Assessing the Resilience of UK Forests to Drought

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Abstract

Widespread impacts on forest productivity from extreme drought events have now been documented on every forested continent on earth, with the frequency and severity of these events expected to increase across much of the world. To meet the challenges of a changing climate, an understanding of how forest systems have responded to extreme droughts in the past and how we can increase the resilience of these systems to future events is needed. This thesis investigates how resilient Scots pine (*Pinus sylvestris*) and Sitka spruce (*Picea sitchensis*) (the two most economically important and abundant UK conifer species) are to historic extreme drought events in the UK. In doing so we aimed to understand how differences in short vs longer term responses might influence our understanding of how these forests recover, how both forest composition and the nature of the drought itself might modify forest resistance and resilience to drought, and whether there are any thresholds of drought tolerance or evidence of drought induced shifts in competitive dominance. Following the implementation of a new methodological approach to quantifying drought resilience over different timescales, we documented evidence of post-drought compensatory growth in both Scots pine and Sitka spruce, which for some trees resulted in the complete recovery of tree size to what might have been expected in a 'no-drought' scenario. We also found evidence that small increases in drought severity were associated with large reductions in the radial growth of Scots pine and a shift in tree growth dominance. Surprisingly, monospecific stands of both species were also more drought resilient than intimate mixtures of the same two species. This research highlights the complexity of operationalising resilience concepts but contributes a strong and comprehensive foundation of evidence which can be used with future modelling work to identify ways to build resilience to future extreme drought events.

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Authors Contributions

Chapter 1

Tom Ovenden wrote the entirety of **Chapter 1** while Maurizio Mencuccini, Alistair Jump and Mike Perks reviewed and commented on the chapter.

Chapter 2 & 3

Tom Ovenden led the conceptual development, methodological approach, all analysis (including the ring-width measurement, crossdating, detrending and analysis of existing dendrochronological disc images) and wrote the manuscripts; Mike Perks contributed to the conceptual development, manuscript production and facilitated data availability; Toni-Kim Clarke contributed to the methodological approach, analysis and the writing of the manuscript; Maurizio Mencuccini contributed to the manuscript production and Alistair Jump contributed to the conceptual development and manuscript production. The cross-sectional disc images utilized in this manuscript were originally collected and digitised during a study supported by the EU Fifth Framework Project (Compression Wood: QLK5-CT-2001- 00177).

Chapter 4

Tom Ovenden led the conceptual development, methodological approach, fieldwork and data collection, analysis (including sample processing, ring-width measurement, crossdating, detrending and analysis of all dendrochronological material) and wrote the manuscript; Mike Perks contributed to the conceptual development, data collection and writing of the manuscript, David Forrester contributed to the conceptual development, methodological approach and writing of the manuscript, Maurizio Mencuccini contributed to the conceptual development and writing of the manuscript, Jazz Rhoades and Danni Thompson contributed to the data collection and writing of the manuscript, Victoria Stokes contributed to the conceptual development methodological approach and writing of the manuscript, Salvo Bonomo contributed to the data collection and Alistair Jump contributed to the conceptual development and writing of the manuscript.

Chapter 5

Tom Ovenden led the conceptual development, methodological approach, analysis and wrote the chapter, Maurizio Mencuccini contributed to the conceptual development and reviewed and commented on the chapter, while Mike Perks and Alistair Jump reviewed and commented on the chapter.

Chapter 6

Tom Ovenden led conceptual development, methodological approach, analysis (including the ring-width measurement, crossdating, detrending and analysis of existing ITRAX images) and the wrote the entire chapter; Mike Perks contributed to the reviewed and commented on the chapter and facilitated data availability; Maurizio Mencuccini reviewed and commented on the chapter; Alistair Jump reviewed and commented on the chapter, and Steven Adams provided the ITRAX images used in the analysis and reviewed and commented on the chapter.

Chapter 7

Tom Ovenden wrote the entirety of **Chapter 7** while Alistair Jump and Mike Perks reviewed and commented on the chapter.

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Thomas Ovenden
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15 August 2019

Dear Thomas,

Re: Ethics Application: Assessing the resilience of UK forests to extreme climate events – GUEP 706

Thank you for your submission of the above to the General University Ethics Panel.

The ethical approaches of this project have been approved by GUEP, and you can now proceed with your research.

Please ensure that your research complies with Stirling University policy on storage of research data which is available at:
https://www.stir.ac.uk/about/faculties-and-services/information-services-and-library/researchers/research-data/before-you-start-your-research/our-policy/

If you have not already done so, I would also strongly encourage you to complete the Research Integrity training which is available at: https://canvas.stir.ac.uk/enroll/CJ43KW

Please note that should any of your proposal change, a further submission (amendment) to GUEP will be necessary. If you have any further queries, please do not hesitate to contact the Panel by email to guep@stir.ac.uk.

Yours sincerely,
Pp.
Katie Hamilton
On behalf of GUEP
Dr William Munro
Deputy Chair of GUEP

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CHAPTER 1 - Introduction

1.1. Extreme drought events

The Intergovernmental Panel on Climate Change (IPCC) warns that temperature extremes, heatwaves and droughts will increase in both frequency, intensity and duration in the coming years (Arias et al., 2021; IPCC, 2014; Shukla et al., 2019). While winter months in the wetter parts of the world are expected to become wetter, drier months and regions will continue to become drier (Skliris et al., 2016; Sohail et al., 2022), with decreases in summer precipitation resulting in progressively more severe and widespread droughts in the next 30-90 years (Dai, 2013; McDowell et al., 2018; Trenberth et al., 2014). Compounding the effects of decreases in summer precipitation and lower soil moisture availability (soil drought) are increases in abnormally high temperatures. These extreme temperatures will result in increased Vapour Pressure Deficit (VPD) (the difference between the amount of moisture in the air and how much moisture air can hold at a given temperature), atmospheric droughts and direct impacts on plant physiology through heat stress. Collectively, the interactions between soil drought, atmospheric drought and heat stress represent a major threat to plant functioning and survival (Hammond et al., 2022), with reductions in gross primary productivity (GPP) linked to recent increases in VPD and widespread tree mortality following hotter droughts already being documented globally (Dannenberg et al., 2022; Hammond et al., 2022; Yuan et al., 2019).

Predicted increases in drought frequency and severity are accompanied by warnings that both marine and terrestrial ecosystems could undergo rapid and irreversible changes in composition, structure and function (IPCC, 2014). These warnings have led to a growing concern for the vulnerability of forest ecosystems globally (Brodribb et al., 2020; McDowell et al., 2020), including those not normally considered to be water-limited (Allen et al., 2010, 2015) such as much of the UK, and the ability of these systems to continue to sequester carbon and provide a range of goods and services (Anderegg et al., 2020). Many studies are already documenting sudden, large-scale changes in composition, structure and function linked to extreme drought events across forest biomes. These changes include shifts in both vegetation composition (Mueller et al., 2005) and the dominance of different species within a community (Cavin et al., 2013), reductions in forest biomass accumulation (Ma et al., 2012), and extensive tree mortality, both directly and indirectly in response to drought (Anderegg et al., 2019; Breshears et al., 2005; Hammond et al., 2022). As a result, understanding how forests have historically responded to drought and how forest managers can increase the resilience of these systems to future extreme drought events is critically important (Field et al., 2020; Sohn et al., 2016).

1.2. How does drought affect trees?

How a plant responds to drought is dictated by the complex interplay of plant functional traits at multiple temporal and spatial scales in concert with individual life histories, the local biotic and abiotic context, and the characteristics of a given drought event (Feng et al., 2018; Fu & Meinzer, 2018; Liu et al., 2019; Mencuccini et al., 2019). Until recently, plants dealing with the demands of water stress imposed by drought were thought to fall into one of two categories (Lambers et al., 2008). Those plants that displayed a *'conservative'* behaviour in response to drought (e.g., by closing their stomata earlier as soil water potentials become increasingly negative) were often categorised as isohydric (Lambers et al., 2008; Tardieu, 1993). In contrast, those species that employed a more *'risky'* strategy, such as those that leave their stomata open for longer under drought conditions were termed anisohydric (Tardieu, 1993; Tardieu & Simonneau, 1998). In practice, it is now accepted that such a dichotomous classification is not representative of the variety of drought responses we see in plants, and that all plant species instead exist somewhere along an isohydric – anisohydric spectrum (Klein, 2014; Meinzer et al., 2016).

Along this isohydric – anisohydric spectrum, more isohydric species generally maintain a more constant leaf water potential in response to atmospheric drying and decreases in soil water availability (McDowell et al., 2008). This approach prevents water loss and limits the risk of drought induced cavitation and embolism, where dissolved air molecules expand to fill xylem under high xylem water tension (Vilagrosa et al., 2012), a process that can ultimately lead to hydraulic failure (Lambers et al., 2008; Thomas, 2014; Vilagrosa et al., 2012). This conservative approach is however not without cost, as the process of closing stomata also restricts the absorption of carbon dioxide needed for photosynthesis, limiting tree growth, and forcing an individual to rely on stored carbohydrate pools.

Carbon starvation is thought to occur when a tree has utilised a large portion of its stored carbohydrate reserves through the demands of respiration, but has been unable to replenish this supply due to ongoing drought conditions that limit stomatal conductance and thus carbon absorption and assimilation (McDowell et al., 2008). Carbon starvation may eventually result in tree death, either directly through the unavailability of resources to satisfy metabolic demand (McDowell et al., 2008), or indirectly as insufficient resources lead to a reduction in vigour and limit tree defences against pests or pathogens (De Grandpré et al., 2018). While all trees along the isohydric – anisohydric spectrum might be effected by carbon starvation, the earlier closing of stomata to maintain leaf water potentials above their hydraulic failure threshold might predispose more isohydric species to carbon starvation than more anisohydric species (McDowell et al., 2008). However, the mechanisms of tree death linked to carbon starvation is likely more complex than this, and far from resolved (Sala et al., 2010). For example, evidence of substantial pools of stored carbon in deceased trees led Sala et al. (2010) to conclude that tree death can still occur before all carbon reserves have been fully exhausted. As the closing of stomata prevents transpiration and influences the hydrostatic pressure along the source-sink gradient between roots and leaves (Dannoura et al., 2018), the “phloem transport failure hypothesis” (where a drastic reduction or even cessation of phloem transport due to stomatal closure impacts a tree’s ability to access the stored carbohydrate reserves needed to maintain metabolism) has been proposed and tested as a mode of tree mortality (Dannoura et al., 2018; Mencuccini et al., 2015; Sevanto et al., 2014). This inability to mobilise stored carbohydrates to meet respiratory demands is also a mechanism by which trees can succumb to carbon starvation whilst still technically having enough stored carbohydrates (Dannoura et al., 2018; Sevanto et al., 2014) and suggests that radial tree growth would also slow or even stop, resulting in narrow or missing annual growth rings during drought years.

In addition to the risk of carbon starvation, the reduction in stomatal conductance and resultant unavailability of CO_2 for photosynthesis rapidly escalates the risk of oxidative stress through the increased production of reactive oxygen species (ROS) and photorespiration (Farooq et al., 2012). ROS are toxic to plants and their overproduction results in a disbalance with internal anti-oxidant defences and leads to inhibited photosynthetic and respiratory activities (Farooq et al., 2012). Similarly, photosynthesis itself is known to be one of the most heat-sensitive physiological processes in plants (Húdoková et al., 2022), meaning that increases in the frequency of hotter droughts carries substantial risks to key physiological processes involved in normal plant functioning due to heat stress.

In contrast to more isohydric species, the xylem of more anisohydric species are generally more tolerant of negative water potentials and continue to operate at much narrower hydraulic safety margins (the difference between the minimum water potential and that causing 50% loss in hydraulic conductivity, i.e. hydraulic dysfunction), meaning more anisohydric species are often more tolerant of drought conditions (McDowell et al., 2008). However, continuing to operate under greater water stress potentially increases the likelihood that drought will result in hydraulic failure (Adams et al., 2017; McDowell et al., 2008).

Differences in morphology and ecophysiology means that all trees exist somewhere along the continuum of these two water-use strategies (isohydric and anisohydric). A wide variety of plant functional traits can be found within a mixed species forest ecosystem (Aranda et al., 2012; Bréda et al., 2006; Manrique-Alba et al., 2018) and differences in these traits likely interact with the characteristics of a particular drought event (e.g. duration, intensity, timing etc.) to partly explaining some of the variability in species responses to climate and extreme drought events. As a results, not all species respond to the same drought event in the same way. In some cases, the disproportionate impact of drought on one species over another has caused long-term shifts in vegetation structure, composition and the competitive dominance of individuals, such that a previously co-dominant species becomes dominant after an extreme drought event (Cavin et al., 2013; Mueller et al., 2005; Suarez & Kitzberger, 2008). However, the long-term impacts of drought on forest structure and composition are complex and still relatively understudied in most forest systems but is important to understand if we are to adapt our forests to deal with the challenges of a changing climate.

1.3. Resilience – an overview

The concept of resilience – here defined as the ability of a system to absorb and recover from disturbance, remaining essentially unchanged – has become popular in applied ecological research as a way of assessing how natural systems such as forests respond to, and recover from extreme climate events such as drought (Gazol et al., 2018; Lloret et al., 2011; Sohn et al., 2016). Similarly, in recognition of the range of challenges that forests will face under future climates, principles of resilience and adaptive management are now seen as integral components of sustainable forest management and feature strongly in international guidelines (e.g. FAO, 2018). To reflect this, research has focused on understanding ways of measuring resilience (Ingrisch & Bahn, 2018; Lloret et al., 2011), the morphological and physiological mechanisms that underlie drought vulnerability (Adams et al., 2017; Anderegg et al., 2018; McDowell et al., 2008), the conditions associated with drought induced tree mortality (Adams et al., 2017; Anderegg et al., 2016, 2018; Sala et al., 2010), the location of ecological thresholds (Adams et al., 2017; Anderegg et al., 2015; Andersen et al., 2009; Choat et al., 2018; Petraitis, 2013) and the resistance and resilience of different forest systems to historic and novel disturbances (DeSoto et al., 2020; Gazol & Camarero, 2016; Sohn et al., 2016; Vitali et al., 2018). In the context of productive forest management, this work has been complemented by studies that seek to understand which widely planted (Boden et al., 2014) or alternative species (Hoffmann et al., 2018; Kunz et al., 2018), species mixtures (Thurm et al., 2016; Vitali et al., 2018) and silvicultural practices (Bottero et al., 2017; Sohn et al., 2016) can best deliver climate resilient forests.

While the concept of ecosystem stability has sat at the heart of ecology for decades (Goodman, 1975; Isbell et al., 2015; McCann, 2000), agreement regarding ways in which stability and resilience can be most effectively measured in ecological systems continues to be the focus of considerable debate (Ingrisch & Bahn, 2018; Lloret et al., 2011; Newton & Cantarello, 2015; Van Meerbeek et al., 2021). Grimm and Wissel (1997) argued that 'stability' cannot be considered as a single property in its own right, instead suggesting that it should be viewed as a descriptive term that encompasses several essential and closely related properties, such as resistance and resilience. Despite a plethora of definitions, resilience terminology primarily distils down into two dominant, though inter-related concepts in ecology: engineering resilience and ecological resilience (Grimm & Calabrese, 2011).

