

Review

Distinct Responses of European Beech (*Fagus sylvatica* L.) to Drought Intensity and Length—A Review of the Impacts of the 2003 and 2018–2019 Drought Events in Central Europe

Shah Rukh ^{1,2,*} , Tanja G. M. Sanders ¹ , Inken Krüger ¹, Tobias Schad ¹ and Andreas Bolte ^{1,2} ¹ Thünen Institute of Forest Ecosystems, Alfred-Möller-Straße 1, Haus 41/42, 16225 Eberswalde, Germany² Department of Silviculture and Forest Ecology of the Temperate Zones, University of Göttingen, Büsgenweg 1, 37077 Göttingen, Germany

* Correspondence: shah.rukh@thuenen.de; Tel.: +49-3334-3820-335

Abstract: A combined severe heatwave and drought, starting in 2018 and lasting for several months, restarted the discussion on the resistance of European beech to climatic changes, with severe growth reductions, early leaf senescence, leaf browning, and diebacks reported across Central Europe. These responses may result in long-term impacts such as reduced vitality of beech, especially under potential future drought periods. While the 2003 drought caused severe crown damage and defoliation and a loss in vitality, resulting in insect and fungal infestations and subsequent dieback, the drought in 2018 was even more severe in terms of geographical scale, duration, and intensity with reports of complete diebacks and severe mortality across Central Europe. These impacts were exacerbated in some regions by the consecutive drought in 2019 and secondary attacks from pathogens, as well as a further loss in vitality. Such enhanced drought exposure of beech trees could push them beyond their hydraulic safety margins. Moreover, growth legacy effects due to past droughts may lead to lower recovery over time, potentially leading to subsequent tree death. In order to better predict the future of beech growth and vitality in Central Europe, both short- and long-term legacy effects of defoliation and their influence on post-drought growth should be explored, and adaptive forest management strategies evaluated. Moreover, synergistic or additive interactions of legacy effects with drought, as well as with biotic disturbances, require further investigation. Long-term forest monitoring data facilitates investigations of drought responses of beech.

Keywords: severe growth reduction; drought stress; heat wave; ecological threshold; legacy effects; forest ecology; ICP forests



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1. Introduction

Driven by varying environmental conditions, trees modify their morphological and physiological responses as part of their adaptation to exogenous conditions. While this allows European beech (*Fagus sylvatica* L.) to grow in a wide natural distribution range, adaptation has its limits [1,2]. These might already have been reached in recent years with visible signs of stress and decline becoming more and more evident across Europe [3–5]. In particular, the reoccurrence of two extreme drought events in 2003 and 2018–2019, in a time span shorter than 20 years, caused severe deterioration and decline of tree crowns as well as growth reductions [6,7]. This loss of vigor might persist as legacy effects [8], including lagged post-drought responses [9]. These may hamper tree recovery, due to carbon depletion through reduced photosynthesis as well as hydraulic dysfunction [10,11], which, if persistent over time, can lead to mortality [9,12].

European beech is distributed across large parts of Europe (Figure 1), but occurs mainly in Central Europe (Austria, Czechia, Germany, Hungary, Poland, Slovakia, Slovenia, and Switzerland) and Western Europe (Belgium, France, Luxembourg, The Netherlands, and the United Kingdom). Its high competitiveness under a wide range of climatic and

soil conditions, its extensive and deep rooting system and low pathogenic pressures make it the most ecologically and economically important deciduous tree species in Central Europe [13–15].

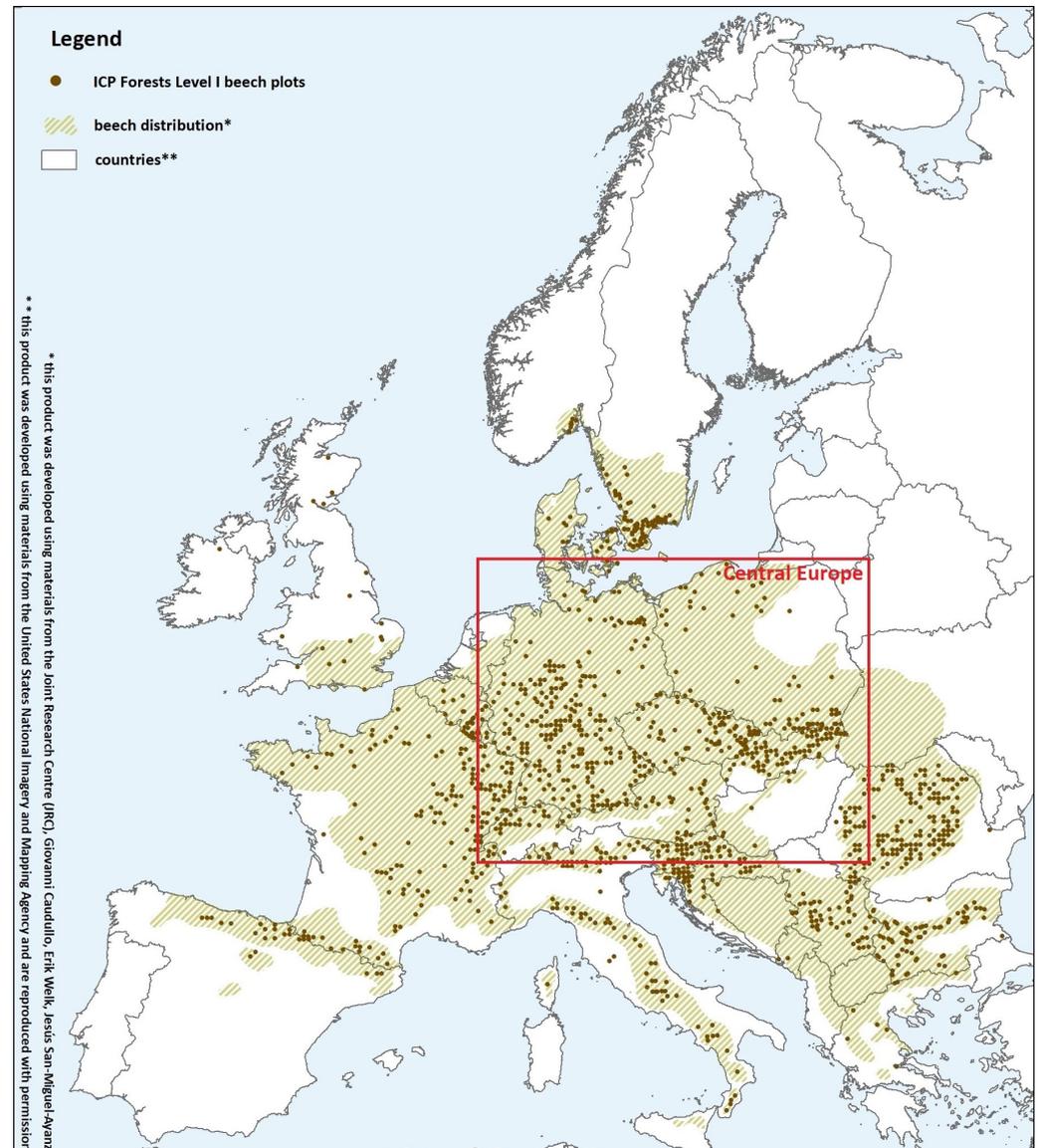


Figure 1. Distribution of European beech (*Fagus sylvatica* L.) across Europe. Eight countries, viz. Austria, Czechia, Germany, Hungary, Poland, Slovakia, Slovenia, and Switzerland, are located in the Central European region. Brown dots are individual ICP Forests Level I beech plots. © Thünen Institute, 2022.

