon, A., Granda, V., Forner, A., Valladares, F., et al., 2021. Unravelling the effect of species mixing on water use and drought stress in Mediterranean forests: a modelling approach. *Agric. For. Meteorol.* 296, 108233.
- DeSoto, L., Cailleret, M., Sterck, F., Jansen, S., Kramer, K., Robert, E.M.R., Aakala, T., Amoroso, M.M., Bigler, C., Camarero, J.J., et al., 2020. Low growth resilience to drought is related to future mortality risk in trees. *Nat. Commun.* 11 (1), 545.
- Dobbertin, M., Eilmann, B., Bleuler, P., Giugliola, A., Graf Pannatier, E., Landolt, W., Schleppl, P., Rigling, A., 2010. Effect of irrigation on needle morphology, shoot and stem growth in a drought-exposed *Pinus sylvestris* forest. *Tree Physiol.* 30 (3), 346–360.
- Dobbertin, M., Mayer, P., Wohlgemuth, T., Feldmeyer-Christe, E., Graf, U., Zimmermann, N., Rigling, A., 2005. The decline of *Pinus sylvestris* L. forests in the Swiss Rhone valley—a result of drought stress? *Phyton* 45 (4), 153.
- Dobbertin, M., Rigling, A., 2006. Pine mistletoe (*Viscum album* ssp. *austriacum*) contributes to Scots pine (*Pinus sylvestris*) mortality in the Rhone valley of Switzerland. *For. Pathol.* 36 (5), 309–322.
- Eilmann, B., Zweifel, R., Buchmann, N., Ponti, P., Rigling, A., 2009. Drought-induced adaptation of the xylem in Scots pine and pubescent oak. *Tree Physiol.* 29 (8), 1011–1020.
- 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. *Front. Plant Sci.* 10.
- Feichtinger, L.M., Eilmann, B., Buchmann, N., Rigling, A., 2014. Growth adjustments of conifers to drought and to century-long irrigation. *For. Ecol. Manag.* 334, 96–105. <https://doi.org/10.1016/j.foreco.2014.08.008>.
- 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. Appl. Ecol.* 53 (6), 1725–1734.
- Forrester, D.I., Hobi, M.L., Mathys, A.S., Stadelmann, G., Trotsiuk, V., 2021. Calibration of the process-based model 3-PG for major central European tree species. *Eur. J. For. Res.* 140 (4), 847–868.
- Franke, A.K., Bräuning, A., Timonen, M., Rautio, P., 2017. Growth response of Scots pines in polar-alpine tree-line to a warming climate. *For. Ecol. Manag.* 399, 94–107.
- Franklin, J.F., Shugart, H.H., Harmon, M.E., 1987. Tree death as an ecological process. *BioSci.* 37 (8), 550–556.
- Galiano, L., Martínez-Vilalta, J., Lloret, F., 2010. Drought-induced multifactor decline of Scots pine in the Pyrenees and potential vegetation change by the expansion of co-occurring oak species. *Ecosystems* 13 (7), 978–991.
- Galiano, L., Martínez-Vilalta, J., Lloret, F., 2011. Carbon reserves and canopy defoliation determine the recovery of Scots pine 4 yr after a drought episode. *N. Phytol.* 190 (3), 750–759.
- Gea-Izquierdo, G., Viguera, B., Cabrera, M., Cañellas, I., 2014. Drought induced decline could portend widespread pine mortality at the xeric ecotone in managed mediterranean pine-oak woodlands. *For. Ecol. Manag.* 320, 70–82.
- Gessler, A., Cailleret, M., Joseph, J., Schönbeck, L., Schaub, M., Lehmann, M.M., Treyde, K., Rigling, A., Timofeeva, G., Saurer, M., 2018. Drought induced tree mortality – a tree-ring isotope based conceptual model to assess mechanisms and predispositions. *N. Phytol.* 219 (2), 485–490.