The focus of engineering resilience is on 'stability' at a single 'equilibrium steady state' (Holling, 1996) and is classically measured through resistance to exogenous disturbances (**Figure 1.1a**) and the time taken to return to this equilibrium (Pimm, 1984) (**Figure 1.1b**). In contrast, ecological resilience differs from engineering resilience by assuming there are multiple potential stable states in which a system could exist, all of which fundamentally differ from one another and into which a system can fall, having crossed some form of threshold (Newton & Cantarello, 2015) (**Figure 1.1c**). In this sense, the ecological resilience of a system is defined more by the ability of a system to absorb change or novel disturbance and maintain its general structure and function. When exposed to a disturbance that exceeds some ecological threshold, the system may cross into a different stable state, potentially governed by a new set of processes or dominated by a new set of species (Holling, 1973; Webb, 2007) (**Figure 1.1c**).

The analogy of a rolling ball in a resilience landscape (analogous to hills and valleys) was originally proposed by Lotka (1956) and has often been employed to help visualise both resilience concepts (Hodgson et al., 2015; Holling, 1996; Peterson, 1997) (**Figure 1.1**). The 'valley' in this context represents the stability domain, with the ball indicating the state of the system (Petraitis, 2013). In engineering resilience, when at the bottom of a valley, the system is thought of as being at some form of stable equilibrium (Holling, 1996). Should an external force or perturbation disturb this system, this would be akin to the ball being pushed up the slopes of the valley. The resilience of the system, as per engineering resilience, is the time taken for the ball to return to the bottom of the valley i.e. the same prior stable state (Holling, 1996). Conversely, in this analogy the amount of 'energy' needed to push the ball up the slopes of the resilience landscape is inversely proportional to the resistance of the system.

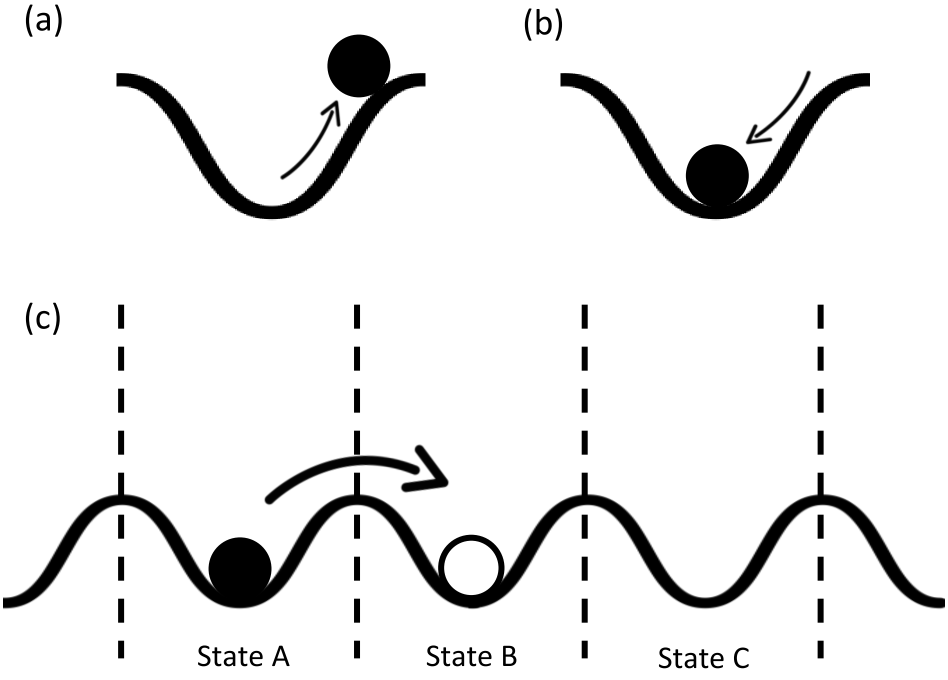

Figure 1.1 *– A 'hill and valley' representation of the concepts of engineering resilience (a and b) and ecological resilience (c). In (a), (b) and (c) the black ball represents the state of an ecological system in a 'resilience landscape'. (a) A perturbation disturbs the system (black circle) pushing it away from its quasi-equilibrium steady state, with the amount of energy required to move the system up the 'hill' being inversely proportional to the resistance of the system. (b) Resilience is the time taken for the system to return to normal following the perturbation. (c) In ecological resilience, if a perturbation is sufficiently strong it may push the system (black circle) into an alternative stable state having crossed one or more thresholds (vertical dashed lines), in which the system (now a white circle) is governed by a different set of processes.*

In contrast to engineering resilience, ecological resilience suggests that there is more than one stability domain within which a system can exist (**Figure 1.1c**). In this analogy, the ball behaves in a similar way as in the engineering resilience example, however here the apex of the 'hill' represents a possible tipping point or 'threshold' where any further disturbance could cause the ball (i.e. the system) to fall into a different basin of attraction (Petraitis, 2013). This 'tipping' signifies the transition of an ecosystem across some form of ecological threshold into an alternative stable state and can, theoretically, occur abruptly. Observed sudden shifts in species composition following what appear to be relatively minor changes in an environment are often cited as evidence for multiple stable states (Petraitis, 2013). Recovery from this state now requires a significant amount of 'work' to push the ball back up the hill and into the previous basin of attraction. This is however where the analogy begins to break down, as the shift to an alternative stable state is generally considered to be an irreversible process. That is, the changes a system has undergone acts as a form of ecological memory or 'legacy' that puts the system on a novel trajectory, making a return to the exact previous system state unachievable.

Despite its appeal as a theoretical concept, designing experiments that can provide convincing evidence of the existence of multiple stable states and translating this theory into rigorously testable hypotheses is difficult and has lead the utility of the ecological resilience concept to be questioned (Newton & Cantarello, 2015; Petraitis, 2013). In turn, this has meant that metrics and indices that measure engineering resilience have been more commonly adopted and more widely implemented in the ecological literature (Ingrisch & Bahn, 2018) and across the forest sciences (Nikinmaa et al., 2020).

1.4. Measuring drought

Droughts are complex, multidimensional and multi-scale phenomena that often vary considerably over both space and time, making them difficult to accurately characterise and study (AghaKouchak et al., 2021; Vicente-Serrano et al., 2020). For studies focused on understanding forest resilience to drought, the Standardised

Precipitation Evapotranspiration Index (SPEI) (Vicente-Serrano et al., 2010) is commonly used as a way of quantifying drought severity (D'Orangeville et al., 2018; Gazol et al., 2018; Huang et al., 2015; Vitasse et al., 2019). The SPEI uses a standardised climatic water balance, calculated as the difference between precipitation and evapotranspiration over different timescales to give a relative measure of drought severity (Beguería et al., 2014; Vicente-Serrano et al., 2010), building on its predecessor, the Standardised Precipitation Index (SPI) (McKee et al., 1993). Despite the widespread adoption of the SPEI, an increasing number of studies are highlighting the importance of considering the different aspects of a drought event (e.g. intensity, duration, frequency, timing etc.) when interpreting tree growth response (Gao et al., 2018; Greenwood et al., 2017; Huang et al., 2018; Kannenberg et al., 2019), rather than relying exclusively on a single measure of severity. The Climatic Water Deficit (the difference between potential evapotranspiration and actual evapotranspiration) has been proposed as a useful absolute measure of aridity to compliment the relative measure of drought severity obtained through the SPEI, particularly in wetter regions of the world such as the UK where there is a risk that the SPEI may mischaracterise a particular event (Zang et al., 2019).

1.5. Forest resilience to drought

Throughout their lifetime, trees keep intra- and inter-annual records of the biotic and abiotic conditions to which they were exposed through radial growth rings. Using this growth record, Lloret et al. (2011) formalised a set of indices that explicitly consider the different components of tree resilience (resistance, recovery, resilience and relative resilience) which broadly reflect the concept of engineering resilience. These indices have now been widely adopted for studying the impact of, recovery from and resilience to drought in both planted and naturally occurring forests (De Grandpré et al., 2018; Fang & Zhang, 2018; Gazol et al., 2018; Olano et al., 2017; Sánchez-Salguero et al., 2013; Zang et al., 2014), with many of these studies highlighting the complex nature of intra- and interspecific responses to drought. As a result, where forests become progressively more limited by water availability, the role that species diversity plays in maintaining ecosystem functioning across a range of temporal and spatial scales is likely to become increasingly important (Ratcliffe et al., 2017).

Despite a growing interest in the role more diverse, mixed-species forests can play in mitigating drought impact (Messier et al., 2021), relatively few detailed studies have been conducted (Haberstroh & Werner, 2022) and fewer species combinations considered (Thurm et al., 2016). As a result, general relationships between tree diversity and drought vulnerability remain unclear (Grossiord, 2019) with contrasting results commonly reported (Ammer, 2019; Haberstroh & Werner, 2022). For example, Vitali et al. (2018b) demonstrated how silver fir (*Abies alba*) benefitted from growing in mixtures with other species under drought conditions, Douglas fir (*Pseudotsuga menziesii*) became more drought stressed in mixtures, and the response of Norway spruce (*Picea abies*) varied depending on the species identity of its immediate tree neighbourhood. Conversely, Douglas fir has been shown to benefit from drought release when mixed with European beech (Thurm et al., 2016), while a summary of recent evidence suggests that whether mixed-species forests are more or less resilient to drought may depend on the characteristics (i.e., severity) of the drought itself (Haberstroh & Werner, 2022). As a result, we should be cautious in assuming that more diverse, mixed-species forests are automatically more drought resistant and/or resilient than less diverse forests. Similarly, these studies illustrate the growing need for additional research on commonly used, but currently under-represented species and species mixtures under a variety of climatic and edaphic conditions. While greater forest resistance or resilience to drought does not always result from increases in tree species diversity (Grossiord et al., 2014), recent work has documented a link between increased functional trait diversity and forest resilience to drought (Anderegg et al., 2018). This understanding makes species diversification an attractive option for adapting planted forests to deal with increases in climate extremes where component species are selected for specific complementary traits.

In addition to species composition, stand management may be an effective way to increase forest resilience to drought. A growing body of evidence suggests that higher stand densities are associated with a greater vulnerability to the climatic and pathogenic challenges associated with drought (Bottero et al., 2017; Sánchez-Salguero et al., 2013; Seidl et al., 2017). As a result, tree density management through thinning has been proposed as a way to decrease the risk of drought induced impacts on tree growth, mortality, and associated pest and fire risks for some time (Bréda et al., 1995; Chmura et al., 2011; Grossiord et al., 2014) in both monospecific (D'Amato et al., 2013; Sohn et al., 2013; Sohn et al., 2016) and mixed species forests (Vernon et al., 2018). However, recent work has demonstrated that the impact of thinning, and its relationship with forest resistance to drought is both spatially and temporally complex. D'Amato et al. (2013) documented a beneficial effect of thinning for both drought resistance and resilience in younger (49 years old) red pine (*Pinus resinosa* Ait.) cohorts, however this positive effect was seen to reverse for older age stands (76 years old) that were maintained at these lower densities. D'Amato et al. (2013) suggest this pattern may be due to faster tree growth in the older cohorts resulting in greater individual tree water demands during subsequent droughts. This explanation is in keeping with evidence that larger trees tend to suffer more during drought (Bennett et al., 2015) and the concept of structural overshoot, where rapid growth during favourable climate conditions becomes maladaptive under drought due to a temporal mismatch of water demand and availability (Jump et al., 2017). Sohn et al. (2016a) also discovered radial growth recovery post-drought was improved in stands of Scots pine (*Pinus sylvestris*) that had been thinned and were, although to a lesser extent, also more resistant. This effect was however seen to diminish with time since thinning, eventually resulting in a negative effect compared to un-thinned stands (Sohn et al., 2016).

A meta-analysis by Sohn et al. (2016b) reviewed the results from 23 thinning experiments to investigate the impact of different thinning intensities on the different resilience indices developed by Lloret et al. (2011). Sohn et al. (2016b) concluded that while there were differences between broadleaves and conifers, any beneficial response for growth resilience and recovery diminishes with time since thinning, and that heavy thinning is better suited in both broadleaves and conifers for mitigating the negative impacts of drought on tree growth (Sohn et al., 2016b). One potential limitation of this analysis is that it groups all study sites by either "moderate" (<40% BA reduction) or “heavy” (>40% BA reduction) thinning, which could obscure some of the variability in the growth response of different species or stands to different thinning approaches e.g. variable density thinning and negative or positive selection (Kerr & Haufe, 2011). There was also a particular emphasis on the genus *Pinus*, with 12 of these 23 studies considering a pine species and most genera only represented by a single study, including *Abies (Abies pinsapo)* and *Picea* (*Picea abies*). The lack of species representation is especially pronounced for *Picea*, many species of which are known to be particularly sensitive to water stress (Savill, 2013; Van Der Maaten-Theunissen et al., 2013) compared to the generally more drought tolerant *Pinus* species (Lévesque et al., 2013).

1.6. The UK context

Across the UK, widespread increases in extreme heat events and the co-localisation of different types of extreme climate events in the last 28 years have already been documented (Dodd et al., 2021), with the risk of both heat and drought stress expected to increase in the future, especially in the southern and eastern regions of the UK (Arnell & Freeman, 2021). These hotter and drier conditions are already being documented, with the recent 2018/19 extreme drought event across much of mainland Europe extending into the UK (Buras et al., 2020) where the 2018 summer (June – August) was the joint hottest on record (Turner et al., 2021). Further increases in the frequency of both moderate and extreme drought events in the UK is expected in the next 60 years (Rahiz, 2009) while the severity of 3-, 6-, 12- and 36-month long droughts is also projected to intensify (Hanlon et al., 2021).

Despite both these historic and predicted future changes to UK drought frequency and severity, to date much of the work examining the resistance and resilience of key forest tree species to drought and the efficacy of management practices in mitigating drought impacts has been conducted in continental Europe or North America. As a result, this research has often focused on those species of greatest importance in those regions. In the UK, the combination of the predominantly maritime UK climate and moist soils has seen *Picea sitchensis* become established as the dominant timber species across much of the UK (particularly in the west and north) where its accounts for more than 51% of all standing conifers (Forestry Commission, 2018), however this species is not widely grown elsewhere in Europe. As a result, very few studies have attempted to quantify the impact of drought on *P. sitchensis* and to our knowledge, no study has yet looked at the resistance or resilience of UK grown trees of this species to historic drought events. This knowledge gap is a concern, as drought induced tree mortality and impacts on timber quality have been document in *P. sitchensis* growing in Scotland (Green et al., 2008) and *P. sitchensis* is considered to be less tolerant than *P. abies* (Savill, 2013), a species which has suffered extensively from recent extreme droughts elsewhere in Europe (Boden et al., 2014; Obladen et al., 2021; Van Der Maaten-Theunissen et al., 2013).