Heatwaves combined with severe droughts such as in 2018 [16,17] caused leaf discoloration, early leaf senescence, severe growth reductions [18–20], crown defoliation [21], and diebacks [17,22,23] in forest ecosystems across Central Europe. Previous drought years, e.g., 1976, 1990, and 2003, posed similar stress to trees [24,25]. However, for this new category of hotter drought of 2018 [26], NDVI (Normalized Difference Vegetation Index) analyses suggested a more severe impact than in 2003 [16]. The drought period of 2018 and 2019 was linked to an unprecedented mortality event [27]. Furthermore, it occurred at a larger spatial scale, was linked to a highly negative climatic water balance (CWB) during the vegetation period and showed highly negative standardized anomalies in Central Europe [28] (ERA-5 Land climate data, Figures 2 and 3). This affected not only beech, as large areas of the

deciduous forests in Austria, Germany, and Switzerland showed signs of damage and leaf discoloration in 2018, twice as much compared to 2003 [17]. The 2018 drought was long; it had begun already in spring and continued through summer, thus imposing multiple months of high temperatures and low precipitation anomalies prior to and during the growing season [29,30]. It was continuously dry from June until November [30]. The drought continued in 2019 in parts of Germany, western Poland, Czechia, and Hungary [29,31,32]. The CWB in the vegetation period of 2019 reached around -250 mm, and anomalies of -1.5 standard deviations (Figures 2d and 3d). Beech diebacks were reported in the spring and summer of 2019 [16,33]. Furthermore, beech was left vulnerable to secondary pathogen attacks, inducing mortality among trees with reduced vitality and defense ability [34–36]. Austria, Slovakia, Slovenia, and Switzerland, however, remained less affected by absolute CWB stress in 2019, with only certain regions subjected to highly negative CWB anomalies.

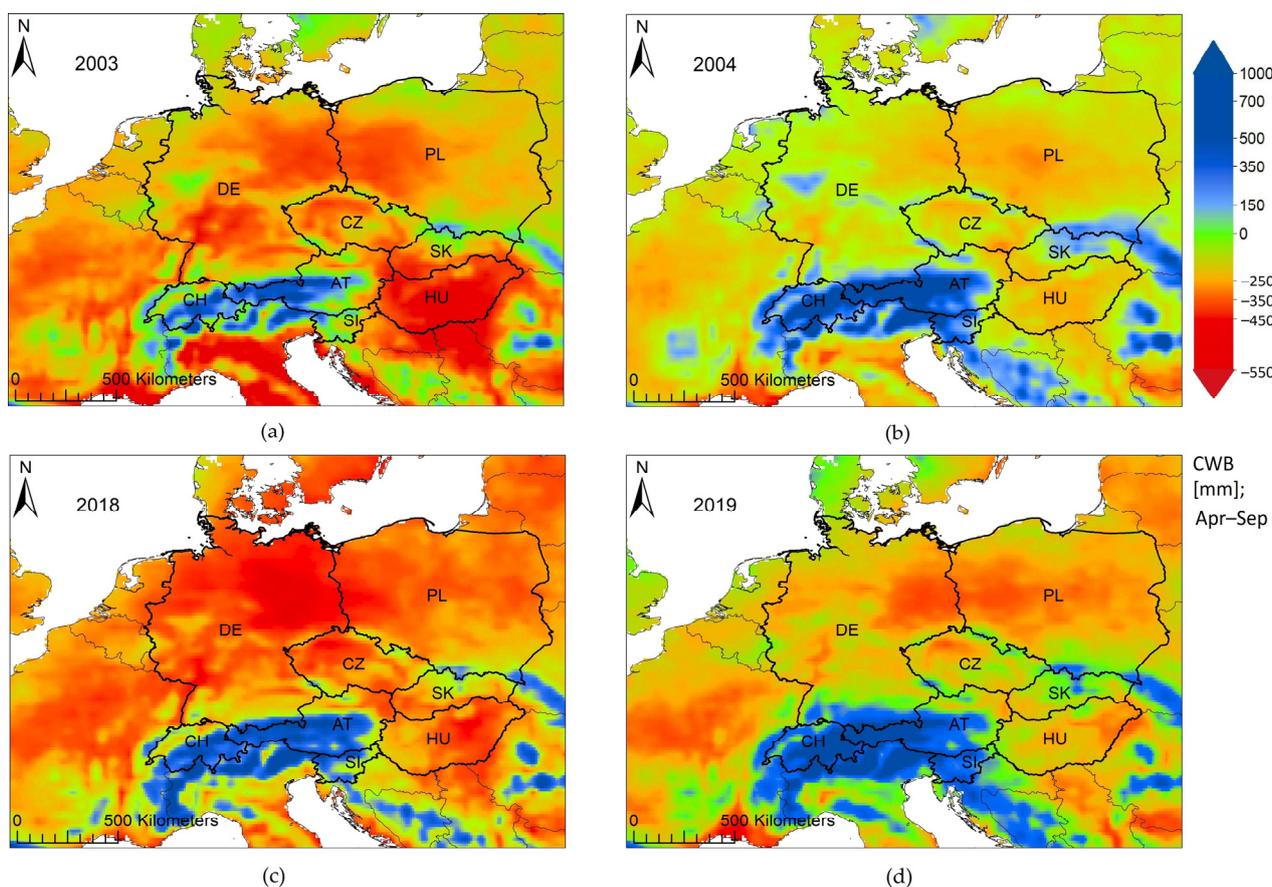


Figure 2. Sum of the climatic water balance (CWB, mm) over the vegetation period from April to September for the years 2003 (a), 2004 (b), 2018 (c), and 2019 (d) over Central Europe. CWB was calculated as the difference between monthly precipitation [28] and monthly potential evapotranspiration (PET, mm). PET was calculated separately [37,38], utilizing the latitude and monthly mean temperature [28] in the *SPEI* package [39] of the R software [40]. Each assessed grid point is 0.1×0.1 degree, roughly 9×9 km. AT: Austria; CH: Switzerland; CZ: Czechia; DE: Germany; HU: Hungary; SI: Slovenia; SK: Slovakia; PL: Poland. Shapefiles of countries downloaded from Eurostat [41]. The downloaded ERA-5 Land climate data for temperature and precipitation [28] existed in NCDF format, was read into R software using the package “ncdf4” [42]. Raster package [43] was used to convert this NCDF data into raster format. See Text S1 for detailed methods description. © Thünen Institute, 2022.