- Gimmi, U., Wohlgemuth, T., Rigling, A., Hoffmann, C.W., Bürgi, M., 2010. Land-use and climate change effects in forest compositional trajectories in a dry Central-Alpine valley. *Ann. For. Sci.* 67 (7), 701.
- Giugliola, A., Bugmann, H., Zingg, A., Dobbertin, M., Rigling, A., 2013. Reduction of stand density increases drought resistance in xeric Scots pine forests. *For. Ecol. Manag.* 310, 827–835.
- Giugliola, A., Ogée, J., Rigling, A., Gessler, A., Bugmann, H., Treyde, K., 2015. Improvement of water and light availability after thinning at a xeric site: which matters more? A dual isotope approach. *N. Phytol.* 210 (1), 108–121.
- 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. *J. Ecol.* 106 (1), 59–75.
- Greenwood, S., Ruiz-Benito, P., Martínez-Vilalta, J., Lloret, F., Kitzberger, T., Allen, C.D., Fensham, R., Laughlin, D.C., Kattge, J., Bönisch, G., et al., 2017. Tree mortality across biomes is promoted by drought intensity, lower wood density and higher specific leaf area. *Ecol. Lett.* 20 (4), 539–553.
- Grossiord, C., 2019. Having the right neighbors: how tree species diversity modulates drought impacts on forests. *N. Phytol.* 228 (1), 42–49.
- Grossiord, C., Buckley, T.N., Cernusak, L.A., Novick, K.A., Poulter, B., Siegwolf, R.T.W., Sperry, J.S., McDowell, N.G., 2020. Plant responses to rising vapor pressure deficit. *N. Phytol.* 226 (6), 1550–1566.
- Grossiord, C., Sevanto, S., Limousin, J.-M., Meir, P., Mencuccini, M., Pangle, R.E., Pockman, W.T., Salmon, Y., Zweifel, R., McDowell, N.G., 2018. Manipulative experiments demonstrate how long-term soil moisture changes alter controls of plant water use. *Environ. Exp. Bot.* 152, 19–27.
- Haberstroh, S., Werner, C., Grün, M., Kreuzwieser, J., Seifert, T., Schindler, D., Christen, A., 2022. Central European 2018 hot drought shifts scots pine forest to its tipping point. *Plant Biol.* 24 (7), 1186–1197.
- Hajek, P., Link, R.M., Nock, C.A., Bauhus, J., Gebauer, T., Gessler, A., Kovach, K., Messier, C., Paquette, A., Saurer, M., et al., 2022. Mutually inclusive mechanisms of drought-induced tree mortality. *Glob. Change Biol.* 28 (10), 3365–3378.
- Hartmann, H., Bastos, A., Das, A.J., Esquivel-Muelbert, A., Hammond, W.M., Martínez-Vilalta, J., McDowell, N.G., Powers, J.S., Pugh, T.A.M., Ruthrof, K.X., et al., 2022. Climate change risks to global forest health: emergence of unexpected events of elevated tree mortality worldwide. *Annu. Rev. Plant Biol.* 73 (1), 673–702.
- Heiniger, U., Theile, F., Rigling, A., Rigling, D., 2011. Blue-stain infections in roots, stems and branches of declining *Pinus sylvestris* trees in a dry inner alpine valley in Switzerland. *For. Pathol.* 41 (6), 501–509.
- Hereş, A.-M., Martínez-Vilalta, J., Claramunt López, B., 2012. Growth patterns in relation to drought-induced mortality at two Scots pine (*Pinus sylvestris* L.) sites in NE Iberian Peninsula. [journal article]. *Trees* 26 (2), 621–630.
- Hereş, A.-M., Petritan, I.C., Bigler, C., Curtu, A.L., Petrea, Ş., Petritan, A.M., Polanco-Martínez, J.M., Rigling, A., Curiel Yuste, J., 2021. Legacies of past forest management determine current responses to severe drought events of conifer species in the Romanian Carpathians. *Sci. Total Environ.* 751, 141851.