The second most abundant conifer in the UK is *P. sylvestris* (Forestry Commission, 2018), and while this species has been the focus of much drought resilience research in recent years (Martínez-Vilalta et al., 2012; Sohn et al., 2016; Steckel et al., 2020; Taeger et al., 2013), to date none of these studies have focused on the historic drought response of this species in the UK. Similarly, while the planting of both *P. sitchensis* and *P. sylvestris* in intimate mixtures has been shown to result in overyielding in the UK (Mason et al., 2021), whether mixtures of these two species are more resistant and/or resilient to drought than either species in monoculture remains untested. As a result, there is a clear and pressing need to establish the drought resilience of these two species in both mixed and monospecific stands under UK conditions if we are to understand the risks posed by climate change for these two economically important species and develop effective management strategies to mitigate any future drought impacts.

This thesis aims to address these knowledge gaps by assessing the resistance and resilience of both monospecific and mixed-species stands of *P. sitchensis* and *P. sylvestris* to a range of historic drought events in the UK. Specifically, I aim to develop an understanding of how tolerant UK grown *P. sylvestris* monocultures are to drought at different stand densities, whether any thresholds of drought severity exist in this species, beyond which impacts on tree growth are detectable, whether patterns of resistance, recovery and resilience are consistent at multiple stem heights and whether any shifts in the tree dominance are associated with extreme drought. Following the development of a new methodological approach that aims to overcome several limitations of how resilience is commonly calculated using dendrochronological datasets, I look for any evidence of compensatory growth that facilitates the recovery of lost basal area after tree growth recovery has occurred. I then investigate how *P. sylvestris* and *P. sitchensis* respond to a spring drought event in intimate mixtures relative to monospecific stands of the same species at the same experimental site to establish if there is any evidence of greater resistance, resilience, or recovery in mixed vs monospecific stands of these two species. Finally, using a 26-site dendrochronological dataset of *P. sitchensis* monocultures, I build a comprehensive understanding of the resistance, resilience, and recovery dynamics of this species to historic drought by investigating whether the different aspects of the drought event (intensity, duration etc.) are linked to drought resilience, and whether there is any evidence of compensatory mechanisms in *P. sitchensis*. I conclude by setting the results of this work in the wider context and suggest areas for future research.

1.7. References

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CHAPTER 2 - Life after recovery: Increased resolution of forest resilience assessment sheds new light on post-drought compensatory growth and recovery dynamics

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2.1. Abstract

Understanding the impacts of extreme drought on forest productivity requires a comprehensive assessment of tree and forest resilience. However, current approaches to quantifying resilience limit our understanding of forest response dynamics, recovery trajectories and drought legacies by constraining the temporal scale and resolution of assessment. We compared individual tree growth histories with growth forecasted using dynamic regression at an annual resolution, allowing drought impact and individual tree and stand level recovery dynamics to be assessed relative to a scenario where no drought occurred. The novel application of this approach allowed us to quantify the cumulative impact of drought legacy on radial growth at multiple stem heights at different stand densities. We show that the choice of pre- and post-drought periods over which resilience is assessed can lead to systematic bias in both estimates and interpretations of resilience indices. In contrast, measuring growth resilience annually revealed clear non-linearities in tree and stand recovery trajectories. Furthermore, we demonstrate that the influence of pre-drought attributes such as tree size, growth rates and stand densities on growth resilience were only detectable at certain stages of recovery. Importantly, we show that the legacy of drought on tree growth can become positive for some individuals, extending up to nine years after the event such that post-recovery growth can result in the reclamation of some lost tree and stand basal area. We demonstrate the importance of increasing the temporal scale and resolution of forest resilience assessment in order to understand both patterns and drivers of drought recovery. We highlight the shortcomings of collapsing growth response into a single average value and show how drought legacy can persist into a post-recovery phase, even positively impacting the growth of some trees. If unaccounted for, this post-recovery growth phase can lead to an underestimation of resilience and an overestimation of above ground losses in productivity, highlighting the importance of considering longer-term drought legacies and compensatory growth on basal area.

2.2. Introduction

Drought-linked losses in forest productivity are now being documented globally (Allen et al., 2010, 2015; Xu et al., 2019). The impact of extreme drought events and other facets of global change on forest systems has direct implications for forest dynamics and ecosystem continuity (Anderegg et al., 2013; Martínez-Vilalta & Lloret, 2016; McDowell et al., 2020) and influences atmospheric feedbacks through reductions in forest carbon stocks and future sequestration potential (Bennett et al., 2015). With extreme drought events expected to increase in both frequency and severity (Szejner et al., 2020), concerns surrounding forest vulnerability to such events (Allen et al., 2015) has seen the application of resilience concepts in forest science become increasingly popular (Nikinmaa et al., 2020).

Our understanding of both ecosystem resilience to extreme drought and losses of net primary productivity (NPP) as a result of these extreme events is intimately linked to both the temporal and spatial scales of assessment. Assessing the resilience of individual trees annually enables the comparison of recovery trajectories between trees, their differential contribution to the stand level response and an estimation of the *time* taken for each tree (and thus the stand collectively) to reach a reference state. Collectively, a fine temporal and spatial scale of assessment could provide much needed insight into the recovery dynamics of the wider forest system.

Understanding when and how a forest recovers following extreme drought has implications for forest management, modelling forest carbon dynamics and our understanding of the structural and functional processes that confer resilience. Forest managers will increasingly depend on knowledge as to which species mixtures (Thurm et al., 2016; Vitali et al., 2017, 2018), stand structures or silvicultural prescriptions (Chmura et al., 2011; Drever et al., 2006; Sohn et al., 2016) are best suited to building resilience and adaptive capacity to deal with the projected increases in frequency and intensity of extreme drought events (Dai, 2013).

Altering tree density or size class distributions is a key mechanism by which the structure of existing forests can be modified to adapt to changing conditions (Jump et al., 2017; Sohn et al., 2016), with the expectation that a lower stand density can increase the water availability for remaining trees and reduce drought stress (Manrique-Alba et al., 2020). Deciding on an optimal stand density, silvicultural prescription or selecting which trees to retain is however complex. A growing body of work is highlighting how the effectiveness of forest management in mitigating the negative effects of drought is contingent on the interplay between the timing and intensity of interventions, stand age, elevation, soil conditions, tree size and species (Gazol et al., 2017; Kerhoulas et al., 2013; Martínez-Vilalta et al., 2012; Seidl et al., 2017; Sohn et al., 2016). As a result, understanding the behaviour of individual trees, their collective contribution to the stand and factors that pre-dispose poor drought performance will be crucial to effectively manage and manipulate stand structure to increase future resilience.

Many assessments of forest resilience to drought focus on measuring the ability of a forest to return to a previous average growth rate and assume the climate driving growth is unchanged (Gazol et al., 2017; Lloret et al., 2011). This view implicitly assumes that the pre-disturbance state is the desirable state to which a system should return and fails to account for how climatically favourable to growth pre- or post-drought years were. As a result, pre-drought growth may not be the most suitable benchmark against which resilience or recovery is assessed, since we may erroneously infer that recovery has or has not occurred and systematically under- or overestimate the true loss of radial growth.

To better quantify the total impact of a particular drought event it is preferable to estimate the cumulative loss of growth over time relative to a scenario where that drought was absent. While rarely quantified in studies of forest resilience (*cf.* Thurm et al., 2016), the loss of basal area (BA) as a direct result of drought is of clear relevance to both forest managers and in modelling carbon dynamics, since it is a direct measure of the cumulative impact of lost radial growth and above ground productivity.

The spatial scale at which resilience is assessed can also influence both our understanding of drought resilience and measures of drought legacy. Hoffmann et al., (2018) showed an increase in resilience with stem height for *Picea abies*, but a decrease or no change with stem height for four other gymnosperms from different genera (*Thuja, Tsuga, Cryptomeria* and *Metasequoia*). Similarly, the magnitude and direction of these changes in resilience with stem height varied between species (Hoffmann et al., 2018). These findings question how representative tree cores collected at breast height (and the indices derived from them) are of whole-tree drought response. Similarly, individual trees can show considerable variability in drought response, with larger trees tending to be more negatively impacted by drought in terms of both growth and mortality (Bennett et al., 2015; Stovall et al., 2019) while faster growing trees sometimes suffer a greater immediate growth impact than their slower growing conspecific neighbours (Martínez-Vilalta et al., 2012). These studies indicate that patterns in growth resilience, drought impact and divergent patters of recovery at the tree level hold key information needed to explain contrasting patterns in drought resilience observed at the stand scale. Similarly, these studies suggest that the pre-drought attributes of individual trees and the stand collectively can be good predictors of drought performance and recovery such that important detail is lost when the temporal resolution of assessment is too coarse or the timescale too short.

Using *Pinus sylvestris* tree-ring chronologies, we compare methods and test for biases in a common approach to calculating forest resilience to an extreme drought event. Then, using dynamic regression to capture individual tree climate-growth relationships and growth histories, we forecasted annual growth rates at three different stem heights and two stand densities for nine years after this same extreme drought event to simulate a scenario where no drought had occurred. We modified the resilience index proposed by Lloret et al., (2011) to calculate growth resilience annually as well as quantifying growth and size deficits over these nine years to test the following hypotheses:

1) Given the differences in resilience with stem height documented in other coniferous species (Hoffmann et al., 2018), we hypothesise that resilience will change with stem height in *Pinus sylvestris*.
2) Patterns in growth resilience over time at the stand level will be due to the disproportionate influence of some trees on stand recovery.
3) Faster growing, larger and more densely spaced trees will show lower growth resilience relative to slower growing, smaller, and lower density trees under extreme drought throughout the post-drought period.

2.3. Materials and Methods

2.3.1. Site description and management history

This research was conducted in a monospecific spacing experiment of *Pinus sylvestris* established in 1935 on a relatively sheltered site in the north-east of Scotland (57° 36′ 23″ N, 4° 16′ 50″ W). The site sits at an elevation of 170m a.s.l with an average slope of 5 degrees. A surface water gley is the dominant soil type throughout and mean annual rainfall over the study period (1961 – 2002) is 851mm, with November being the wettest month on average.

Two spacing treatments were used in the present study representing high (ρ_H) and low (ρ_L) density stands. At the time of sampling (2002-2003), these plots were stocked at 1047 live trees per hectare (ρ_H) and 647 live trees per hectare (ρ_L). Some pruning was carried out in the 1950's and 1960's but no thinning or other management has been carried out during the life of the stand.

2.3.2. Dendrochronological data

34 trees from each of the two treatments (ρ_H and ρ_L) were felled in 2002-2003 and cross-sectional discs were taken along the length of each tree approximately every metre. These discs were digitised and all disc images within ± 30cm from 0.3, 1.3m and 3.3m high were selected from both ρ_H and ρ_L for use in the present study. This approach ensured that measurements were consistently taken from a similar stem height, whilst allowing for some variation in the precise location of each disc (e.g., due to the location of branch whorls). As a result of these criteria, not all trees are represented at all three stem heights.

Annual ring widths were measured using two separate radii from each scanned disc image using WinDENDRO image analysis software (Regents Instruments, Quebec). Both radii were averaged to give a mean annual radial increment for each disc and each chronology was subsequently crossdated following the leave-one-out principle on overlapping segments using the *dplR* package (Bunn et al., 2019) to ensure each ring was accurately dated. Raw ring width (RW) data were then converted into individual tree annual basal area increments (BAI) (**Figure S2.1**) following **Eq. 2.1,**

Eq. 2.1

$$BAI = \pi(R_t^2 - R_{t-1}^2)$$

where *R* is the radius of the tree in year *t*. BAI was used instead of raw ring widths as it better represents annual tree growth than linear measures such as ring width (Biondi & Queaan, 2008) and was required for calculations of both growth and size deficit.

Basal area (BA) was then calculated annually for each tree as the cumulative sum of BAI records up to and including each year as a measure of annual tree size. Crossdating and the conversion of raw ring width data into BAI for each disc was conducted using *dplR* package (Bunn et al., 2019) using R version 3.6.1 (R Core Team, 2019).

2.3.3. Extreme drought year identification

We calculated both the Standardized Precipitation Evapotranspiration Index (SPEI) (Vicente-Serrano et al., 2010) for August using a six-month integration window ($SPEI_{Aug6}$) and the Climatic Water Deficit (CWD) over the study period (1961 – 2002) to identify any extreme drought events in the climate record. CWD was calculated monthly using a Thornthwaite-type water-balance model following (Lutz et al., 2010) as the difference between Potential Evapotranspiration (PET) and Actual Evapotranspiration (AET) using code developed by (Redmond, 2019). Interpolated climate data at 1km resolution, obtained from the Climate Hydrology and Ecology Research Support System (CHESS) meteorology dataset for Great Britain (Robinson et al., 2017) for the study period (1961 – 2002) was used for both SPEI and CWD. Both drought indices were used since the reliance on SPEI as the only drought index has been shown to occasionally misclassify drought conditions (Zang et al., 2019). More negative SPEI values indicate progressively more severe drought conditions, with extreme droughts commonly considered to be at an SPEI threshold of < -2 (Hoffmann et al., 2018; Vanhellemont et al., 2018), which was also the threshold adopted here. To identify extreme drought years using CWD values, we summed monthly CWD values over 12 months (Jan – Dec) every year. Only 1984 was classified by SPEI as an extreme drought year while the CWD analysis confirmed this year showed the largest CWD across years in the study period. 1984 also corresponds to a period of growth depression in the tree-ring record at all disc heights in both treatments (**Figure S2.1**). As such the 1984 drought year was selected for further analysis in the present study.

2.3.4. Climate variables

To include climate variables that correlate strongly with radial growth in *P. sylvestris* (Jyske et al., 2014; Misi et al., 2019) as both predictors in dynamic regression models and when forecasting BAI values in a no-drought scenario, we calculated total precipitation and growing degree days above 5°C (gdd) annually from 1961- 1993 using 1km resolution interpolated climate data (Met Office et al., 2019). Annual precipitation ($Precip_{sum}$) was calculated by summing daily precipitation across the whole year while gdd was calculated for each year using temperature data from Jan – Sept (273 days) in the *pollen* package in R (Nowosad, 2019) following **Eq. 2.2**,

Eq. 2.2

$$gdd = \sum_{i=j}^{273} (T_i - 5), \quad if \quad T_i > 5$$

where annual gdd is the sum of the positive differences between daily mean air temperature (T_i) with a threshold value of +5°C from Jan – Sept (273 days). We chose *gdd* as it has previously been used to effectively study the onset and duration of tracheid production in *P. sylvestris* (Jyske et al., 2014), with 5°C frequently used as a *gdd* threshold in this species (Jyske et al., 2014; Seo et al., 2008). We included late winter temperatures (Jan-Feb) in the calculation of gdd as it has been found to be positively correlated with ring width in previous studies of *P. sylvestris* in Scotland (Grace & Norton, 1990), though its inclusion had a minimal effect on final gdd values. Equally, we chose to include all of September in calculating gdd to accommodate for the extended growing season and duration of tracheid development at our more southerly study site than documented in *P. sylvestris* at more northern latitudes (Jyske et al., 2014).