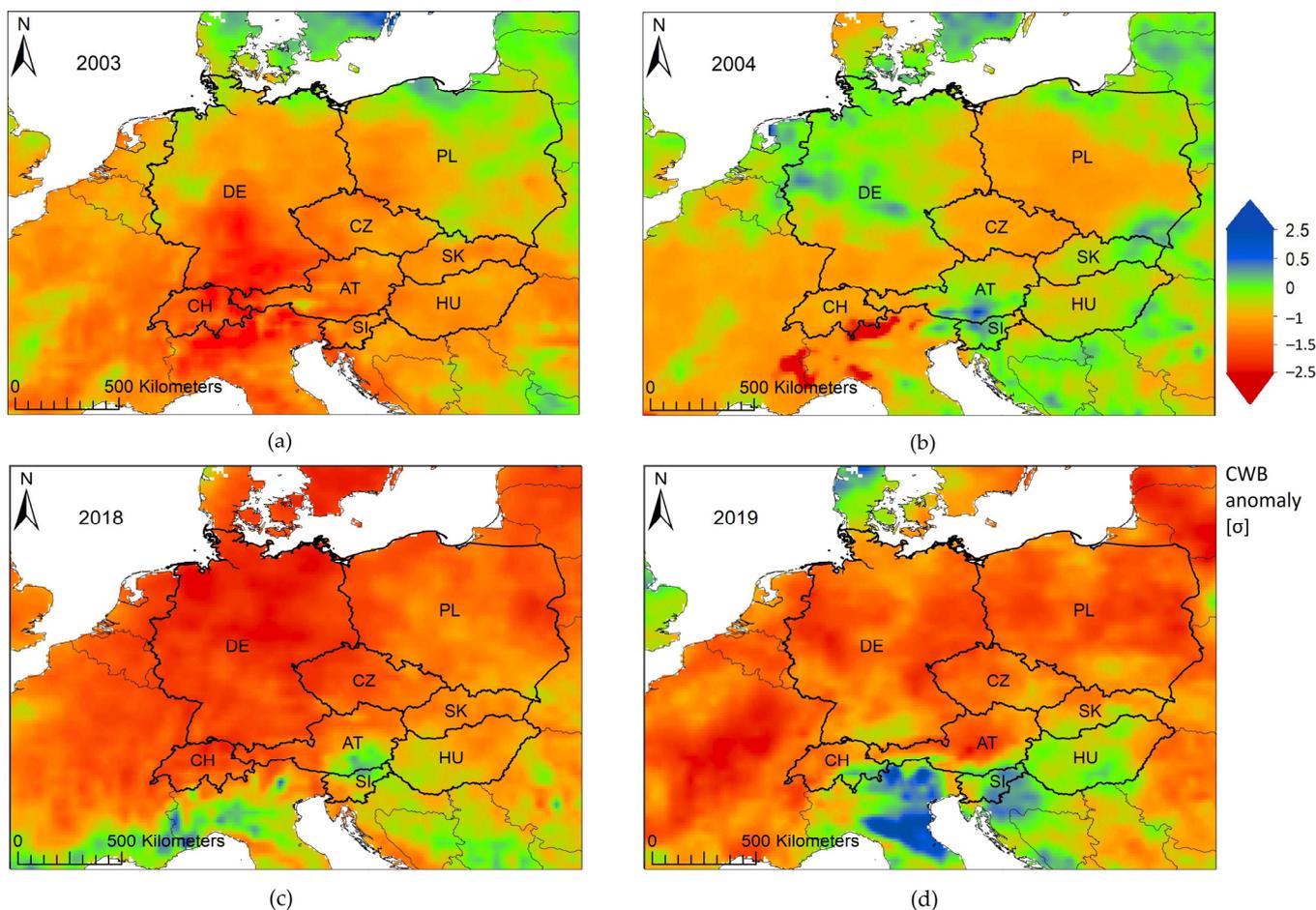


Figure 3. Standardized anomaly of the climatic water balance (CWB, mm) given as sigma (σ) for the years 2003 (a), 2004 (b), 2018 (c), and 2019 (d) as the deviation from the summated mean of the vegetation period (April–September) from the reference time of 1991–2020. CWB was calculated as the difference between monthly precipitation [28] and monthly potential evapotranspiration (PET, mm). PET was calculated separately [37,38], utilizing the latitude and monthly mean temperature [28] in the *SPEI* package [39] of the R software [40]. Each assessed grid point is 0.1×0.1 degree, roughly 9×9 km. AT: Austria; CH: Switzerland; CZ: Czechia; DE: Germany; HU: Hungary; SI: Slovenia; SK: Slovakia; PL: Poland. Shapefiles of countries downloaded from Eurostat [41]. The downloaded ERA-5 Land climate data for temperature and precipitation [28] existed in NCDF format, was read into R software using the package “ncdf4” [42]. Raster package [43] was used to convert this NCDF data into raster format. See Text S1 for detailed methods description. © Thünen Institute, 2022.

In 2003, precipitation was severely low during summer and remained generally lower from February until June compared to the long-term average of 1961–1990 [44]. However, in contrast to 2018, the heat in Central Europe mainly started to build up in May and peaked in June [44]. It was complemented by high evapotranspiration in spring, which intensified the summer conditions [45]. Drought subsided in 2004 [31], a year that was relatively wet and that started with above-average precipitation [29].

Hence, the hot drought of 2018 followed by a subsequent drought in 2019 was unique in terms of length, timing, and climatic anomalies. Such drought periods could reoccur in the future [20], with an increase in their intensity and frequency expected under current climate change [46]. High temperatures during a drought, especially in spring and summer, can lead to an exponential increase in vapor pressure deficit (VPD) [47,48], while soil moisture depletion occurs via evapotranspiration. When there is a negative balance between precipitation and evapotranspiration, the depleting soil moisture makes trees vulnerable to

hydraulic failure if stomata are not sensitively regulated and transpiration is sustained [48] as is the case in species classified as anisohydric, such as beech.

Such unfavorable conditions severely affect tree growth and physiology. For example, they can lead to the modification of allometric properties of beech trees with changes in biomass partitioning strategies [24,49] among coarse roots and shoots [50,51]. Moreover, physiological responses such as stomatal conductance, governed by the underlying biochemical reactions to drought, may be disrupted. The production of abscisic acid (ABA) in roots regulates stomatal closure in leaves [52–54], and increased concentrations of ABA in the xylem sap signals drought stress [55]. Moreover, stomatal conductance could be subject to hysteresis [56] and affect the net photosynthetic rate [52], thereby limiting the synthesis and availability of nonstructural carbohydrates (NSCs) [56]. Furthermore, the risk of xylem cavitation and lethal embolism formation may strongly increase when the xylem tension under water shortages becomes too high [57,58]. Due to its larger leaf area compared to other deciduous species, beech is more vulnerable to drought [7]. At drier sites, for example, beech may be exposed to lower minima of leaf water potential and steep water gradients under drought, most likely coinciding with great deficits of water in leaves and thus higher risk of embolism. Adaptation strategies on such sites include the reduction in mean vessel diameter and the lowering of the P50 (50% loss of hydraulic conductivity). This may, on one hand, avoid xylem embolism, but at the same time affect the water supply to the leaves [59].

The synthesized NSCs and other assimilates are translocated from the leaves (source) to other parts of the plant (sink) via the phloem. Phloem transport is another important pathway governing plant growth, which is rather less explored [60]. It may be disrupted under mild or severe drought stress [60], due to lower water input into the phloem, which leads to more viscous phloem sap reducing the sap flow velocity [59,61], to lower hydrostatic pressure between the sink and the source, and to the formation of sieve tubes of smaller radii. This ultimately reduces the conductivity of the phloem [59]. Phloem transport disruption may therefore be another cause of carbon starvation [59], affecting xylem, leaves, and root formation in a post-drought year, causing a drought memory [56,62]. Morphologically, impaired leaf formation [63–65] also reduces primary and secondary growth due to reduced stomatal conductance [64].