- Hereş, A.-M., Voltas, J., López, B.C., Martínez-Vilalta, J., 2014. Drought-induced mortality selectively affects Scots pine trees that show limited intrinsic water-use efficiency responsiveness to raising atmospheric CO₂. *Funct. Plant Biol.* 41 (3), 244–C0256.
- Herguido, E., Granda, E., Benavides, R., García-Cervigón, A.I., Camarero, J.J., Valladares, F., 2016. Contrasting growth and mortality responses to climate warming of two pine species in a continental Mediterranean ecosystem. *For. Ecol. Manag.* 363, 149–158.
- Hermes, D.A., Mattson, W.J., 1992. The dilemma of plants: to grow or defend. *Q. Rev. Biol.* 67 (3), 283–335.
- Hilmers, T., Schmied, G., Pretzsch, H., 2022. Legacy effects of past thinning modulate drought stress reactions at present. *Scand. J. For. Res.* 37 (3), 182–199.
- Hunziker, S., Begert, M., Scherrer, S.C., Rigling, A., Gessler, A., 2022. Below average midsummer to early autumn precipitation evolved into the main driver of sudden Scots pine vitality decline in the Swiss rhone valley. *Front. For. Glob. Change* 5.

- Irvine, J., Perks, M.P., Magnani, F., Grace, J., 1998. The response of *Pinus sylvestris* to drought: stomatal control of transpiration and hydraulic conductance. *Tree Physiol.* 18 (6), 393–402.
- Jaime, L., Batllori, E., Margalef-Marrase, J., Pérez Navarro, M.Á., Lloret, F., 2019. Scots pine (*Pinus sylvestris* L.) mortality is explained by the climatic suitability of both host tree and bark beetle populations. *For. Ecol. Manag.* 448, 119–129.
- Jiang, Y., Marchand, W., Rydval, M., Matula, R., Janda, P., Begović, K., Thom, D., Fruleux, A., Buechling, A., & Pavlin, J. (2023). Drought Resistance of Major Tree Species in Central Europe. Available at SSRN 4524632.
- Jonas, O., Jan, S., Jordi, M., Vilalta, 2014. The effect of fungal pathogens on the water and carbon economy of trees: implications for drought-induced mortality. *N. Phytol.* 203 (4), 1028–1035.
- Jucker, T., Grossiord, C., Bonal, D., Bouriaud, O., Gessler, A., Coomes, D.A., 2017. Detecting the fingerprint of drought across Europe's forests: do carbon isotope ratios and stem growth rates tell similar stories? *For. Ecosyst.* 4 (1), 24.
- Jump, A.S., Ruiz-Benito, P., Greenwood, S., Allen, C.D., Kitzberger, T., Fensham, R., Martínez-Vilalta, J., Lloret, F., 2017. Structural overshoot of tree growth with climate variability and the global spectrum of drought-induced forest dieback. *Glob. Change Biol.* 23 (9), 3742–3757.
- Krakau, U.-K., Liesebach, M., Aronen, T., Lelu-Walter, M.-A., Schneck, V., 2013. Scots pine (*Pinus sylvestris* L.) Forest Tree Breeding in Europe. Springer, pp. 267–323.
- Lamelas, L., López-Hidalgo, C., Valledor, L., Meijón, M., & Cañal, M.J. (2024). Like mother like son: Transgenerational Memory and Cross-tolerance from Drought to Heat Stress Are Identified in Chloroplast Proteome and seed provisioning in *Pinus radiata*. *Plant, Cell & Environment*, in press.
- Lebourgeois, F., Rathgeber, C.B.K., Ulrich, E., 2010. Sensitivity of French temperate coniferous forests to climate variability and extreme events (*Abies alba*, *Picea abies* and *Pinus sylvestris*). *J. Veg. Sci.* 21 (2), 364–376.
- Lemaire, J., Venetier, M., Prévosto, B., Cailleret, M., 2022. Interactive effects of abiotic factors and biotic agents on Scots pine dieback: a multivariate modeling approach in southeast France. *For. Ecol. Manag.* 526, 120543.