2.3.5. Dynamic regression analysis and BAI forecasting

Focusing on the 1984 extreme drought year, we fitted dynamic regression models to each chronology at each stem height in both density treatments from 1961 – 1983 (the year before the 1984 drought) following **Eq. 2.3**,

Eq. 2.3

$$BAI_t = \beta_0 + \beta_1 Precip_{sum_{1,t}} + \beta_2 gdd_{2,t} + \beta_3 SPEI_{Aug6_{3,t}} + \eta_t$$

where BAI_t is the annual BAI at time t, β_0 is the overall intercept, $Precip_{sum}$, gdd and $SPEI_{Aug6}$ are climate predictors at time *t*, and the errors from the regression, η_t are modelled as an autoregressive integrated moving average (ARIMA) *p, d, q* process (where *p, d* and *q* represent the auto-regressive order, the degree of differencing and the moving average order, respectively). The multiple regression part of the model captures each chronology's relationship between growth and climate prior to the 1984 drought event. The ARIMA part of the model accounts for each chronology's unique short-term time series dynamics, with each forecasted value incorporating lagged values of the dependant variable (or its forecasted values) as well as lagged model errors (to the order of *p* and *q* respectively). As such, dynamic regression combines exogenous predictors with the history of the time series in a single model (Hyndman & Athanasopoulos, 2018).

For each chronology at each stem height in both density treatments a large number of possible *p, d, q* values were calculated to identify the best fitting ARIMA model for the regression errors. The number of differences (*d*) to achieve stationarity of the data was calculated using a KPSS test (Hyndman & Athanasopoulos, 2018), while optimal *p* and *q* values were chosen by minimising the AICc values. To ensure the maximum number of possible ARIMA models were fitted and the minimum AICc value was found, both approximation parameters and the use of stepwise procedures were relaxed. For each chronology's best fitting dynamic regression model, we checked that the residuals were normally distributed and that the ARIMA errors were free of autocorrelation by plotting an autocorrelation function (ACF), resulting in the successful fitting of individual dynamic regression models to 120 chronologies.

For 1984 (the drought year), values for all three climate variables ($Percip_{sum}$, gdd and $SPEI_{Aug6}$) were replaced by their average values for the period between 1961-1983, thus replacing the observed extreme climate values in 1984 with average climate values. The mean 1984 values for these three climate variables and the observed annual values for these same variables from 1985-1993 were then used in conjunction with each chronology's individually fitted dynamic regression model to forecast annual BAI values (BAI_{for}) and 95% confidence intervals for each year between 1984 - 1993 in a scenario where no drought had occurred (**Figures S2.2–S2.7**). Forecasted BAI values for each tree were then plotted and visually sense checked. We chose to forecast BAI for nine years following the 1984 drought to avoid the influence of any conditions immediately preceding 1995, the next (though less severe) drought identified in the climate record.

Each chronology's BA in 1983 was calculated by summing all observed annual BAI values up to and including 1983. Forecasted annual BAI values were then added to the same chronology's BA in 1983 to calculate the forecasted annual basal area (BA_{for}) of each chronology at all three stem heights in both treatments. As such BAI_{for} and BA_{for} represent individual tree annual growth and size, respectively in a scenario where the extreme drought of 1984 had never occurred but was instead a climatically average year. All dynamic regression modelling and forecasting was carried out using the *forecast* package in R (Hyndman et al., 2020).

2.3.6. Pre- and post-drought average growth resilience

Resilience (*Rs*) assessment, as proposed by Lloret et al., (2011), compares a pre-drought growth average with a post drought growth average following **Eq. 2.4**,

Eq. 2.4

$$\text{Resilience } (Rs) = \frac{Post_{Dr}}{Pre_{Dr}}$$

where Pre_{Dr} and $Post_{Dr}$ are the average pre- and post-drought growth rates (respectively), calculated using the same number of pre- or post- drought years. We refer to the size of this period over which growth is averaged as an integration period throughout the remainder of this text. The same number of pre-drought and post-drought years were always used to calculate the respective averages for an integration period. To assess the influence of the size of the chosen integration period on our interpretation of resilience, we calculated resilience for all three stem heights in both density treatments for 2, 3, 4, 5 and 6 year integration periods following **Eq. 2.4** using the *PointRes* package (van der Maaten-Theunissen et al., 2015) to reflect a range of integration periods commonly chosen in studies of forest resilience.

To investigate differences in *Rs* between integration periods, we used *lme4* (Bates et al., 2015) to fit a linear mixed effects model following **Eq. 2.5**,

Eq. 2.5

$$Rs_{ij} = X_{ij}\beta + b0_i + b1_i X_{ij} + \varepsilon_{ij}$$

Where Rs_{ij} is the resilience for the *j*th measure of the *i*th tree, X is an *n* x *p* matrix of fixed effect variables, including integration period, stem height and stand density, β is a *p* x *1* column vector of regression estimates, $b0_i$ represents the random effect of tree, where $b0_i$ ~ $N(0,\sigma^2_0)$ and the random slope is $b1_i$ ~ $N(0,\sigma^2_1)$. We used log transformed *Rs* values as this improved model fit. The most parsimonious model was selected using *pbkrtest* (Halekoh & Højsgaard, 2014), dropping stand density as a non-significant fixed effect ($p > 0.05$). The final model fit integration period and stem height as fixed effects and tree ID and integration period as random effects. Significance values were obtained from model output using the *lmerTest* package (Kuznetsova et al., 2017).

2.3.7. Growth resilience

We combined the growth rates forecasted using dynamic regression with the observed growth rates at an annual scale to calculate resilience. In doing so we quantified resilience of both individual trees and average stand response for growth resilience (*Gr*) (the ability to return to forecasted growth rates) using **Eq. 2.6**. For *Gr*, we modified the resilience calculation introduced by Lloret et al., (2011) by replacing the pre-drought growth average with the forecasted growth rate (BAI_{for}) in a given year,

Eq. 2.6

$$\text{Growth resilience } (Gr) = \frac{BAI_{obs}}{BAI_{for}}$$

where BAI_{obs} is the observed basal area increment in a given year, BAI_{for} is the forecasted basal area increment for that same year. We calculated *Gr* for 1984 and then annually for the following 9 years (1985 – 1993) for each chronology individually and on average at all three stem heights in both treatments.

We subsequently fit mixed-effect models using *nlme* (Pinheiro et al., 2020) to investigate the change in *Gr* over time and assess the importance of stand density (ρ_H and ρ_L), stem height (0.3m, 1.3m or 3.3m) and individual tree pre-drought growth rate (BAI_{1983}) and size (BA_{1983}) for the year preceding the extreme drought of 1984. We used *nlme* over *lme4* for this analysis as it allowed us to fit a correlation structure. Both pre-drought growth rate and size were standardised to have a mean of zero and a SD of one to ensure estimated coefficients were on the same scale, while *Gr* was log transformed to improve both the normality of the residuals and satisfy model assumptions. To account for the non-linearity in *Gr* over time, we first identified the optimal number of degrees of freedom to fit natural cubic splines to year using AIC values. The optimal autocorrelation structures were also determined using AIC values and log likelihood ratio tests. The correlation structure for *Gr* was modelled using a corARMA correlation structure set to $p=1$, $q=1$ and four degrees of freedom were specified for the natural splines fit to year. Initially, BAI_{1983}, BA_{1983}, stem height and stand density were fit as fixed effects along with their interaction with year/time. As all interactions were significant ($p < 0.05$), the final model was fit following **Eq. 2.7**,

Eq. 2.7

$$Gr_{ij} = X_{ij}\beta + b0_i + \varepsilon_{ij}$$

Where Gr_{ij} is the growth resilience for the *j*th measure of the *i*th tree, X is an *n* x *p* matrix of fixed effect variables, including *year* fit using natural cubic splines with four degrees of freedom, *stem height*, *stand density*, BAI_{1983} and BA_{1983}, with retained significant interactions ($p < 0.05$) between all fixed effects and *year*, β is a *p* x *1* column vector of regression estimates, $b0_i$ represents the random effect of *tree*, where b0i ~ N $(0,\sigma^2_0)$ and ε represents error term, where ε_i ~ N (0, σ2). No residual autocorrelation was detected using ACF plots. Adjusted marginal means and unadjusted 95% confidence intervals were obtained using the R package *emmeans* (Lenth, 2016) and comparisons for retained interactions made using the *'contrast'* function to assess effects at the annual scale. As pre-drought growth and size are continuous variables, the effect of BAI_{1983} and BA_{1983} was compared in *emmeans* annually using quantiles.

2.3.8. Annual size and growth deficit

To fully capture both growth and size recovery trajectories, we calculated the annual (BAI) and cumulative (BA) loss of radial increment for individual trees and summed across all trees at each stem height in both treatments by subtracting forecasted from observed values every year between 1984-1993. The year in which an individual tree achieved the forecasted annual growth rate (BAI), or size (BA) was considered to represent the year in which a given tree fully recovered to a growth rate or size expected in a scenario where no drought had occurred i.e., complete recovery. We also forecasted annual ring width index values for all trees at 0.3m in both ρ_H and ρ_L using the same ring width data detrended using a cubic smoothing spline with a 30-year cut off. We then used these forecasted values to calculate tree and stand level annual size and growth deficits in the same way as for the BAI data to ensure our results derived from BAI values were robust.

2.4. Results

2.4.1. Growth Resilience

Mixed-model results comparing *Rs* calculated over different integration periods indicates a significant linear increase in *Rs* with the size of the integration period ($p = < 0.001$) (**Figure 2.1** and **Table 2.1**). Stem height showed a significant ($p = 0.023$) but weak negative relationship with *Rs*, indicating *Rs* decreases with increasing stem height (**Table 2.1**).

Table 2.1 *- Mixed-effects model output for resilience values calculated using different numbers of pre- and post-drought years (integration periods = 2, 3, 4, 5 and 6 years) at three different stem heights (0.3m, 1.3m and 3.3m) for trees in both high (ρ_H) and low (ρ_L) density stands considered collectively.*

Fixed effect	**Estimate**	**Std. Error**	***df***	**t value**	**p-value**
(Intercept)	**-0.279**	**0.018**	**73.586**	**-15.800**	**<0.001**
Integration period	**0.044**	**0.003**	**61.962**	**14.833**	**<0.001**
Stem height	**-0.007**	**0.003**	**514.627**	**-2.287**	**0.023**

The analysis of growth resilience calculated annually using forecasted values shows a contrasting and more complex pattern in resilience over time than that observed using pre- and post-drought growth averages, with a clear non-linear pattern in *Gr* emerging for all stem heights in both high density (ρ_H) and low density (ρ_L) treatments (**Figure 2.1**). Mixed-effects model results that account for both this non-linearity and autocorrelation in annual values of *Gr* show significant interactions between year and stem height, stand density, BAI_{1983} and BA_{1983} (**Table 2.1**).

A comparison of the estimated marginal means for *Gr* at each year for stand density and for different quantiles of BAI_{1983} and BA_{1983} found that differences were only detectable at certain periods during drought recovery (**Figure S2.8**). Differences in *Gr* between trees based on pre-drought growth rate (BAI_{1983}) were only detected between 1985 and 1987 (the three years following drought), during which trees with higher BAI_{1983} showed significantly higher *Gr* (**Figure S2.8a**). Similarly, higher density stands (ρ_H) showed greater *Gr* than lower density stands (ρ_L), but only between 1985-1986 (**Figure S2.8c**), corresponding to the two-year period of continued growth decline post-drought (**Figure 2.2–2.4**). In contrast, smaller trees (lower BA_{1983}) showed consistently higher Gr, from 1986 – 1993 (**Figure S2.8b**).

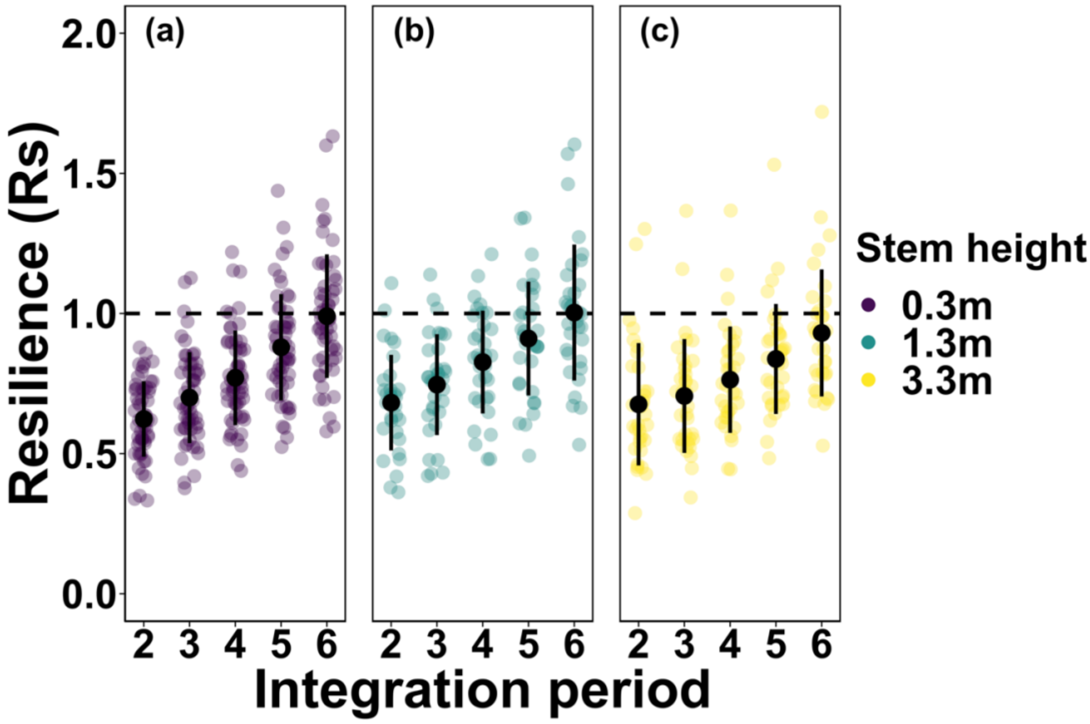

Figure 2.1 *Resilience values calculated using different numbers of pre- and post-drought years (integration periods = 2, 3, 4, 5 and 6 years) for three stem heights (a) = 0.3m with n = 56, (b) = 1.3m with n = 33 and (c) = 3.3m with n = 35, pooled across both high (ρ_H) and low (ρ_L) density treatments. The same number of pre- and post-drought years were used to calculate pre- and post-drought growth averages for each integration period. Each coloured dot represents a tree while black dots and lines represent the mean resilience value ±1 SD respectively for each integration period. Individual points are displayed as 'jittered' (small amount out random variation added to the x axis values) to better discern individual data points.*

At the individual tree level, patterns in *Gr* trajectories show considerable differences in the time taken to recover, with some trees at all stem heights in both density treatments never achieving forecasted levels (**Figure 2.2**). Across all stem heights in both density treatments, full recovery occurred anywhere between one- and six-years post drought (**Figure 2.2**), however the majority of those trees that recovered to forecasted growth rates did so between three- and six-years post drought.