For the whole tree, these responses are signs of reduced carbon reserves [64] and a decreasing buffering capacity, shown by a declining autocorrelation in tree rings [66,67]. They are also potential signs of legacy effects, which could be either negative or positive [68]. Legacy effects are mediated by drought and are a struggle of a system between recovery and a path towards decline [8]. They can last from three to four years [68] and may even have long-term cumulative impacts on tree growth leading to mortality [9]. Moreover, beech is found to be unable to recover by active vessel refilling from xylem embolism leading to sustained branch hydraulic dysfunction [10,69]. This points to an additive or even interactive effect of carbon shortage and hydraulic limitation on impaired recovery of beech from extensive drought events [10] and explains why consecutive drought events such as 2019 may worsen the impact of the 2018 drought [46], by affecting not only the xylem but also the phloem pathway. Combined with biotic disturbances [27], they may further exacerbate the negative legacy effects in beech [20,46].

To understand the implications of consecutive drought periods on the development of legacy effects, in Sections 2 and 3 we compare the climatic and edaphic conditions in beech dominated areas in Central Europe linked to the drought conditions in 2018–2019 and 2003. Based on the reviewed literature [70,71] and existing knowledge of the morphological and physiological, as well as biochemical, reactions of beech to drought, we hypothesize that: (i) the recent hotter and repetitive drought events are responsible for pushing beech beyond its functional limits causing a large-scale decline as well as mortality, and, (ii) legacy effects and weakened vitality may contribute to future beech decline and mortality if post-drought conditions are unfavorable.

In Section 4, we summarize the existing literature that is available on drought reactions of beech in 2018–2019 vs. 2003. We explore the implications on morphological and physiological reactions of beech to drought in Section 5 and discuss the significance of resilience and recovery under the status quo for beech. This leads us to highlighting the current research gaps to be investigated to broaden our understanding of drought impacts on beech at the end of Section 4.2, Section 5.1, and Section 5.2 (also see Appendix A). Finally, we explore various forest management strategies in Section 6, which could be used to potentially buffer negative legacy effects in beech, and improve its future drought tolerance.

2. Climatic and Edaphic Conditions in Beech Dominated Areas

Climate in Central Europe ranges from sub-Atlantic in the northern and central distribution of beech to the mountainous continental and Mediterranean climate towards its southern distribution. Sub-Atlantic climate occurs in eastern and southern Germany, Poland, Czechia, and parts of Slovakia, where beech is found in areas with a minimum of 470 to 500 mm annual precipitation. Mountainous climate occurs in the southern part of Central Europe, e.g., in Slovakia and Slovenia (the latter also experiencing Mediterranean climate), the Alps of Austria, Germany, and Switzerland [15,59,72,73]. Continental climate occurs in Hungary [74,75].

Major soil types are cambisol, luvisol, and podzol [76]. However, beech generally does not occur on very dry sandy soils, on peat, or on marsh [72,73]. Growing on soils with a pH ranging from around 3 to 7 and a base saturation (<5%–100%) [59], beech most frequently exists on limestone derived soils [73]. A competitive advantage of beech in its distribution areas is the ability of its rooting system to reach beyond 1 m soil depth [77]. However, most of its fine roots are located in the topsoil [78], between 0 and 30 cm [79], and even down to 50 cm [77]. Therefore, beech is predicted to lose its advantage across the range of natural occurrence and regeneration under conditions of water shortages [14,72,77].

3. Single Year vs. Consecutive Drought Periods

Climatically extreme years occurred in Central Europe during the last two decades (Table 1). The single drought year 2003 with considerably higher temperatures and lower precipitation than the long-term average and its negative impacts on trees was considered a benchmark of possible future heatwaves and drought events. It was followed by a relatively favorable year 2004. In 2003, mean monthly temperatures in summer were at least 4 °C above the long-term average of 1961–1990 over large areas across Europe, even reaching up to 6 °C across regions in south-west Germany and western Switzerland in Central Europe [44]. The higher than normal temperatures began in May 2003 and lasted until September. In June and August, minimum and maximum air temperatures across Central Europe reached at least 4 °C above the long-term average. Hungary, parts of Slovakia and Poland already experienced maximum temperature anomalies by at least 4 °C in May [44]. Lower than the long-term average precipitation (or negative precipitation anomalies) was observed from February until June across large parts of Central Europe with an additional dry period in August [44,80]. Moreover, a higher than usual spring evapotranspiration, which is associated with a high VPD [45,48], intensified the drought in summer [45].

Table 1. Overview of climatic conditions in the drought years 2003 and 2018, and in their post-drought periods.

Year	Unusual Weather Patterns	Temperature Anomalies (1961–1990) ^a	Precipitation Anomalies % (1961–1990) ^b	CWB ^c absolute sum (mm)	Standardized CWB Anomalies (1991–2020) ^d	References
2003	Heat: starting in May, peaking in June and August; Lower than average precipitation from February until June and then again in August	Mean temperature during June and August at least +2 to +4 °C above the long-term average over large areas across Europe; Min temperatures: at least +2 °C of the long-term average in June and August over large CE areas Max temperatures: warmest months June and August, anomalies beyond +4 °C across almost all CE countries	–50% to –75% of the long-term monthly mean values in June and August across Germany, Poland, Austria, Slovakia, Czechia and Hungary; September precipitation decreasing to –75% in southern Germany and Switzerland	–225 mm; 49% of the grid points across CE below –250 mm	–1.5 σ (standard deviation)	[28,29,44,45,80]
2004	Relatively favorable climatic conditions compared to 2003 with on average milder temperatures and higher precipitation months	Mean temperatures remaining 3 °C below the long-term average (1981–2010) in May, June and July and 0 up to +4 °C above the long-term average in April, August and October	Precipitation in March between –20% and –60% in Germany, Austria Switzerland, parts of Poland in April; from –20% to +150% in May, July and August, with the exception of Czechia and Poland: –40% to –80% in August and September, respectively	–38 mm	+0.1 σ	[28,29]
2018	Impact on a larger area than in 2003; Heat: began in April (mean temperature +4 to +6 °C of long-term average); Lower than average precipitation in February, April, June, July, August, and October; Germany being constantly under stress of below-average precipitation	Mean temperature: +4 to +6 °C in April and May over large CE areas, even above +6 °C in April across large parts of Czechia, small parts of Germany, Poland and Austria, varying between +2 and up to +6 °C from June to September; maximum temperature anomalies +4 σ over larger CE than the long-term average in July (1981–2018; Buras et al. [16])	In February down to –80% to –100%, in April –40% to –80% lower than long-term average and impacting a large CE region, with June/July anomalies down to –60% to –80% in Austria, Germany and Switzerland; August again –40% to –80% in Germany, Poland and Czechia; also below average in October again in parts of Germany and Hungary; November, also dry down to –80% across almost all of Germany and Poland (smaller regions down to –100%), larger parts of Czechia and parts of Austria, Switzerland and Slovakia	–253 mm; 71% of the grid points across CE below –250 mm	–1.9 σ	[16,17,28–30,45]
2019	Secondary drought after 2018; As a post-drought year more unfavorable than 2004, with a lower climatic water balance during the vegetation period	+2 to +4 °C higher mean temperatures than the long-term average in February, April, July, August, October; June being the warmest with +3 up to +6 °C above average, reaching up to +7 °C across large areas in Poland	Down to –60% to –80% in Germany, Switzerland, Austria, Hungary and Slovakia in February; April ranging from –40% to –80% in Germany, Czechia, parts of Slovakia and Austria; and up to –100% on large parts of Poland; June and July from –60% to –80% over a large CE region; August down to –60% in eastern Germany and central and western Poland	–132 mm	–0.8 σ	[28,29]