- Lerdau, M., Litvak, M., Monson, R., 1994. Plant chemical defense: monoterpenes and the growth-differentiation balance hypothesis. *Trends in Ecology & Evolution* 9 (2), 58–61.
- Lévesque, M., Saurer, 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. *Glob. Change Biol.* 19 (10), 3184–3199.
- Linderholm, H.W., 2002. Twentieth-century Scots pine growth variations in the central Scandinavian mountains related to climate change. *Arct., Antarct. Alp. Res.* 34 (4), 440–449.
- Linderholm, H.W., Moberg, A., Grudd, H., 2002. Peatland pines as climate indicators? A regional comparison of the climatic influence on Scots pine growth in Sweden. *Can. J. For. Res.* 32 (8), 1400–1410.
- Lloret, F., Jaime, L.A., Margalef-Marrase, J., Pérez-Navarro, M.A., Batllori, E., 2022. Short-term forest resilience after drought-induced die-off in Southwestern European forests. *Sci. Total Environ.* 806, 150940.
- Madrigal-González, J., Ballesteros-Cánovas, J.A., Zavala, M.A., Morales-Molino, C., Stoffel, M., 2020. Forest stocks control long-term climatic mortality risks in Scots pine dry-edge forests. *Ecosphere* 11 (8), e03201.
- Mantova, M., Herbette, S., Cochar, H., Torres-Ruiz, J.M., 2022. Hydraulic failure and tree mortality: from correlation to causation. *Trends Plant Sci.* 27 (4), 335–345.
- Martínez-Vilalta, J., Cochar, H., Mencuccini, M., Sterck, F., Herrero, A., Korhonen, J.F. J., Llorens, P., Nikinmaa, E., Nolè, A., Poyatos, R., et al., 2009. Hydraulic adjustment of Scots pine across Europe. *N. Phytol.* 184 (2), 353–364.
- Martínez-Vilalta, J., López, B.C., Loepfe, L., Lloret, F., 2012. Stand- and tree-level determinants of the drought response of Scots pine radial growth. *Oecologia* 168 (3), 877–888.
- Mátyás, C., Ackzell, L., and, & Samuel, C.J.A. (2004). EUFORGEN Technical Guidelines for Genetic Conservation and Use for Scots Pine (*Pinus sylvestris*). International Plant Genetic Resources Institute, Rome, Italy. 6 pages.
- McDowell, N., Brooks, J., Fitzgerald, S., Bond, B., 2003. Carbon isotope discrimination and growth response of old *Pinus ponderosa* trees to stand density reductions. *Plant, Cell & Environment* 26 (4), 631–644.
- 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? *N. Phytol.* 178 (4), 719–739.
- McDowell, N.G., Sevanto, S., 2010. The mechanisms of carbon starvation: how, when, or does it even occur at all? *N. Phytol.* 186 (2), 264–266.
- Moir, A.K., Leroy, S.A.G., Helama, S., 2011. Role of substrate on the dendroclimatic response of Scots pine from varying elevations in northern Scotland. *Can. J. For. Res.* 41 (4), 822–838.
- Oberhuber, W., 2001. The role of climate in the mortality of Scots pine (*Pinus sylvestris* L.) exposed to soil dryness. *Dendrochronologia* 19 (1), 45–55.
- Oberhuber, W., Stumböck, M., Kofler, W., 1998. Climate-tree-growth relationships of Scots pine stands (*Pinus sylvestris* L.) exposed to soil dryness. *Trees* 13 (1), 19–27.
- Ogle, K., Barber, J.J., Barron-Gafford, G.A., Bentley, L.P., Young, J.M., Huxman, T.E., Loik, M.E., Tissue, D.T., 2015. Quantifying ecological memory in plant and ecosystem processes. *Ecol. Lett.* 18 (3), 221–235.
- Ogle, K., Whitham, T.G., Cobb, N.S., 2000. Tree-ring variation in pinyon predicts likelihood of death following severe drought. *Ecology* 81 (11), 3237–3243.