***Table 2.2** - Type 3 ANOVA summary of the mixed-effects model output for growth resilience (Gr) calculated annually for all stem heights and both density treatments (n = 120) and reported on the log transformed scale. Chisq = Wald Chi-square, df = degrees of free*

Fixed effect	**Chisq**	***df***	**p-value**
(Intercept)	**22.24**	**1**	**<0.001**
Year	**160.63**	**4**	**<0.001**
Stem height	3.00	2	0.224
Plot	3.28	1	0.070
BA_{1983}	0.24	1	0.627
BAI_{1983}	2.78	1	0.095
Year × Stem height	**17.64**	**8**	**0.024**
Year × Stand density	**22.56**	**4**	**<0.000**
Year × BA_{1983}	**12.62**	**4**	**0.013**
Year × BAI_{1983}	**18.84**	**4**	**<0.001**

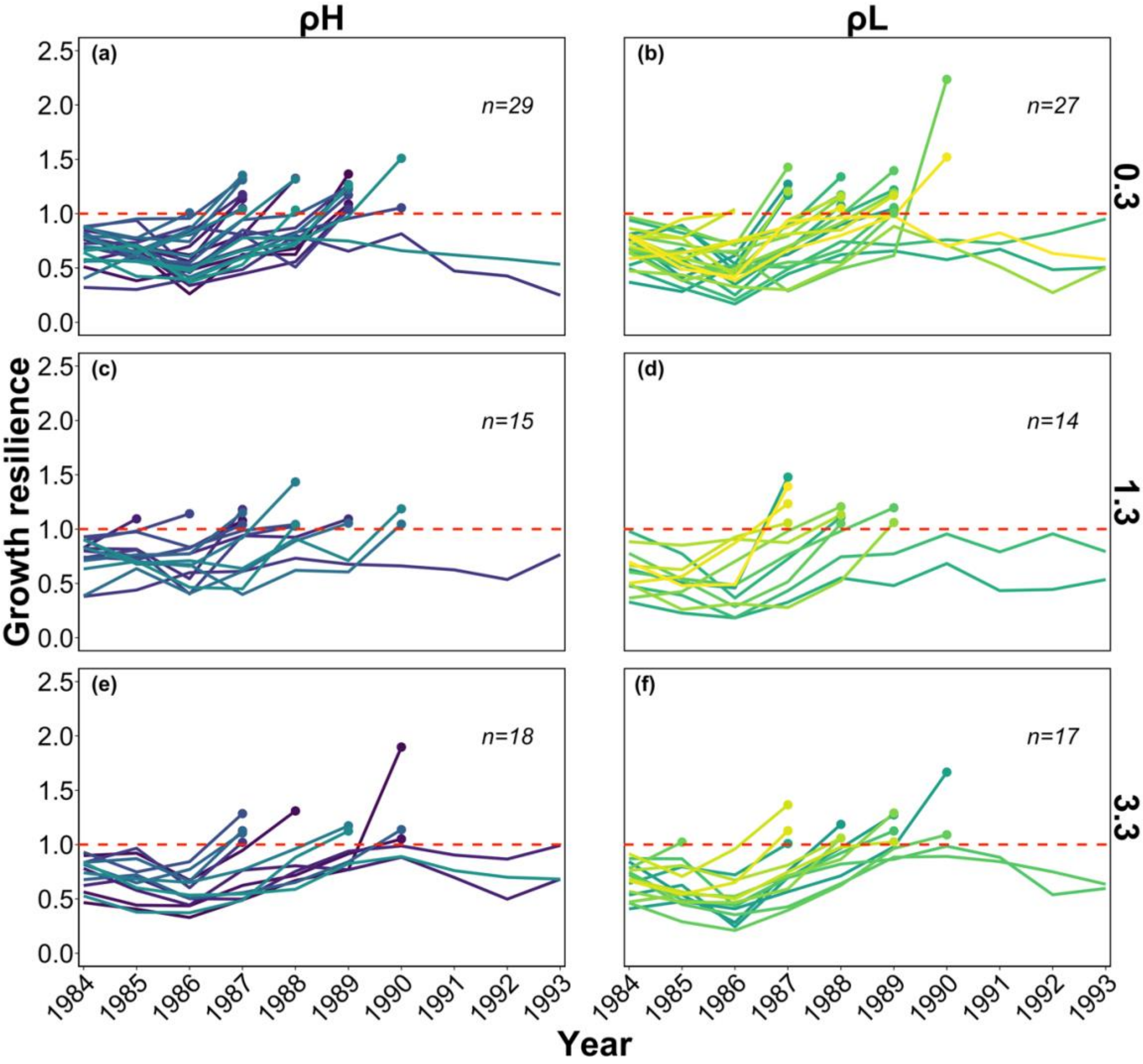

Figure 2.2 *- Individual tree annual growth resilience (Gr) values for (a, b) 0.3m, (c, d) 1.3m and (e, f) 3.3m stem heights in both high (ρ_H) and low (ρ_L) stand density treatments. Values >1 (above the red dashed line) indicate growth recovery has occurred (observed growth rates achieved forecasted values) while values < 1 (below the red dashed line) indicate a tree is still in growth recovery. Each line represents a different tree and points at the terminus of the same line correspond to the year in which that same tree reached forecasted growth rates. Gr values for years following growth recovery are not displayed.*

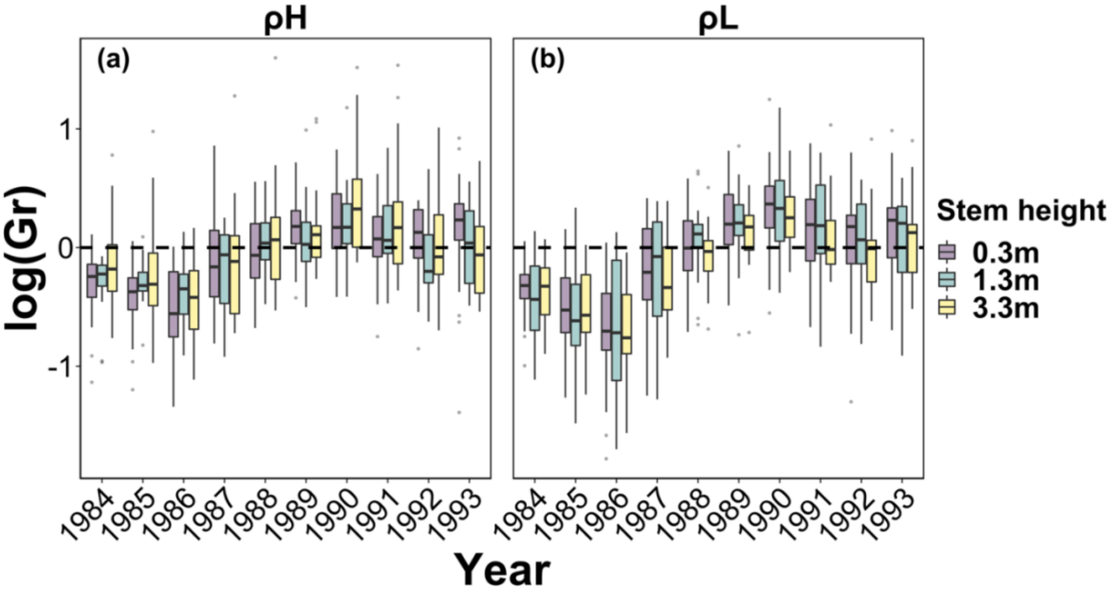

Figure 2.3 *- Box-plots showing median growth resilience (Gr) for (a) high density (ρ_H) and (b) low density (ρ_L) treatments for all three stem heights considered in this study (0.3m, 1.3m and 3.3m) calculated annually for the drought year (1984) and the subsequent 9 years (1985-1993). The dashed horizontal black line indicates whether growth recovered (above) or not (below), relative to forecasted values. Hinges show first and third quantiles while whiskers show largest and smallest values (excluding outliers) while outliers are indicated by points beyond the whiskers.*

2.4.2. Size and growth deficit

In terms of absolute loss of annual growth, all three stem heights in both density treatments showed a progressive growth decline in the two years following the 1984 drought, with the lowest annual growth record for all three stem heights in both treatments being 1986 with the exception of 1.3m in ρ_L which was marginally lower in 1985 (**Figure 2.4, Table S2.1**).

In 1987, summed annual growth rates for all trees in each treatment and at all three stem heights showed a large reversal of the progressive growth decline of the previous three years (the pattern of continued growth decline reversed, and growth recovery began) (**Figure 2.4**). Despite a reversal of the continued decline in growth performance, annual stand growth at each stem height and in both treatments continued to underperform relative to forecasted growth. As a result, the cumulative loss of basal area continued to decline into 1987 for 1.3m in both ρ_H and ρ_L, and into 1988 for all remaining stem heights in both treatments (**Figure 2.4, Table S2.1**).

By 1989 observed annual stand growth rates in both ρ_H and ρ_L were better than forecasted at all stem heights (**Figure 2.4** and **Table S2.1**)**.** This return to forecasted growth indicates that complete stand level growth recovery had effectively occurred by 1989, five years after drought. In subsequent years, stand growth rates at all stem heights and in both treatments continued exceeding forecasted growth rates which in turn resulted in a reversal and progressive reclamation of lost BA in the years following 1989 (**Figure 2.4**).

While growth recovery at all stem heights in both density treatments occurred at the stand level, full size recovery (that is, observed tree size achieving forecasted tree size in a no drought scenario) never occurred for any stem height in either treatment, despite the growth rate of many trees exceeding forecasted values. For 3.3m and 1.3m heights in both density treatments, observed annual growth for all trees collectively (summed) dropped back to values that were almost indistinguishable from forecasted values in 1992 and 1993, which in turn resulted in size recovery plateauing at below forecasted levels (**Figure 2.4**). In contrast, summed annual growth always remained above forecasted values at 0.3m in both density treatments from 1989 onwards. Of particular note is a clear apex in annual growth rate in 1990 for summed annual growth across all trees both collectively (**Figure 2.4**) and on average (**Figure 2.4**) relative to forecasted growth rates.

The observed patterns of summed annual growth and partial size recovery is the result of a stratification of individual growth performances in the years following drought and the disproportionate contribution to summed growth of overperforming individuals (**Figure 2.4**). Conversely, some trees never fully recovered to forecasted growth rates (**Figure 2.2**) or sufficiently overcompensated their growth to recover lost BA (**Figure 2.4**). On average, all three stem heights in both ρ_L and ρ_H no longer showed a negative growth resilience by 1989 (**Figure 2.3**), indicating that by 1989, median tree size was no longer different from a scenario where the 1984 drought had never occurred.

The general pattern of a progressively severe growth depression (and thus decreasing resilience) in the years following the 1984 drought (**Figures 2.2** and **2.3**), followed by an overcompensation of growth (**Figure 2.4**), is also clear from the mean BAI values for each stem height in both treatments (**Figure S2.1**). The observed patterns and timing of both growth and size recovery trajectories were also observed using ring width data detrended using cubic smoothing spline with a 30-year cut off for all trees at 0.3m in both density treatments (**Figure S2.9**).

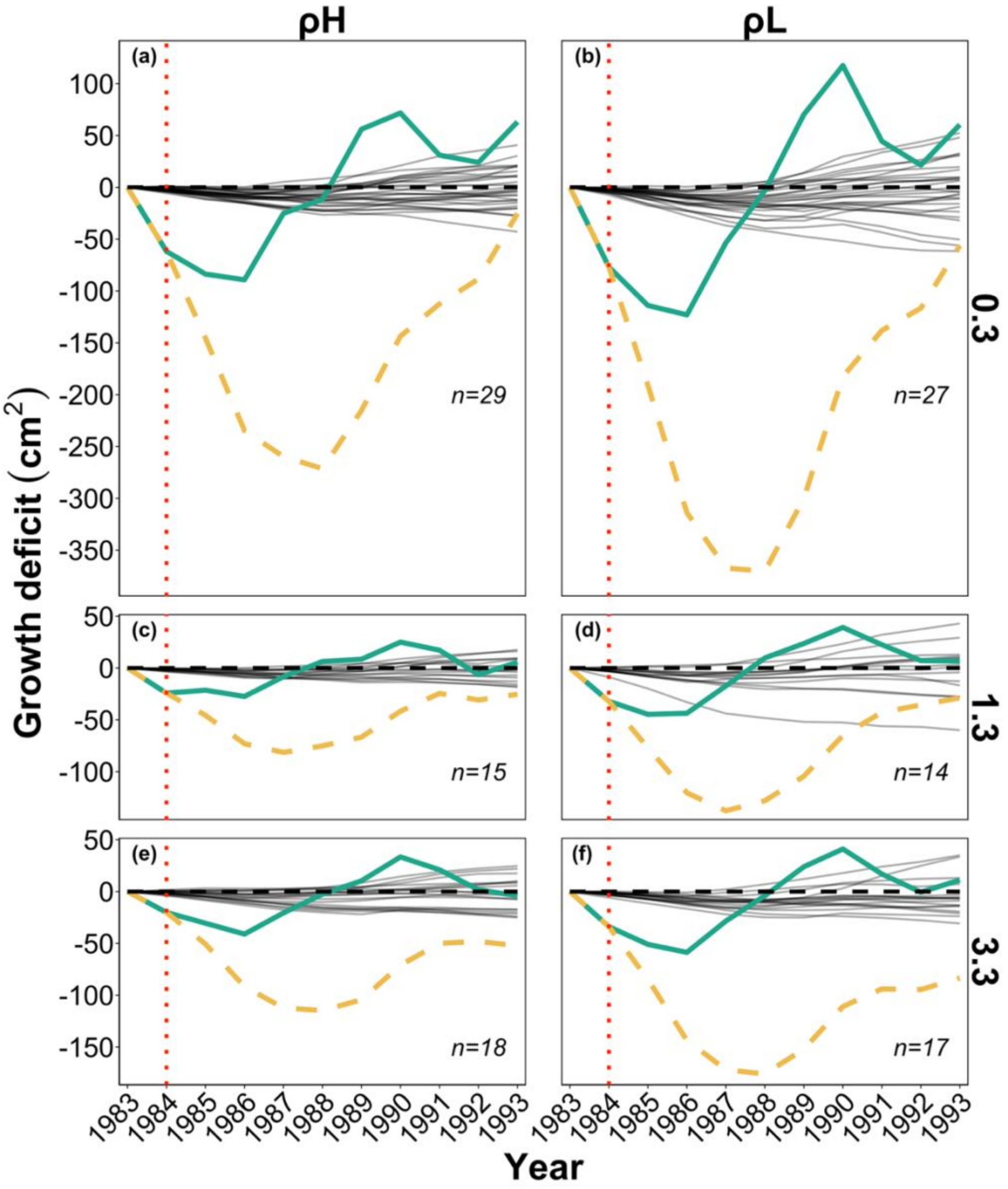

Figure 2.4 *- Growth deficit derived from the difference between observed and forecasted growth (BAI). Chronology level annual growth deficit summed over time, representing individual tree cumulative growth deficit at a given stem height (grey lines), stand annual deficit calculated by summing annual growth deficit for all chronologies at a given stem height in a given year (solid green line) and the cumulative stand growth deficit calculated annually by summing the annual stand deficit over time (dashed yellow line) in the high density (*ρ_H*) and low density (*ρ_L*) stands at 0.3m (a, b), 1.3m (c, d) and 3.3m (e, f) stem heights. Annual values were calculated for the drought year in 1984 (vertical dotted red line) and the subsequent 9 years (1985-1993) while n= the sample size for each stem height in the respective density treatment.*