CE: Central Europe. ^a Reference period (1961–1990) for specifying absolute anomalies of monthly mean values, unless mentioned in the text. ^b Deviation from mean monthly precipitation in % (100% value = monthly mean over the reference period of 1961–1990). ^c Mean over Central European grid of the CWB absolute sum during the vegetation period (April–September). Evaluated using ERA5-Land data for temperature and precipitation [28]; PET (Potential Evapotranspiration) was calculated using the Thornthwaite method [37,38]. ^d This is the latest reference period and reflects both drought years 2003 and 2018. Deviations from the vegetation period (April–September). See Text S1 for calculation.

2018 was exceptionally sunny, warm and dry as early as in spring. The drought impacted a larger area of Central Europe compared to 2003 [16,45]. However, the main difference compared to 2003 was the drought's longer duration and its continuation into 2019 and even into 2020 across some regions [31].

In Austria, Germany, and Switzerland, mean temperatures in the growing season of 2018 were 1.2 °C higher than in 2003 [17]. Mean temperatures reached an anomaly of 4 to 6 °C above long-term average, especially in April, May, July, and August. The temperature anomalies even reached above 6 °C already in April in parts of Germany and Austria [29] (Table 1). The temperature anomalies peaked in July, with maximum temperatures for the month up to four standard deviations above normal observations across Central Europe [16]. A dry period lasting from June until November in Central Europe [30], with average precipitation falling below 80% of the normal values occurred across an extended region of Germany and Poland [29]. The year started with lower than normal precipitation [29] and the cumulative precipitation in spring, summer, and autumn was less than 80% of the reference period of 1981–2010 [81]. Evapotranspiration gradually increased in the months leading to summer. This intensified the summer conditions, even more than in 2003 [16,45]. Thus, a negative CWB was observed in spring and over the total vegetation period (April to September, Figures 2c and 3c). Coupled with VPD [48], it potentially depleted soil water and affected further soil water recharge. Countries most affected by low amounts of precipitation were Germany, Czechia, and western Poland [82].

Our evaluation of the ERA5-Land climate data [28] (see Text S1 for CWB calculation) showed a large area impacted with a highly negative CWB across Central Europe in 2018. A total of 71% of the assessed grid points lay below a value of –250 mm as opposed to 2003, which impacted only 49% of this area with a value below –250 mm (Figures 2 and 3; Table 1). Other single drought events like 2015 also occurred in the region [83,84]. However, the time period 2018–2019 was unique compared to other past drought years in terms of duration, intensity, and magnitude [31]. Continuing also in some regions into 2020,

the drought period from 2018 to 2019/2020 condenses to an average of twelve months. The drought period during 2003 lasted on average five months and the drought intensity peaked in summer but slowly subsided in 2004. Therefore, the recent events beginning in 2018 can be classified as unprecedented [31].

4. Stress Response under Extreme Events

The impacts of the 2003 and 2018 drought periods on European beech were similar in terms of stress responses expressed in reduced growth and deteriorating crown condition such as defoliation and premature discoloration of leaves [7]. In 2018, however, mortality of beech was observed which might be linked to hydraulic failure induced by drought. This was not reported for 2003 [17]. The mortality in 2003 occurred mainly due to secondary pathogen infestations in weakened trees [85,86].

4.1. Negative Impacts of the 2003 Drought

In 2003, partial or full branch diebacks, along with severe growth reductions were reported [87–91]. Growth recovery was often slow [3,24,92,93] and trees exhibited a significant growth decline after 2003 [3,94]. Upper branch dieback and formation of stag-headed patterns on the side branches led up to 70% loss of foliage on intermediate (height on average 10 m) and suppressed beech trees (below 10 m height) in Südbaden in Germany [92,95]. A pan-European assessment of crown condition under the ICP Forests at Level I sites revealed an increase in crown deterioration and defoliation in the sub-Atlantic region of Central Europe (most of Germany, Poland and Czechia) and the Atlantic region (north-west Germany, UK, France, Denmark, parts of southern Norway and Sweden). In the Atlantic region the overall percentage of damaged trees increased by 17% after 2003 (29% to 46%, from 2003 to 2004). This was also the case in the sub-Atlantic region where the percentage of damaged beech trees increased from 23% to 38% from 2003 to 2004 [75]. Mountainous regions showed an increase in the percentage of damaged trees from 12% to 33% from 2002 to 2003 [75]. At plot level, 26% of the assessed plots across Central Europe experienced moderate (>25%) to severe mean plot defoliation (>60% up to 99%), with Germany having been most affected followed by Poland and Slovakia. The number of plots showing mean defoliation >25% increased in 2004 (internal study; Text S2; Figures S1 and S2).

Mortality of beech following the 2003 drought was observed across some regions in Central Europe. This was associated with the loss of tree vigor among predisposed trees [85], defoliation, decrease in root-biomass, and follow-up pathogen attacks by, e.g., fungi such as *Phytophthora* species (north-east Austria and Bavaria, Germany) [34,86], *Botryosphaeria corticola*, *Neonectria ditissima* [35], and *Biscogniauxia nummularia*, inducing stem bark necrosis, as well as from insects such as *Agrilus viridis* (green jewel beetle) and *Taphrorychus bicolor* or beech bark beetle (south-west Hungary) [96]. Brück-Dyckhoff et al. [85] report for Bavaria (south-east Germany) that beech trees showed visual damage of sunburn and spears (dead branches protruding from upper crown) due to vitality loss after the drought of 2003. Moreover, they were predisposed to infestation by *Agrilus viridis*. Percentages of *Agrilus*-infested trees with sunburn and spears were 83% and 68%, respectively.

Cases of pathogen infestations on beech were also reported from other Central European countries, irrespective of the 2003 drought [97,98] (south-west Poland and central Slovakia). However, we only found studies from Germany, Hungary, and Austria, which link pathogen infestation after the 2003 drought to European beech decline and mortality.