- Ovenden, T.S., Perks, M.P., Clarke, T.-K., Mencuccini, M., Jump, A.S., 2021. Life after recovery: Increased resolution of forest resilience assessment sheds new light on post-drought compensatory growth and recovery dynamics. *J. Ecol.* 109 (9), 3157–3170.
- Ovenden, T.S., Perks, M.P., Forrester, D.I., Mencuccini, M., Rhoades, J., Thompson, D.L., Stokes, V.J., Jump, A.S., 2022. Intimate mixtures of Scots pine and Sitka spruce do not increase resilience to spring drought. *For. Ecol. Manag.* 521, 120448.
- Peltier, D.M.P., Guo, J., Nguyen, P., Bangs, M., Wilson, M., Samuels-Crow, K., Yocom, L. L., Liu, Y., Fell, M.K., Shaw, J.D., et al., 2022. Temperature memory and non-structural carbohydrates mediate legacies of a hot drought in trees across the southwestern USA. *Tree Physiol.* 42 (1), 71–85.
- Peltier, D.M.P., Ogle, K., 2020. Tree growth sensitivity to climate is temporally variable. *Ecol. Lett.* 23 (11), 1561–1572.
- Poorter, H., Niklas, K.J., Reich, P.B., Oleksyn, J., Poot, P., Mommer, L., 2012. Biomass allocation to leaves, stems and roots: meta-analyses of interspecific variation and environmental control. *N. Phytol.* 193 (1), 30–50.
- Poyatos, R., Aguadé, D., Galiano, L., Mencuccini, M., Martínez-Vilalta, J., 2013. Drought-induced defoliation and long periods of near-zero gas exchange play a key role in accentuating metabolic decline of Scots pine. *N. Phytol.* 200 (2), 388–401.
- Poyatos, R., Martínez-Vilalta, J., Cermák, J., Ceulemans, R., Granier, A., Irvine, J., Köstner, B., Lagergren, F., Meiresonne, L., Nadezhkina, N., et al., 2007. Plasticity in hydraulic architecture of Scots pine across Eurasia. *Oecologia* 153 (2), 245–259.
- Pretzsch, H., 2021. Trees grow modulated by the ecological memory of their past growth. Consequences for monitoring, modelling, and silvicultural treatment. *For. Ecol. Manag.* 487, 118982.
- Pretzsch, H., Biber, P., 2022. Fertilization modifies forest stand growth but not stand density: consequences for modelling stand dynamics in a changing climate. *For. Int. J. For. Res.* 95 (2), 187–200.
- Pretzsch, H., Biber, P., Durský, J., 2002. The single tree-based stand simulator SILVA: construction, application and evaluation. *For. Ecol. Manag.* 162 (1), 3–21.
- Pretzsch, H., Bravo-Oviedo, A., Hilmers, T., Ruiz-Peinado, R., Coll, L., Löf, M., Ahmed, S., Aldea, J., Ammer, C., Avdagić, A., et al., 2022. With increasing site quality asymmetric competition and mortality reduces Scots pine (*Pinus sylvestris* L.) stand structuring across Europe. *For. Ecol. Manag.* 520, 120365.
- Pretzsch, del Río, H., Arcangeli, M., Bielak, K., Dudzinska, K., Forrester, M., Klädtke, D.I., Kohnle, J., Ledermann, U., Matthews, T., R, et al., 2023. Forest growth in Europe shows diverging large regional trends. *Sci. Rep.* 13 (1), 15373.
- Pretzsch, del Río, H., Schütze, M., Ammer, G., Annighöfer, C., Avdagic, P., Barbeito, A., Bielak, I., Brazaitis, K., Coll, G., L, et al., 2016. Mixing of Scots pine (*Pinus sylvestris* L.) and European beech (*Fagus sylvatica* L.) enhances structural heterogeneity, and the effect increases with water availability. *For. Ecol. Manag.* 373, 149–166.