2.5. Discussion

Using dynamic regression models to forecast both tree growth rates and sizes in a scenario where extreme drought was absent enabled us to estimate patterns of forest response to drought. Our approach ensured annual climate is explicitly accounted for in both the pre-drought and forecasted periods, capturing each chronology's historical relationship between climate and growth prior to the drought event, as well as the autocorrelated nature inherent in radial tree growth from year to year. In doing so, we identified that post-drought annual growth rates can recover or even exceed those that might have been expected if no drought had occurred. This pattern of compensatory growth in a post-recovery phase resulted in the reclamation of some of the lost BA at all stem heights in both high and low density stands. Equally, we showed how patterns in growth resilience at the stand level are the product of the temporal stratification of drought recovery at the level of individual trees, meaning assessments based purely on the average or stand level response (Huang et al., 2018) miss important variation and non-linearities in growth and size recovery dynamics. These non-linearities are only detectable when the temporal scale and resolution of assessment is over longer (up to nine years in this study) and finer (annually) timescales than commonly practiced (Bose et al., 2020; Gazol et al., 2017). By demonstrating how the importance of some stand attributes (e.g., stand density and pre-drought growth rates and sizes) on growth recovery dynamics varies depending on the point during the recovery period, we provide evidence that assessing forest resilience annually over an extended post-drought period can provide a more comprehensive understanding of forest response to drought whilst highlighting limitations in approaches that use pre- and post-drought growth averages.

2.5.1. The temporal frame of resilience assessment

The linear increase in resilience (*Rs*) with the size of the integration period used to calculate average growth can be explained by observing the pattern of growth recovery. In this study, two years post-drought (1986) is the point of lowest absolute annual growth, after which a period of progressive growth recovery begins. As resilience (*Rs*) is often calculated as the ratio of pre-drought and post-drought growth averages (Gazol et al., 2018), continually increasing the size of this post-drought integration period will inevitably be reflected by a corresponding increase in resilience. As we demonstrate, the choice of integration period risks systematically biasing the calculation of resilience since increasingly large integration periods result in increasingly high values of resilience at all stem heights, influencing both our interpretation and understanding drought response. Similarly, this property makes the comparability of resilience values difficult across study systems where the same integration period has not been used to calculate pre- and post-drought growth averages e.g. Merlin et al. (2015) and Serra-Maluquer et al. (2018). This change in resilience with the choice of pre- and post-drought period is in keeping with other recent work that highlights the limitations of considering only a single post-drought integration window (Schwarz et al., 2020). Instead, we advocate assessing resilience at an annual resolution (Anderegg et al., 2015; Huang et al., 2018; Kannenberg et al., 2019; Martínez-Vilalta et al., 2012) to retain important information regarding the temporal dynamics of forest drought response.

While mixed-model results indicate that *Gr* changes over time at all stem heights (**Table 2.2**), contrary to our hypothesis, there was no differences in *Gr* between stem heights at any point during drought recovery (**Figure 2.3** and **Figure S2.8d**). However, mechanisms allowing the targeted allocation of carbon below ground or above ground could indicate a decoupling of tree-ring signals from gross primary productivity (Kannenberg et al., 2019), which in turn should lead us to question how representative resilience indices based solely on radial growth are of whole tree resilience.

The observed non-linearities in *Gr* and drought legacy may be linked to post-drought alterations in carbon allocation strategy. Such alterations could occur at the expense of radial growth via the upregulation of photosynthesis (Kannenberg et al., 2019), the reparation and expansion of the canopy (Kannenberg et al., 2019) or roots and fungal hyphae (Børja et al., 2017). Such shifts in carbon allocation under drought have been documented in *P. sylvestris* (Fernández-De-Uña et al., 2017) and could lead to the continued decline in radial growth immediately after drought observed in this study.

Subsequent radial growth recovery may only then begin once the repair and expansion of roots and mycorrhizal networks and repair of foliage have been made, shifting allocation patterns back to compensate for losses in radial growth. Similarly, drought induced damage to xylem and hydraulic architecture (Adams et al., 2017) may conceivably lead to reductions in radial growth at the expense of metabolically costly repair. While the ecophysiological processes that drive these observed patterns were not the focus of this study, mechanisms that allow the preferential allocation of carbon (Hagedorn et al., 2016) could indicate a more plastic and adaptive plant response to drought than current indices based on radial growth imply and question current estimates of drought induced losses in biomass.

2.5.2. Overgrowth, size recovery and post-recovery dynamics

Stand-level growth recovery occurred around 4-5 years after drought, varying slightly with stem height and density treatment (**Figure 2.4**). However, individual trees were highly variable in the time taken to recover (**Figure 2.2**). Stand level recovery time is slightly longer than global averages of 1-4 years (Anderegg et al., 2015) but two years longer than reported in a similar study of *P. sylvestris* (Martínez-Vilalta et al., 2012). We continued to track annual growth performance relative to forecast growth rates up to nine years post-drought and identified a widespread pattern of 'overgrowth' i.e., growth that occurred in excess of that forecasted. While the year in which annual stand growth turned from a deficit to a surplus (indicating complete growth recovery) was relatively synchronous across stem heights and stand densities, the magnitude of stand overgrowth differed. This pattern of radial overgrowth for some trees in a post-recovery phase meant that all stem heights in both density treatments recovered a considerable portion of the BA lost in the years immediately following drought (relative to the forecasted no-drought scenario).

Patterns in *Gr* and overgrowth at the stand level were clearly the result of the disproportionate influence of individual trees in both density treatments at all stem heights, supporting our second hypothesis. The staggered return of individuals to forecasted growth rates (**Figure 2.2**) was reflected in the increasing stratification of individual tree performance over time (**Figure 2.4**). While most trees recovered to forecasted growth rates, some trees appeared to benefit from drought (being larger than forecasted in a no-drought scenario), particularly in the latter stages of the observed nine-year period, while others remained smaller than forecasted (**Figure 2.4**), the net effect of which resulted in the observed reclamation of some lost BA.

To our knowledge this is the first study to document such patterns of overgrowth and size recovery following extreme drought in mature trees by extending the temporal window and increasing the temporal resolution of assessment. While attempts to quantify the cumulative impact of drought on radial growth during the recovery period are uncommon (*c.f.* Thurm et al., 2016), we demonstrate the importance of considering post-recovery growth dynamics when measuring the totality of drought impact. As noted by Gessler et al. (2020), the existence of compensatory growth *i.e.* increased function post-drought relative to pre-drought, is widely acknowledged in other ecological systems but has received little attention in stress-ecological studies. Indeed, compensatory growth has been documented in fish (Álvarez, 2011; Won & Borski, 2013), moths (Kecko et al., 2017), grasses (Østrem et al., 2010) and recently in seedlings of *P. sylvestris* (Seidel et al., 2019). By constraining the period of resilience assessment to either a pre-defined post-drought period or to the point at which growth returns to a historic norm implicitly assumes this point is where drought legacy ends. However, our findings show that this assumption is not necessarily justified, with the legacy of drought extending far beyond a return to reference growth levels and even becoming positive for some trees.

By failing to document patterns in the recovery of lost BA, management decisions to increase overall forest resilience such as targeted tree removal or the selection of species for climate adaptation may be made prematurely on incomplete information. To illustrate this point using data from the present study, an assessment of the studied trees at a stem height of 0.3m in the lower density stand (ρ_L) (*n = 27*) three years after drought would indicate a cumulative loss of BA of 367 cm^2 (**Table S2.1**). However, the same assessment after nine years would indicate a much smaller loss in BA of only 56 cm^2 relative to forecasted values (**Table S2.1**). Thus, the severity of drought impact and choice of management designed to increase forest resilience depends on the post-drought period being considered. With a global push towards forest expansion to help deal with the challenges of a changing climate yet an increasing awareness of the associated risks and trade-offs (Anderegg et al., 2020; Doelman et al., 2020), decisions that are informed by the interplay between forest structure, drought resilience and the temporal dynamics of forest recovery will become increasingly important to ensure the continuity of forests ecosystems.

We caution that the patterns of overgrowth documented here are from a single experimental site and dependant on the accuracy of forecasted growth values. As such, the existence of patterns of overgrowth elsewhere needs to be established before wider conclusions can be drawn as to the importance or pervasiveness of such a mechanism. However, where extreme droughts are occurring with increasing frequency, intensity or duration, the presence of overgrowth in a post-recovery phase could itself become maladaptive by leaving trees more susceptible to future drought impacts, the concept of *structural overshoot* (Jump et al., 2017). As a result, we argue that understanding the longer-term temporal dynamics of both growth and size recovery are crucial but largely overlooked components in studies on forest resilience, with clear implications for estimates of both historic and future drought induced losses of above ground biomass.

2.5.3. Temporal dependency of structural drivers

By explicitly modelling the observed non-linearity in *Gr*, we were able to explore the temporal dynamics of drought impact and investigate whether stand attributes such as pre-drought size, growth rate or stand density were (dis)advantageous for *Gr* throughout recovery. Contrary to our third hypothesis, we found that there was no simple relationship between faster growing, larger or more densely spaced trees and *Gr*. When considered annually, the interaction between growth rates in the pre-drought year (BAI_{1983}) and time highlighted that trees growing faster prior to drought had significantly higher *Gr,* but only between 1985 and 1987 and not during the drought year itself (1984) or in the post-recovery phase. These results differ to those reported by Martínez-Vilalta et al., (2012) who noted faster pre-drought growth negatively impacted drought recovery in *P. sylvestris* for three years immediately following drought. However, in contrast to this present study, Martínez-Vilalta et al., (2012) did not include climate variables as predictors when estimating growth in this post-drought period, or consider post-drought timescales longer than three years.

Stand density and pre-drought tree size also showed clear temporal dependacies in their relationship with *Gr*, corresponding to particular phases of the post-drought period. Again, contrary to our expectations, the higher density stand showed significantly higher *Gr* than the lower density stand but only for two years, during the period of continued growth decline (1985 -1986). In contrast and as expected, larger trees did show consistently lower *Gr*, but only from 1986 onwards (once the continued growth decline reversed and recovery began) and not during the drought year itself. This latter result is in keeping with other work that found larger trees suffer more under drought (Bennett et al., 2015). The opposing positive and negative influence of pre-drought growth and stand density vs pre-drought size respectively, highlights the importance of not reducing stand structure down to a single metric (Forrester, 2019).

The positive or negative impact of pre-drought stand attributes on individual recovery trajectories may result in changes in the competitive or functional dominance of individual trees. The decoupling of size and growth means that some trees contribute disproportionately to stand growth relative to their size (West, 2018). As such, directional shifts in stand level growth rates will depend on how drought differentially impacts those trees that contribute more or less to stand growth. While not the focus of this study, persistent drought-induced shifts in functional dominance both within and between species have been documented previously (Cavin et al., 2013) and the persistance with which pre-drought growth impacted meausres of *Gr* documented here could indicate a shift or amplification in the competitive status of individuals. Our analysis highlights that not all trees contributed equally to stand level recovery. The divergence of recovery responses seems to show that those trees that recovered early became dominant in terms of growth and stayed dominant, while those that failed to recover settled into a new, lower-than-average growth regime.

As lower drought resilience is emerging as a good indicator of future mortality risk (DeSoto et al., 2020), lower historic resilience may be adapted in the future as a management tool to selectively remove susceptible trees and improve overall forest resilience. However, our results demonstrate that the importance of stand attributes that might be used to inform targeted tree removal to increase forest resilience (such as pre-drought tree growth rates, tree sizes or target stand densities) is temporally dependant. For example, in this study higher density stands were only found to be more resilient than lower density stands for two years (1986-1993), indicating that stand density was only important for increasing *Gr* for a small period of the overall recovery landscape. Consequently, we caution that if resilience concepts are to be successfully deployed to guide forest management, the selection of an appropriate temporal scale and resolution of resilience assessment will be key.

2.6. Conclusion

Growing concern as to the vulnerability of forests globally means a comprehensive understanding of forest response to drought is becoming increasingly important. Here we show that the temporal scale and resolution of approaches to assessing resilience are critical if we are to understand drought impact on stand growth and recovery dynamics. The application of dynamic regression to ecological questions using dendrochronological data demonstrated here is a promising approach to achieving such an increased understanding.

Notably, we identified the capacity of both tree and stand growth rates to return to, or even exceed those forecasted in a scenario where no drought occurred, a pattern that resulted in the partial reclamation of lost basal area. This process of overgrowth appears to be the product of the disproportionate influence of individual trees on stand level recovery. Higher pre-drought growth rates and stand density but lower pre-drought tree size is of clear importance for explaining patterns in growth resilience in our study, however the importance of these structural variables is temporally dependent, indicating more nuanced patterns of drought recovery than previous studies have suggested.

Future work should aim to investigate the roles of mortality and shifts in the competitive dominance of individual trees and their neighbourhoods to further understand the drivers of these temporally dependant patterns in stand behaviour. Similarly, investigating the pervasiveness of overgrowth, compensatory growth and the structural overshoot phenomenon in a post-recovery phase will be an important step in quantifying drought impact, with implications for both forest management targeted at increasing resilience, carbon budgeting and our understanding of drought legacy (Kannenberg et al., 2020).