4.2. Negative Impact of the Consecutive Droughts in 2018 and 2019

During the 2018 drought, partial or whole crown diebacks, early fruit abortion [99], leaf discoloration [18], early leaf senescence [19], and severe growth reductions [20] occurred in beech. Physiological stress seemed to be greater in 2018 compared to 2003. Due to the extensive mortality, it can be hypothesized that some beech trees had reached a limit of functioning under these extreme drought conditions. This might be linked to highly negative water potentials leading to embolism as Schuldt et al. [17] measured negative values

of midday leaf water potentials on around 25 beech trees from -1.17 MPa in Göttingen (Germany) to -3.32 MPa in Hölstein (Switzerland). These measurements indicate embolism and were likely the cause of a partial or complete canopy dieback due to hydraulic failure induced by drought [17]. Walthert et al. [22] found increased stress on shallow soils with lower water holding capacity leading to embolism, which was also confirmed by Weithmann et al. [100]. They report beech trees transpiring (proxies of transpiration: $\delta^{13}\text{C}$; midday leaf water potential—predawn water potential, $\Psi_{\text{leaf, md}} - \Psi_{\text{leaf, pd}}$) at high embolism levels and critical negative predawn water potentials of around -1.3 to -2.1 MPa, after which a distinct transpiration reduction occurred and defoliation followed to avoid water loss. Between -2.1 and -2.8 MPa, defoliation occurred as a result of stress rather than as a mechanism of preventing stress. Embolism exceeded 50% and early defoliation in 2018 was followed by crown dieback. In other studies, 50% loss of hydraulic conductivity (P50) were reported around negative predawn water potentials of -2.8 to -3.8 MPa [58,100–104]. Such water status in 2018 might have been critical for beech trees, affecting the whole crown rather than just the branches and leaves, leading to its dramatic decline at some sites.

Carbon isotope $\delta^{13}\text{C}$ in leaves is a useful indicator of drought resistance in stressed plants and is linked to stomatal conductance. The higher discrimination of $\delta^{13}\text{C}$ under drought shows higher stomatal conductance in an anisohydric species such as beech, which is also reflected in its intrinsic water use efficiency (iWUE) [105]. Higher discrimination and less reduction in negativity reflect the higher resistance to drought stress [54]. High net photosynthetic rate and high $\Psi_{\text{leaf, md}}$ reflect higher drought resistance in trees [54].

Under drought stress, the production of reactive oxygen species (ROS) is triggered, which may result in cell death [54,59]. Fine roots and leaves in beech produce antioxidants and secondary metabolites such as flavonoids against ROS as a protection mechanism, and they detoxify ROS, stabilize enzymes and proteins, and protect membranes. Thus, they biochemically improve drought resistance. However, drought stress may disrupt the phloem transport and affect these protective mechanisms [54,60]. From this angle, the hotter and repetitive drought events, when pushing beech trees beyond their functional limits, can put them at the verge of carbon starvation, hydraulic failure in the xylem, and water stress in the phloem. This may limit the protective mechanisms of beech trees if these pathways are continuously subject to stress. Recent tree growth decline and enhanced stress were linked to past drought events such as 2003 [3] and to unfavorable climatic conditions of previous years [106,107]. Meyer et al. [3] reported beech growth decline after 2003 in north-eastern Bavaria where the investigated beech trees were unable to recover. In their tree ring study using stem discs, Obladen et al. [106] reported 7% of the sampled beech trees to be dead at lower elevation and on clay-rich soil in northern Bavaria in 2018. These dying trees showed a higher growth sensitivity to past spring–summer droughts after the 1990s. An increasing influence of spring temperature starting in April on this site was found, combined with a negative influence of the current year's June temperature and a positive influence by soil moisture of the current year's July. This illustrates the role of not only climatic conditions but also soil conditions in governing stress responses to drought.

Furthermore, links between significantly lower basal area growth, crown transparency, and leaf browning were reported in beech by Rohner et al. [19] on 75 Swiss National Forest Inventory plots. Trees with severe leaf browning and crown transparency showed a significantly lower basal area growth in 2018 compared to the unaffected trees and compared to their past seven-year average basal area growth.

Crown condition is an important indicator to assess forest condition, and defoliation during the growing season indicates the loss of leaves or needles due to external stress factors such as drought. This reaction to stress was observed on beech dominated ICP Forests Level I plots in 2018 [21,108], when 36% of the plots across Central Europe showed moderate to severe mean plot defoliation (>25 up to 99%) compared to 26% in 2003. Plots exhibiting moderate to severe defoliation ($>40\%$ –99%) were mostly located in Germany (Figure S3). This increased crown transparency has also been documented in the forest assessment reports of Germany in 2020 [6] and has mainly been linked to the consecutive

drought period. The increase in crown transparency in 2019 was generally observed in almost all the federal states but evidently exceeded the one in 2004 in Berlin [109], Brandenburg [110], Thuringia [111], and Mecklenburg-Vorpommern [112]. This could be either due to the consecutive drought event or the lagged impact of 2018 in 2019, or both. Also see Figures S4 and S5.

Low site water supply and CWB have been associated with crown decline [113], branch dieback [114], and premature leaf discoloration [18]. Brun et al. [115] reported early wilting and leaf shedding during the summer of 2018 in Germany and Czechia and suggest shallow soils and steep slopes as a potential risk factor for such a response. High available soil water capacity (AWC) was reported to reduce crown dieback in Germany and Switzerland [116]. Water availability to plants has thus been addressed differently in various studies. However, there is a link between site climate and water availability to plants [117,118]. In regions where the CWB is low due to high potential evapotranspiration (PET) linked to higher temperature, soil AWC may buffer soil drought, especially if winter conditions are favorable with high precipitation and soil water recharge is enough not to be further limited by dry summer conditions [118]. Thus, AWC seems to be a predisposing factor for crown defoliation rather than just the CWB, which is mainly of meteorological nature. Nevertheless, how these interactions govern the drought responses and recovery processes in beech in Central Europe requires further investigation. Furthermore, the role of soils and the site climate in buffering the negative impacts of drought on tree vitality should be further investigated in relation to the biotic disturbances that may follow. Not only AWC, but also site climate along with soil nutrients [119,120], and especially their interactions, should be incorporated into statistical models to better quantify crown condition in terms of drought and legacy effects.

After 2018, trees affected by drought also became vulnerable to secondary pathogen attacks such as *Botryosphaeria corticola* and *Neonectria ditissima* [35,36]. These studies are, however, more local and do not represent all of Central Europe.

5. Unravelling Legacy Effects of Defoliation in the Wake of the 2018 Drought

Unlike long-term studies based on tree rings, topics such as reduced leaf area and defoliation, or per se their legacy effects, are rather less explored [121]. Climatic conditions of the previous year can limit the formation and mobilization of carbohydrates [122], leading to a limited leaf development, smaller leaf area and clumping of foliage [63,64], loss of vigor [46], and reduced greenness in next year's spring [115,123]. Drought can further cause embolism in twigs leading to defoliation [64]. The embolism may persist post-drought [114]. Although defoliation is an attempt of a tree to protect itself from xylem hydraulic failure, it is a sign of stress that can lead to carbon starvation and result in tree mortality [124]. A recent review by McDowell et al. [125] describes tree mortality as a complex process governed by underlying mechanisms that begins at the cellular level until it sets off a chain of events that affect the entire tissue or organ. Hydraulic failure begins at the cellular level and is governed by underlying mechanisms such as cascading cell death due to cell wall rupture, or "cytorrhysis," caused by a drop in water level below a critical value [125]. Carbon pools prior to drought also affect plant defense mechanisms and may also influence the hydraulic conductivity of the plant system. How much carbon is allocated to roots, sapwood, and foliage, and how much is invested to tolerate cytorrhysis or for tree defense, can alleviate or increase the risk of hydraulic failure [125] and thus mortality.