- Pretzsch, H., Steckel, M., Heym, M., Biber, P., Ammer, C., Ehrbrecht, M., Bielak, K., Bravo, F., Ordóñez, C., Collet, C., et al., 2020. Stand growth and structure of mixed-species and monospecific stands of Scots pine (*Pinus sylvestris* L.) and oak (*Q. robur* L., *Quercus petraea* (Matt.) Liebl.) analysed along a productivity gradient through Europe. *Eur. J. For. Res.* 139 (3), 349–367.
- Rigling, A., Bigler, C., Eilmann, B., Feldmeyer-Christe, E., Gimmi, U., Ginzler, C., Graf, U., Mayer, P., Vacchiano, G., Weber, P., 2013. Driving factors of a vegetation shift from Scots pine to pubescent oak in dry Alpine forests. *Glob. Change Biol.* 19 (1), 229–240.
- Rigling, A., Bräker, O., Schneider, G., Schweingruber, F., 2002. Intra-annual tree-ring parameters indicating differences in drought stress of *Pinus sylvestris* forests within the Erico-Pinion in the Valais (Switzerland). *Plant Ecol.* 163 (1), 105–121.
- Rigling, A., Brühlhart, H., Bräker, O.U., Forster, T., Schweingruber, F.H., 2003. Effects of irrigation on diameter growth and vertical resin duct production in *Pinus sylvestris* L. on dry sites in the central Alps, Switzerland. *For. Ecol. Manag.* 175 (1), 285–296.
- Rigling, A., Eilmann, B., Koechli, R., Dobbertin, M., 2010. Mistletoe-induced crown degradation in Scots pine in a xeric environment. *Tree Physiol.* 30, 845–852.
- Riofrio, J., del Río, M., Pretzsch, H., Bravo, F., 2017. Changes in structural heterogeneity and stand productivity by mixing Scots pine and Maritime pine. *For. Ecol. Manag.* 405, 219–228.
- Ruiz-Peinado, R., Pretzsch, H., Löf, M., Heym, M., Bielak, K., Aldea, J., Barbeito, I., Brazaitis, G., Drössler, L., Godvod, K., et al., 2021. Mixing effects on Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) Karst.) productivity along a climatic gradient across Europe. *For. Ecol. Manag.* 482, 118834.
- Salmon, Y., Lintunen, A., Dayet, A., Chan, T., Dewar, R., Vesala, T., Hölttä, T., 2020. Leaf carbon and water status control stomatal and nonstomatal limitations of photosynthesis in trees. *N. Phytol.* 226 (3), 690–703.
- Salmon, Y., Torres-Ruiz, J.M., Poyatos, R., Martínez-Vilalta, J., Meir, P., Cochar, H., Mencuccini, M., 2015. Balancing the risks of hydraulic failure and carbon starvation: a twig scale analysis in declining Scots pine. *Plant Cell Environ.* 38 (12), 2575–2588.
- Sánchez-Salguero, R., Camarero, J.J., Hevia, A., Madrigal-González, J., Linares, J.C., Ballesteros-Cánovas, J.A., Sánchez-Miranda, A., Alfaro-Sánchez, R., Sangüesa-Barreda, G., Galván, J.D., et al., 2015. What drives growth of Scots pine in continental Mediterranean climates: drought, low temperatures or both? *Agric. For. Meteorol.* 206, 151–162.
- Sánchez-Salguero, R., Navarro-Cerrillo, R.M., Swetnam, T.W., Zavala, M.A., 2012. Is drought the main decline factor at the rear edge of Europe? The case of southern Iberian pine plantations. *For. Ecol. Manag.* 271, 158–169.
- Sangüesa-Barreda, G., Linares, J.C., Julio Camarero, J., 2013. Drought and mistletoe reduce growth and water-use efficiency of Scots pine. *For. Ecol. Manag.* 296, 64–73.