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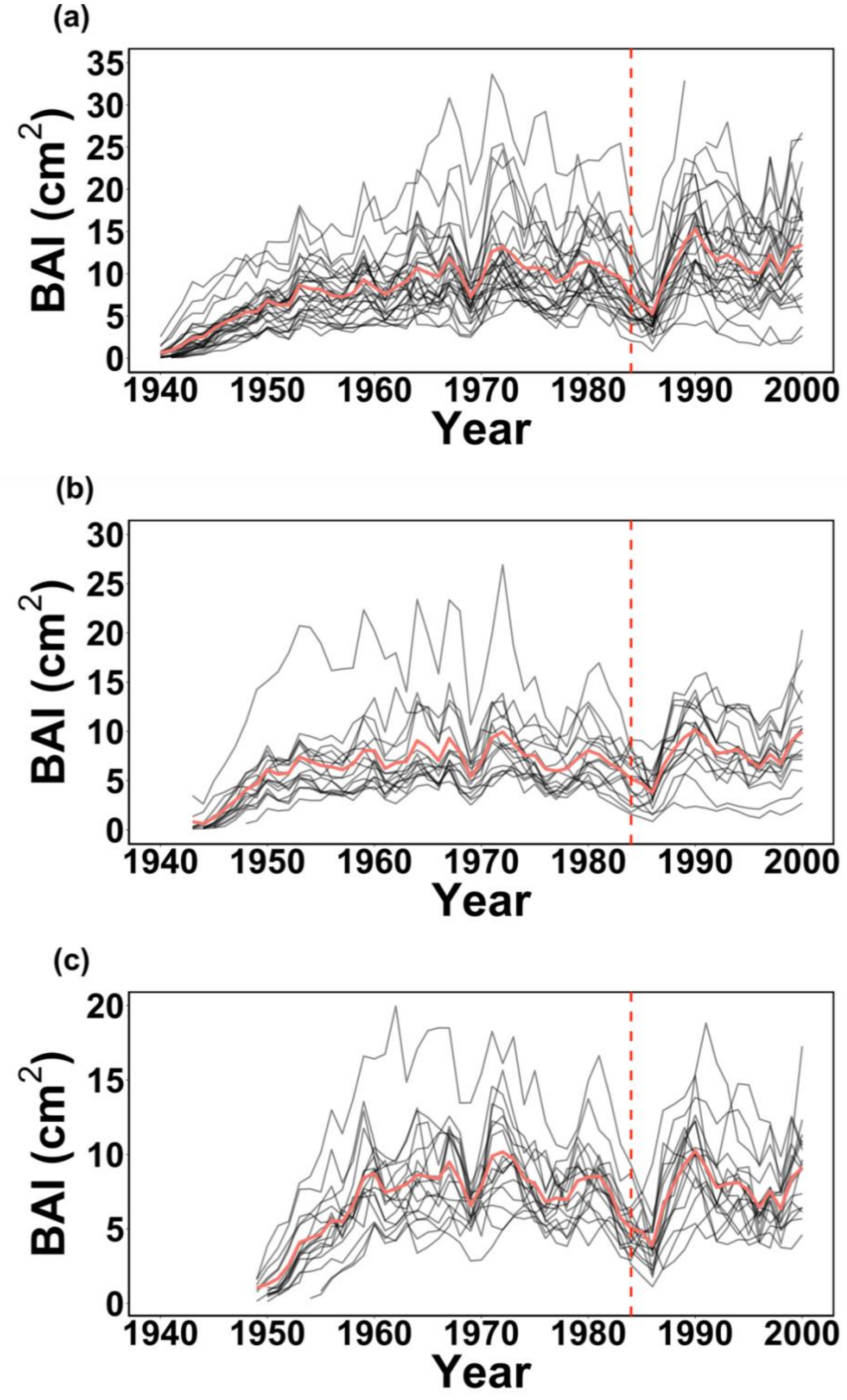
2.8. Supplementary Material



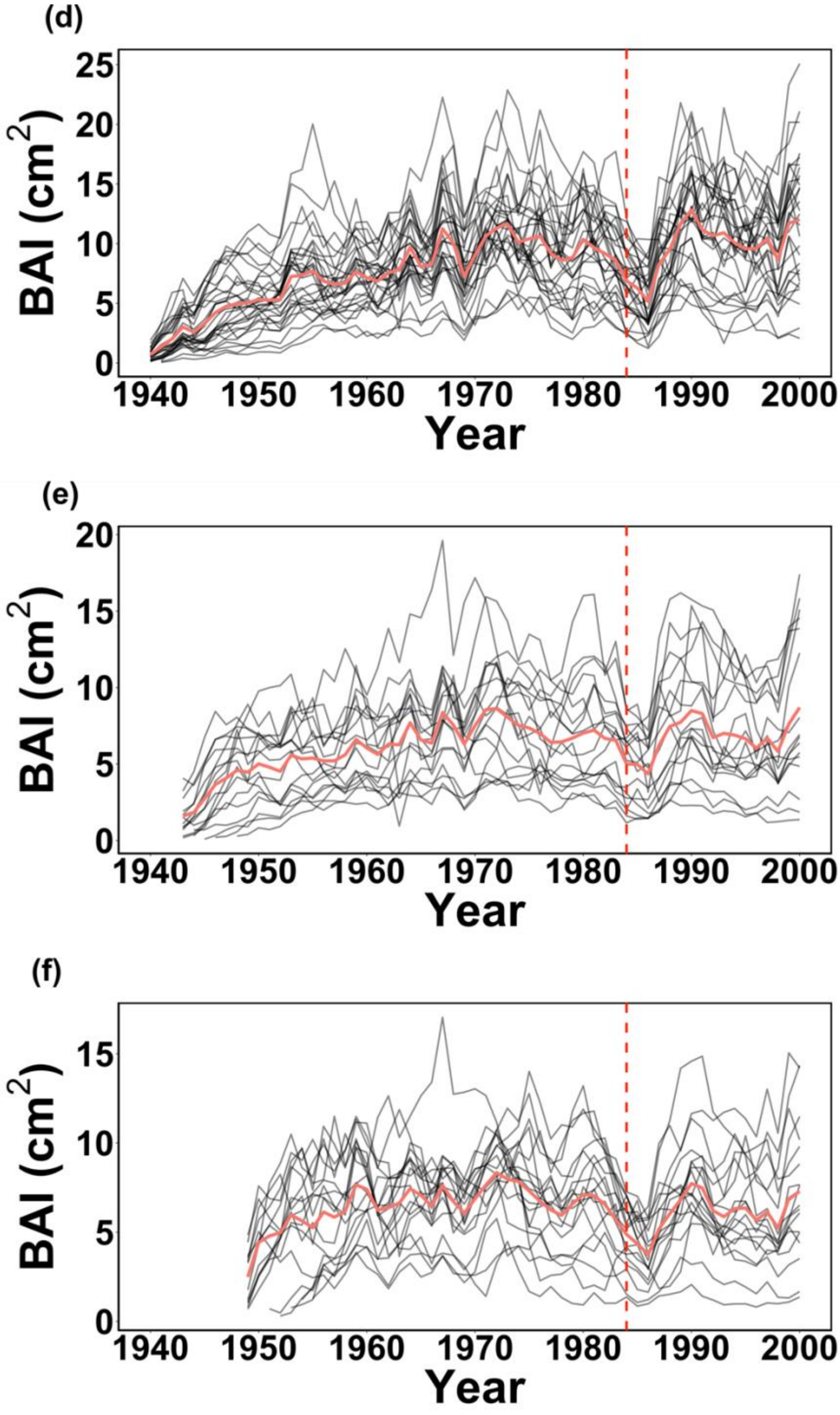


Figure S2.1 *- Individual tree (grey lines) and mean (solid red lines) annual basal area increments (BAI) for a) 0.3m, b) 1.3m and c) 3.3m in the lower density stand (ρ_L) and for d) 0.3m, e) 1.3m and f) 3.3m in the higher density stand (ρ_H). The vertical red dashed line marks the extreme drought year in 1984.*

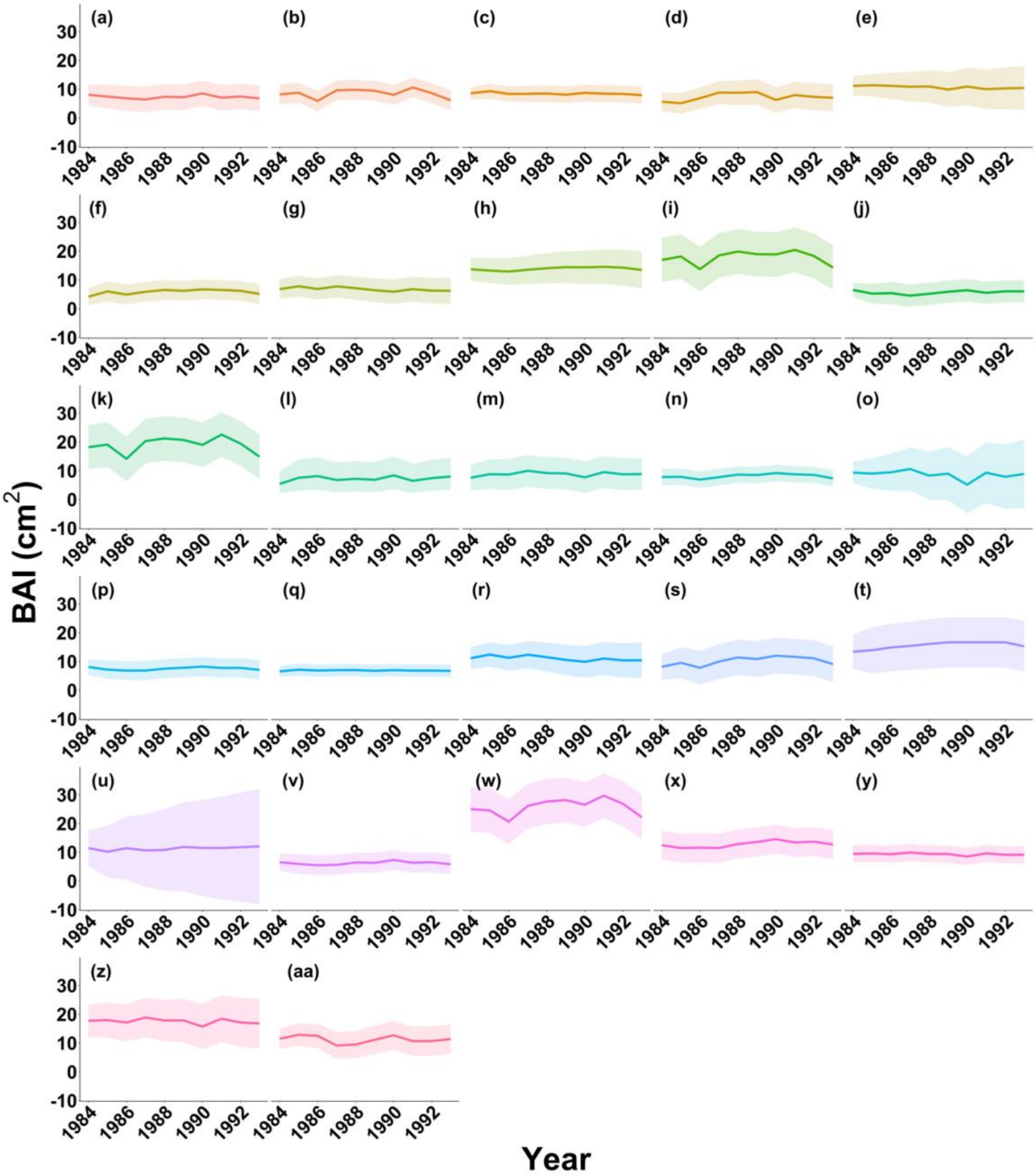


Figure S2.2 *- Individual tree (a – aa, n = 27) annual basal area increment (BAI) forecasts (solid lines) and corresponding 95% confidence intervals (shaded areas) for 1984 and the following nine years in a no-drought scenario at the 0.3m stem height in the low density (*ρ_L*) stand generated using the dynamic regression approach detailed in the main text.*

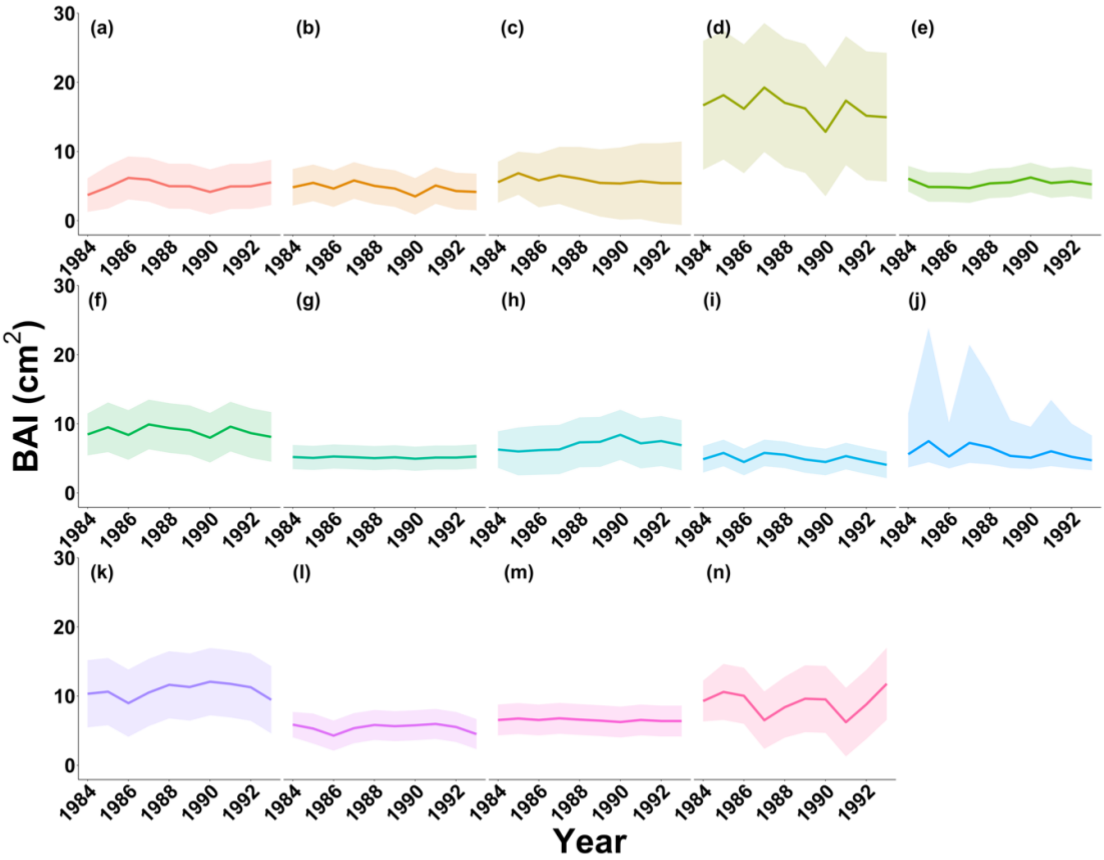


Figure S2.3 *- Individual tree (a – n, n = 14) annual basal area increment (BAI) forecasts and corresponding 95% confidence intervals (shaded areas) for 1984 and the following nine years in a no-drought scenario at the 1.3m stem height in the low density (ρ_L) stand generated using the dynamic regression approach detailed in the main text.*