5.1. Linking Defoliation and Growth

Defoliation could thus be an important proxy of legacy, providing information on reduced canopy cover as well as a direct link to growth [126]. Both are negatively correlated [126] and are complementary as indicators of stress under drought because one may become evident before the other [90]. When conditions such as reduced canopy cover persist over time, tree growth could decline. New growth trajectories arise, and trees eventually get pushed beyond their hydraulic safety margins [68,124]. Physiologically,

the limited assimilation of carbohydrates (NSCs) becomes an ecophysiological drought memory (lower recovery of growth; lower resilience), the span which may lengthen due to frequent drought events as “negative carbon balances” increase [56]. This makes the trees unfit and prone to mortality due to hysteresis in stomatal conductance and limited synthesis and assimilation of NSCs under drought, which in turn limits future biomass allocations in trees to construct xylem tissues and fine roots [56], and may even result in smaller leaves [65]. Frequent or consecutive drought events such as 2018–2019 slow down growth recovery [127] and increase the mortality risk as growth and leaf development may also be impaired by low water availability in the previous summer [64,107,128].

The concept of recovery and resilience can be applied to unravel the legacy of defoliation in beech and complement studies of growth resilience with defoliation resilience. Recovery from stress of a parameter such as growth or crown condition can be expressed as its status post-drought vs. under drought; resilience can be expressed as post-drought vs. pre-drought [129]. Recovery is central to resilience [130] and it is a bridge between drought response and tree condition. Drought-induced mortality is associated with previously lower resilience and resistance in trees, which were previously exposed to stress and carry on a low-growth legacy over the years [131]. These growth legacy effects may be short- or long-term. Long-term growth depressions or legacy effects persisting over 20 years were found to be associated with tree mortality [59,113]. It is useful to determine the severity of these effects following a drought and to understand physiological responses of trees and how they may react under future drought events [132]. Stochastic modelling approaches can complement drought studies in determining this cause–effect relationship by incorporating exogenous conditions of the past as a covariate to explain the physiological responses, such as defoliation and growth, in the current year [133].

Growth trajectories are species-specific, site-specific, dependent on species mixing and stand density [134] as well as length, timing, seasonality, frequency, and intensity of drought [38,134,135]. In order to better understand at which sites beech may grow better and be more resilient, linking resilience, legacy, mortality and forest management is crucial. The drought events starting in 2018 were a combination of longer length, early timing and higher intensity than past droughts like in 2003, which may have increased the negative impact on both short- as well as long-term legacy effects of beech. Linking drought exposure, which is primarily a water deficit, and its history [136] with resilience can further our understanding into determining the severity of legacy effects.

Furthermore, links between vitality indicators such as defoliation and growth require more exploration [63,137] to determine if and in which regions beech may recede in the future due to water shortages and high temperatures [14,77]. Delineating legacy effects and impacts of a recurring drought like 2019, and to understand whether the interaction of legacy effects and drought is additive or synergistic in terms of depleting carbon, and how the legacy effects of defoliation could influence post-drought growth, remains open to investigate.

5.2. Beech Rooting Depth, Allometry, and Legacy Effects

Another factor of drought response is the rooting depth of beech, mediated by the activity of aquaporin [138] and access to water from deeper soil layers under drought [139,140]. However, results are ambiguous. For example, no compensation effect in beech under drought to reach water from deeper soil layers was observed by Gessler et al. [78], and water uptake was mostly restricted to topsoil, presumably because the root density in the topsoil was high and a smaller amount of fine roots were present in the deeper soil layers [78]. Difference in the allometric properties of trees might be a contributing factor for water use [141]. Larger trees had coarser root biomass than smaller trees. Nevertheless, in their study, Lüttschwager and Jochheim [141] found larger trees to be more water conserving and drought adapted than smaller trees, and found that the water uptake from deeper soil layers decreased [141]. Interactions of rooting depth with soil type and its

hydrological properties such as AWC and how they govern the growth and drought legacy effects should be explored to better quantify drought responses of beech [9,142].

6. Future Management Decisions for Beech

The current status of European beech may be at risk if extreme weather events like the 2018 drought recur, and the planting of beech trees to establish mixed forests has to be reconsidered. The question of how forest management must be adapted to ensure that beech maintain a sustainable legacy over time remains open. European beech is well known to be drought sensitive [5,89,143,144] and precipitation, especially during the summer [145–147], is often a limiting factor for its growth [148–150]. Soil water capacity is also negatively related to the growth sensitivity of beech [14,151], with trees growing under limiting conditions being more vulnerable towards growth decline [152].

6.1. Site Conditions and Drought Response of Beech

Better post-drought recovery and higher radial growth of beech on less xeric sites or sites with higher water holding capacity were reported [92,144,152]. Trees growing at these sites might therefore not experience severe drought stress even under low rainfall [22]. Dry sites and sites with lower water holding capacity experience higher crown decline and mortality of beech [22,113]. In other studies, beech has been projected to decline at lower elevation sites with warmer climate and lesser precipitation [153], as reported in a study for Germany [154]. An increase in tree mortality under such conditions may occur [155,156]. On the other hand, high temperatures at high elevation sites (above 600 m) with sufficient water supply and precipitation [149] may benefit beech growth [122,154]. This is due to the fact that the utilization rate of assimilated glucose in leaves and tissues, as well as the rate of cell division at higher elevations, is generally restricted by lower temperatures but increases under higher temperatures [122]. This may be beneficial to beech on sites at which water supply is not a problem.

6.2. Mixed versus Pure Stands of Beech

Intra- and interspecific competition may also influence beech growth, especially during drought conditions. Tree responses depend on site conditions and neighborhood density. Several mixture types of beech and other species were studied for resistance, resilience, and recovery of growth under drought. For example, beech admixtures with sessile oak have shown to be more beneficial for beech than admixtures with spruce [24]. Beech is much more drought sensitive than deciduous oak species, but benefits from the presence of oak, e.g., sessile oak [157], in terms of lower stomatal conductance sensitivity compared to pure beech stands. With admixture of coniferous silver fir, both silver fir and beech benefitted in terms of stem diameter growth [158]. In one long-term study [159], beech with co-occurring species in the neighborhood showed superior growth performance and also better recovery after the drought of 1976 and 2003 than the trees in monoculture. Deeper roots and capture of belowground water by oak and silver fir in the admixture benefits the stem diameter growth of relatively shallow-rooted beech [160] by virtue of hydraulic lift [77,161,162]. On the other hand, in mixtures of beech and Douglas fir, Douglas fir recovers more quickly whereas beech recovery slowed down [163]. Therefore, future silviculture practices for beech should involve early mixing with more drought-tolerant species such as sessile or pedunculate oak and silver fir on xeric sites where the latter species are at an advantage due to their deeper rooting system [158,164]. Mixing with Scots pine also seems to be a promising adaptation strategy for European beech [165]. However, in existing mature beech stands with a closed canopy, an admixture of other species may be difficult because of poor light availability in the understory, so early mixing is advised. It may also be that assisted migration [166,167] of southern beech provenances, which have been shown to be more drought resistant [168,169], can help to improve drought tolerance of this species in Central Europe and perhaps prevent future mortality under extreme events.