- Schönbeck, L., Gessler, A., Hoch, G., McDowell, N.G., Rigling, A., Schaub, M., Li, M.-H., 2018. Homeostatic levels of nonstructural carbohydrates after 13 yr of drought and irrigation in *Pinus sylvestris*. *N. Phytol.* 219 (4), 1314–1324.
- Searle, E.B., Chen, H.Y.H., Paquette, A., 2022. Higher tree diversity is linked to higher tree mortality. *Proc. Natl. Acad. Sci.* 119 (19) e2013171119.
- Senf, C., Pflugmacher, D., Zhiqiang, Y., Sebald, J., Knorn, J., Neumann, M., Hostert, P., Seidl, R., 2018. Canopy mortality has doubled in Europe's temperate forests over the last three decades. *Nat. Commun.* 9 (1), 4978.

- Sensula, B., Wilczyński, S., Opała, M., 2015. Tree growth and climate relationship: dynamics of Scots pine (*Pinus sylvestris* L.) growing in the near-source region of the combined heat and power plant during the development of the pro-ecological strategy in Poland. *Water Air Soil Pollut.* 226 (7), 220.
- Sidor, C.G., Bosela, M., Büntgen, U., Vlad, R., 2018. Mixed effects of climate variation on the Scots pine forests: age and species mixture matter. *Dendrochronologia* 52, 48–56.
- Simon, J., Dannemann, M., Pena, R., Gessler, A., Rennenberg, H., 2017. Nitrogen nutrition of beech forests in a changing climate: importance of plant-soil-microbe water, carbon, and nitrogen interactions. *Plant Soil* 418 (1), 89–114.
- Sohn, J.A., Hartig, F., Kohler, M., Huss, J., Bauhus, J., 2016a. Heavy and frequent thinning promotes drought adaptation in *Pinus sylvestris* forests. *Ecol. Appl.* 26 (7), 2190–2205.
- Sohn, J.A., Saha, S., Bauhus, J., 2016b. Potential of forest thinning to mitigate drought stress: a meta-analysis. *For. Ecol. Manag.* 380, 261–273.
- Steckel, M., del Río, M., Heym, M., Aldea, J., Bielak, K., Brazaitis, G., Černý, J., Coll, L., Collet, C., Ehbrecht, M., et al., 2020. Species mixing reduces drought susceptibility of Scots pine (*Pinus sylvestris* L.) and oak (*Quercus robur* L., *Quercus petraea* (Matt.) Liebl.) – Site water supply and fertility modify the mixing effect. *For. Ecol. Manag.* 461, 117908.
- Taeger, S., Zang, C., Liesebach, M., Schneck, V., Menzel, A., 2013. Impact of climate and drought events on the growth of Scots pine (*Pinus sylvestris* L.) provenances. *For. Ecol. Manag.* 307, 30–42.
- Thrippleton, T., Bugmann, H., Folini, M., Snell, R.S., 2018. Overstorey–understorey interactions intensify after drought-induced forest die-off: long-term effects for forest structure and composition. *Ecosystems* 21 (4), 723–739.
- Timofeeva, G., Treydte, 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 Physiol.* 37 (8), 1028–1041.
- Torano Caicoya, A., Biber, P., del Río, M., Ruiz-Peinado, R., Arcangeli, C., Matthews, R., Pretzsch, H., 2024. Self-thinning of Scots pine across Europe changes with solar radiation, precipitation and temperature but does not show trends in time. *For. Ecol. Manag.* 552, 121585.
- Trotsiuk, V., Babst, F., Grossiord, C., Gessler, A., Forrester, D.I., Buchmann, N., Schaub, M., Eugster, W., 2021. Tree growth in Switzerland is increasingly constrained by rising evaporative demand. *J. Ecol.* 109 (8), 2981–2990.
- Tymińska-Czabańska, L., Hawryło, P., Janiec, P., Socha, J., 2022. Tree height, growth rate and stand density determined by ALS drive probability of Scots pine mortality. *Ecol. Indic.* 145, 109643.