6.3. Stand Thinning to Mitigate Negative Legacy Effects in Beech

Furthermore, the problem of declining growth of beech can be addressed by controlling stand density. For example, thinning can decrease drought sensitivity by reducing the above- or belowground competition among individuals [124,170] and boosting growth by prolonging the growth duration in a year, and by increasing drought tolerance in beech [171,172]. It can reduce competition, leading to better acquisition of belowground resources. Thinning may also reduce defoliation under stress by reducing belowground competition, potentially preventing embolisms induced by drought [173]. This is because a lower number of trees would experience lower stress for transpiration under water shortage with better redistribution [174]. On the other hand, Meyer et al. [175] found no overall influence of tree removal on mortality rates in the drought years 2018–2019, although it led to a shift in mortality patterns from smaller to larger trees. Studies on the effect of silvicultural practices on drought responses should, however, consider longer periods after drought and larger climatic gradients [175].

Forest management, including the advancement of tree mixtures and reduction of tree competition for enhanced acquisition of limited water resources, plays an important role for stabilizing beech vitality on sites with increasing drought stress. However, those management measures can only attenuate the ongoing range shift of beech from drought-exposed lowland and lower-elevated mountainous regions to higher elevated sites, e.g., Stojnić et al. [58]. Thus, assisting the beech range shift in the future to more suitable mountainous areas by transforming coniferous forests mostly dominated by Norway spruce in broadleaved forests with beech should be prioritized [176].

7. Outlook and Conclusions

Projections show an increase in frequency and intensity of combined drought and heatwaves under current climate change [177], potentially leading to mortality of trees in forest stands across the globe [46,178]. The drought of 2018 in Central Europe, being a new category of hot drought [46], had a negative impact on beech in terms of its vitality, with the following drought in 2019 worsening the impact on already weakened trees. Although 2003 was dry, the following years were overall quite sufficient in terms of CWB and the conditions for the trees to grow and recover were favorable. However, the analysis of tree ring chronologies shows high resilience of beech trees towards drought [67], which raises the question whether the unprecedented decline in 2018–2019/2020 is already fully understood. It is presently an open question as to how the interaction of changes in biochemical cycling and drought will affect beech [179]. In addition, depleting carbon reserves and recurring hydraulic dysfunction caused by drought events may further threaten beech vitality. The interaction between these two remains open to investigation. The impacts of the droughts in 2003 and 2018–2019 are both important for understanding the long-term legacy effects and changing sensitivity of beech trees to extreme conditions over time.

It is also important to note that the recent 2018 drought did not impact all beech sites in Central Europe equally. This was due to differences in precipitation, soil conditions, and stand composition. Nevertheless, the severity of the impacts and physiological responses of trees to these events were so far unprecedented.

In addition, we emphasize that alternatives should be explored for (nearly) pure stands of beech in particular on (future) drought and heat exposed sites. Management measures such as the admixture of more drought-tolerant tree species such as native oak species, hornbeam, winter lime, silver fir, and Scots pine in beech regeneration could create potentially more favorable conditions for beech growth. In addition, mixtures with drought-adapted non-native tree species such as Douglas fir, grand fir, and red oak would be an option if nature-conservation targets do not conflict with this mixing approach. Moreover, site-specific thinning could also be prescribed to reduce (intra- or interspecific) competition among trees [171].

These measures could potentially mitigate the impacts of severe drought events on beech growth and vitality and buffer negative legacy effects, but only to a certain extent.

Under the conditions of ongoing climate change and a more frequent occurrence of climatic extremes, we may have to face the loss of several lowland and lower elevated regions in Central Europe as suitable sites for beech. That may be balanced or even overcompensated with site gains in mountainous areas. Moreover, the review shows the importance of long-term forest monitoring and the value of analyzing data on both growth and crown defoliation. Correlating longer chronologies of defoliation and growth might establish a stronger link between legacy, tree mortality, resilience, and forest management.

This review summarizes recent studies on drought response of beech in Central Europe. Central to our hypotheses, we lay the ground for future research by highlighting current research gaps and by emphasizing that the existing knowledge should be bridged with future frontiers by investigating these gaps. Furthermore, this review is the first comprehensive approach to specifically address the differing responses of beech to the 2003 and 2018–2019 drought events, and it is the first to quantify the CWB and its anomalies for 2003–2004/2018–2019 during the vegetation period across Central Europe. It provides an anchor for future research to better understand beech responses to drought and supports future forest management decisions.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/f14020248/s1>, Text S1: Methods description for the calculation of the climatic water balance and creating Figures 2 and 3. Text S2: Evaluation of the ICP Forests Level I data. Figure S1: (left) Defoliation Plots on ICP Forests Level I in Central Europe in 2003; (right) Total number of plots on Level I in Central Europe, in each defoliation category in 2003. Moderate to severe defoliation (>26% and up to 99%) has been shown as a single category. Figure S2: (left) Defoliation Plots on ICP Forests Level I in Central Europe in 2004; (right) Total number of plots on Level I in Central Europe, in each defoliation category in 2004. Moderate to severe defoliation (>26% and up to 99%) has been shown as a single category. Figure S3: (left) Defoliation Plots on ICP Forests Level I in Central Europe in 2018; (right) Total number of plots on Level I in Central Europe, in each defoliation category in 2018. Moderate to severe defoliation (>26% and up to 99%) has been shown as a single category. Figure S4: (left) Defoliation Plots on ICP Forests Level I in Central Europe in 2019; (right) Total number of plots on Level I in Central Europe, in each defoliation category in 2019. Moderate to severe defoliation (>26% and up to 99%) has been shown as a single category. Figure S5: (left) Defoliation Plots on ICP Forests Level I in Central Europe in 2020; (right) Total number of plots on Level I in Central Europe, in each defoliation category in 2020. Moderate to severe defoliation (>26% and up to 99%) has been shown as a single category.

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Appendix A

Drought is the result of a complex mixture of environmental variables. Not only is the role of temperature and precipitation crucial for tree growth, but also other variables such as the vapor pressure deficit (VPD). VPD regulates evapotranspiration and affects

the water pools, especially in spring and summer when the temperature is highest. The conditions could exacerbate, in case of lower than average precipitation, as occurred in 2018, for a longer duration compared to previous drought events. The drought was more severe than previous drought periods in terms of duration, high temperatures, and affected area. It caused the decline of growth and tree vitality in the form of early leaf senescence, leaf browning, and crown burning, as well as partial to whole crown diebacks, and even mortality [17–23]. Vitality reflects the previously stored carbon pools and can determine the resilience of a tree. A plant's defense ability is affected by carbohydrate concentrations and can explain post-drought defensiveness or vulnerability. A consecutive drought such as 2019 worsens the impact.

A holistic approach towards understanding the detailed responses of beech is emphasized. A variety of exogenous climatic factors such as VPD, relative humidity (RH%), solar radiation, and wind speed can be integrated into systematic research frameworks in addition to temperature and precipitation. These frameworks should not only incorporate the response at the level of the individual tree, but also the response at the organ level and down to the cellular level, into statistical and simulation models. Drought response begins as a cascading chain of events from emboli in the water conduits, changes in water tension within the cell wall and up to the organ, affecting the hydraulic conductivity and the carbon pools [125]. A tree as a whole can be prone to mortality under critical water levels and carbon reserves [11,12,22,64]. Recent drought events such as 2018–2019 emphasized the need of a more integrated approach to observe, hypothesize, and investigate the drought response of European beech.

Bringing all the information together is often difficult due to logistical constraints. However, long-term forest monitoring data, with not only ecological observations but also the measurements at the organ level and studies at the cellular level, may further add to the understanding of the drought response of beech under different conditions.

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