- Urfli, M., Porté, A.J., Cochard, H., Guengant, Y., Burlett, R., Delzon, S., 2013. Xylem embolism threshold for catastrophic hydraulic failure in angiosperm trees. *Tree Physiol.* 33 (7), 672–683.
- Vacchiano, G., Garbarino, M., Borgogno Mondino, E., Motta, R., 2012. Evidences of drought stress as a predisposing factor to Scots pine decline in Valle d'Aosta (Italy). *Eur. J. For. Res.* 131 (4), 989–1000.
- Venturas, M.D., Todd, H.N., Trugman, A.T., Anderegg, W.R.L., 2021. Understanding and predicting forest mortality in the western United States using long-term forest inventory data and modeled hydraulic damage. *N. Phytol.* 230 (5), 1896–1910.
- Vertui, F., Tagliaferro, F., 1998. Scots pine (*Pinus sylvestris* L.) die-back by unknown causes in the Aosta Valley, Italy. *Chemosphere* 36 (4), 1061–1065.
- Vilà-Cabrera, A., Martínez-Vilalta, J., Galiano, L., Retana, J., 2013. Patterns of forest decline and regeneration across Scots pine populations. *Ecosystems* 16 (2), 323–335.
- Vilà-Cabrera, A., Martínez-Vilalta, J., Vayreda, J., Retana, J., 2011. Structural and climatic determinants of demographic rates of Scots pine forests across the Iberian Peninsula. *Ecol. Appl.* 21 (4), 1162–1172.
- Volta, J., Camarero, J.J., Carulla, D., Aguilera, M., Ortiz, A., Ferrio, J.P., 2013. A retrospective, dual-isotope approach reveals individual predispositions to winter-drought induced tree dieback in the southernmost distribution limit of Scots pine. *Plant Cell Environ.* 36 (8), 1435–1448.
- von Arx, G., Arzac, A., Fonti, P., Frank, D., Zweifel, R., Rigling, A., Galiano, L., Gessler, A., Olano, J.M., 2017. Responses of sapwood ray parenchyma and non-structural carbohydrates of *Pinus sylvestris* to drought and long-term irrigation. *Funct. Ecol.* 31 (7), 1371–1382.
- Wang, A., Bose, A.K., Lehmann, M.M., Rigling, A., Gessler, A., Yu, L., Li, M., 2023. Water status and macronutrient concentrations, but not carbon status, of *Viscum album* ssp. *album* are determined by its hosts: a study across nine mistletoe–host pairs in central Switzerland. *Front. Plant Sci.* 14.
- Weber, P., Bugmann, H., Fonti, P., Rigling, A., 2008. Using a retrospective dynamic competition index to reconstruct forest succession. *For. Ecol. Manag.* 254 (1), 96–106.
- Weiskittel, A.R., Hann, D.W., Kershaw Jr, J.A., Vanclay, J.K., 2011. *Forest Growth and Yield Modeling*. John Wiley & Sons.
- Wermelinger, B., Rigling, A., Schneider Mathis, D., Dobbertin, M., 2008. Assessing the role of bark- and wood-boring insects in the decline of Scots pine (*Pinus sylvestris*) in the Swiss Rhone valley. *Ecol. Entomol.* 33 (2), 239–249.
- Williams, P.A., 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., 2012. Temperature as a potent driver of regional forest drought stress and tree mortality. *Nat. Clim. Change* 3, 292.
- Wilmking, M., van der Maaten-Theunissen, M., van der Maaten, E., Scharnweber, T., Buras, A., Biermann, C., Gurskaya, M., Hallinger, M., Lange, J., Shetti, R., et al., 2020. Global assessment of relationships between climate and tree growth. *Glob. Change Biol.* 26 (6), 3212–3220.
- Zweifel, R., Etzold, E., Sterck, F., Gessler, A., Anfodillo, T., Mencuccini, M., von Arx, G., Lazzarin, M., Haeni, M., Feichtinger, L., et al., 2020. Determinants of legacy effects in pine trees - implications from an irrigation-stop experiment. *N. Phytol.* 227 (4), 1081–1096.