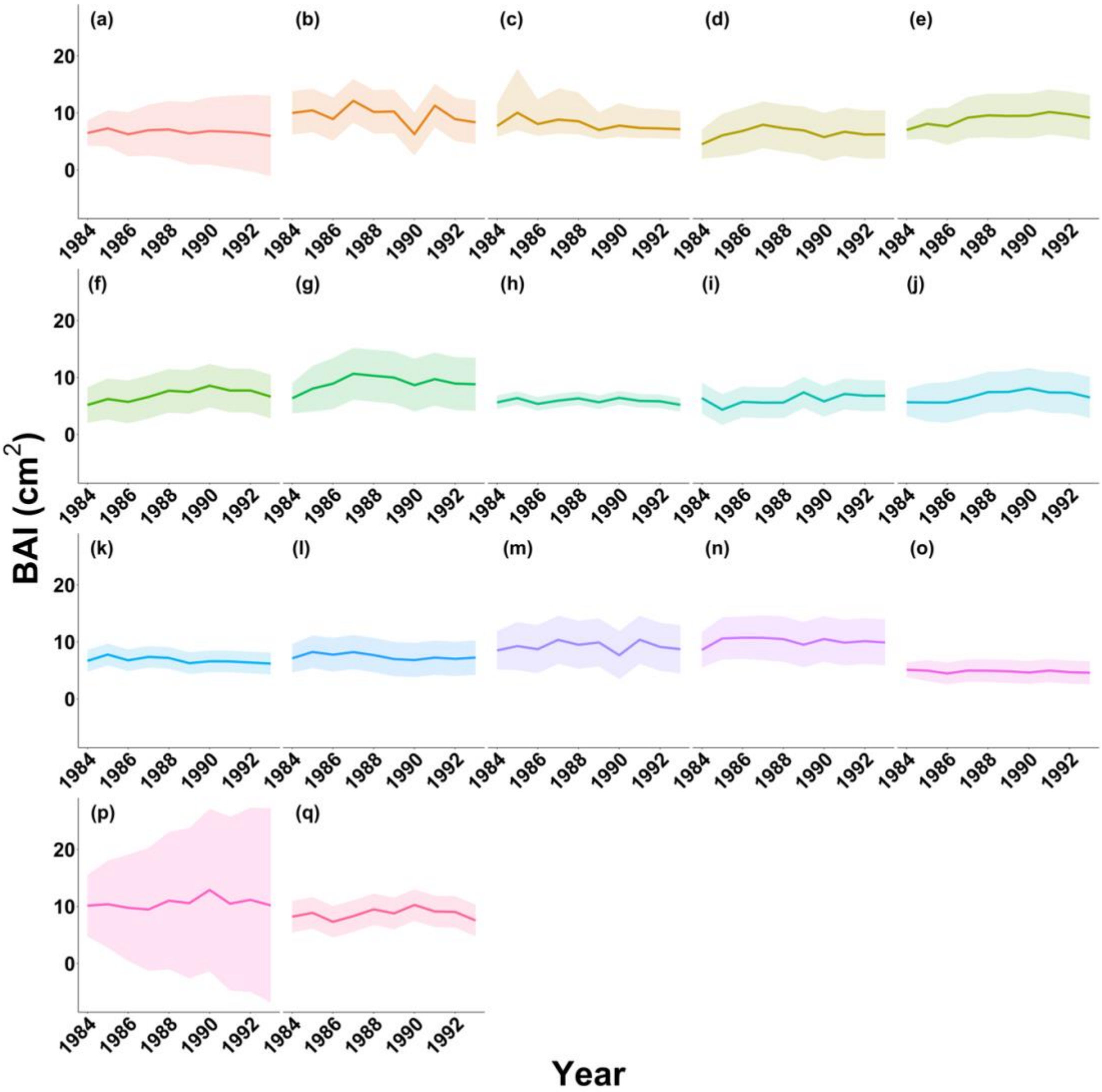


Figure S2.4 *- Individual tree (a – q, n = 17) annual basal area increment (BAI) forecasts (solid lines) and corresponding 95% confidence intervals (shaded areas) for 1984 and the following nine years in a no-drought scenario at the 3.3m stem height in the low density (ρL) stand generated using the dynamic regression approach detailed in the main text.*

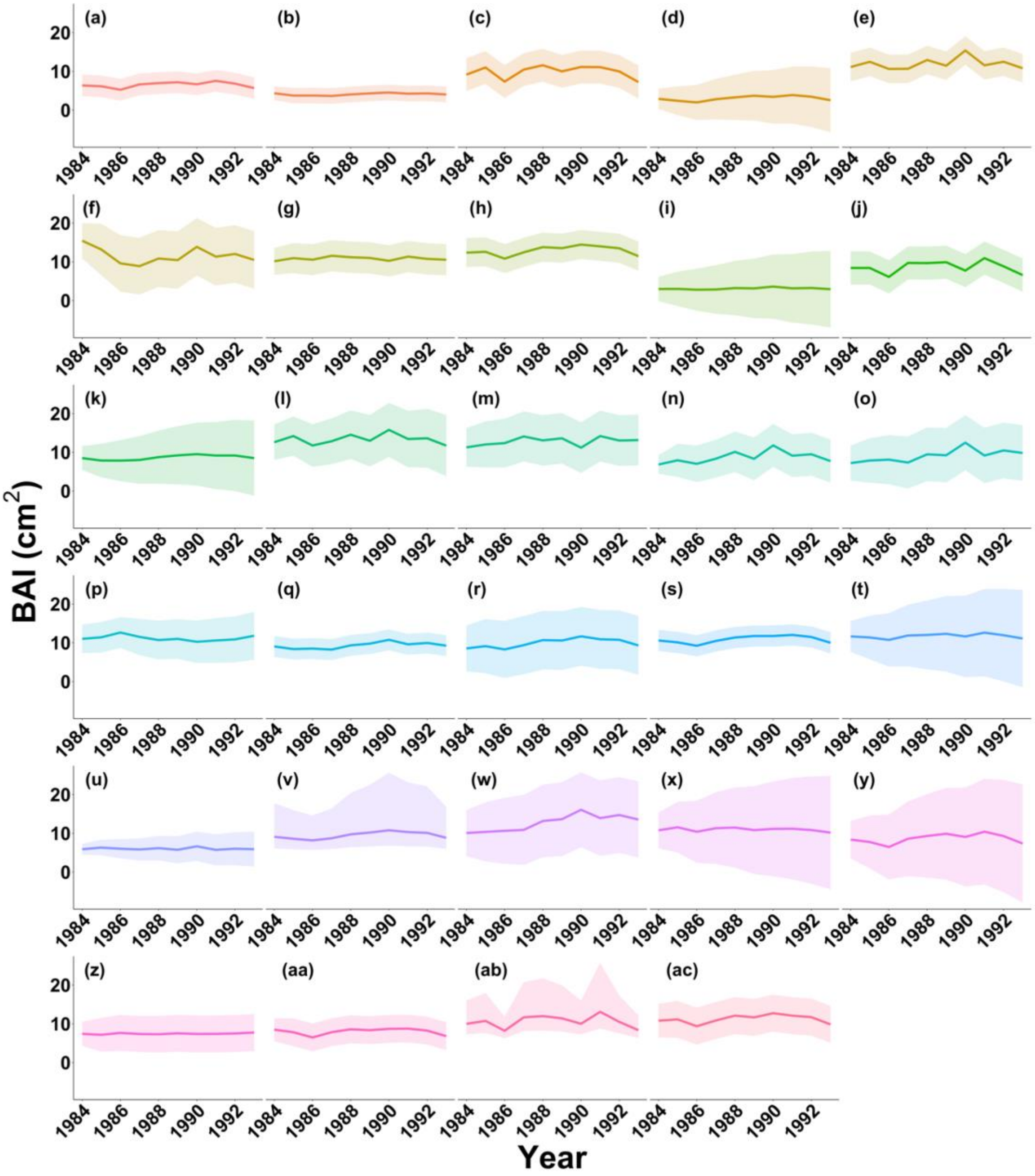


Figure S2.5 *- Individual tree (a – ac, n = 29) annual basal area increment (BAI) forecasts (solid lines) and corresponding 95% confidence intervals (shaded areas) for 1984 and the following nine years in a no-drought scenario at the 0.3m stem height in the high density (ρH) stand generated using the dynamic regression approach detailed in the main text.*

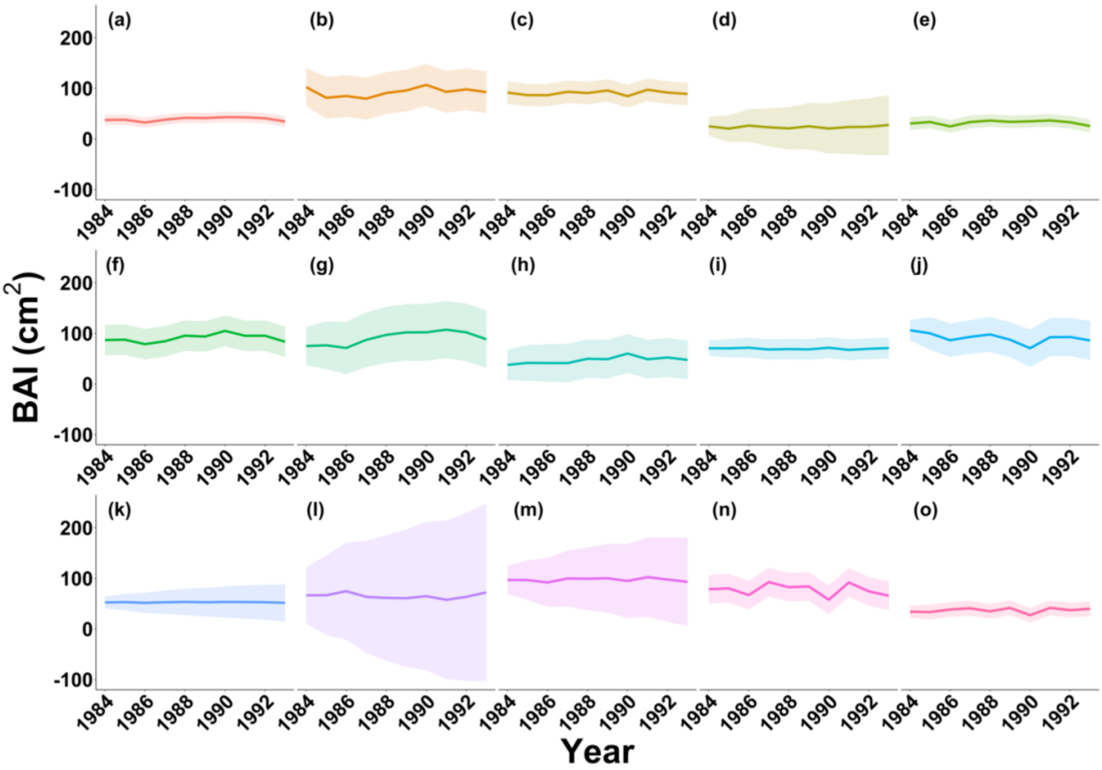


Figure S2.6 *- Individual tree (a – o, n = 15) annual basal area increment (BAI) forecasts (solid lines) and corresponding 95% confidence intervals (shaded areas) for 1984 and the following nine years in a no-drought scenario at the 1.3m stem height in the high density (ρH) stand generated using the dynamic regression approach detailed in the main text.*

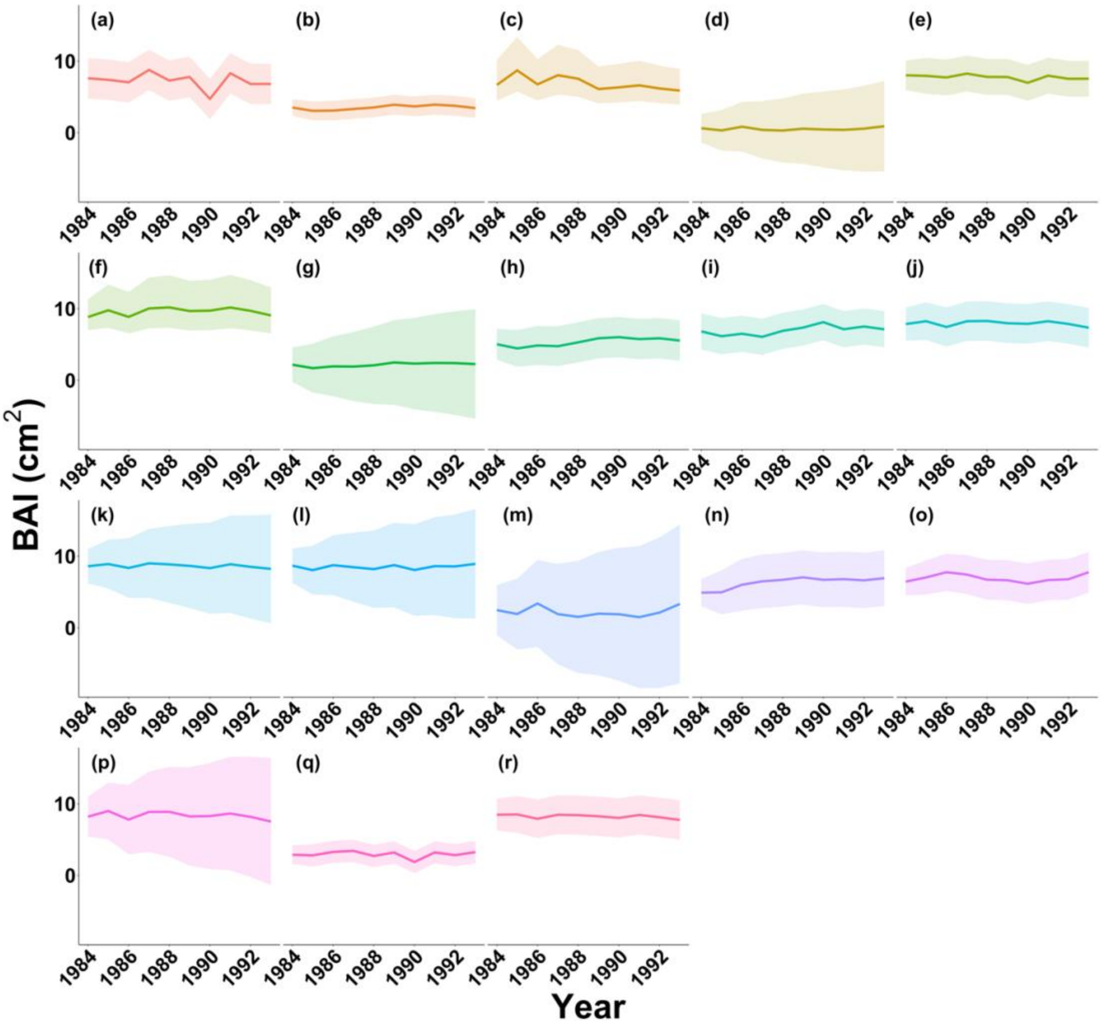


Figure S2.7 *- Individual tree (a – r, n = 18) annual basal area increment (BAI) forecasts (solid lines) and corresponding 95% confidence intervals (shaded areas) for 1984 and the following nine years in a no-drought scenario at the 1.3m stem height in the high density (ρ_H) stand generated using the dynamic regression approach detailed in the main text.*

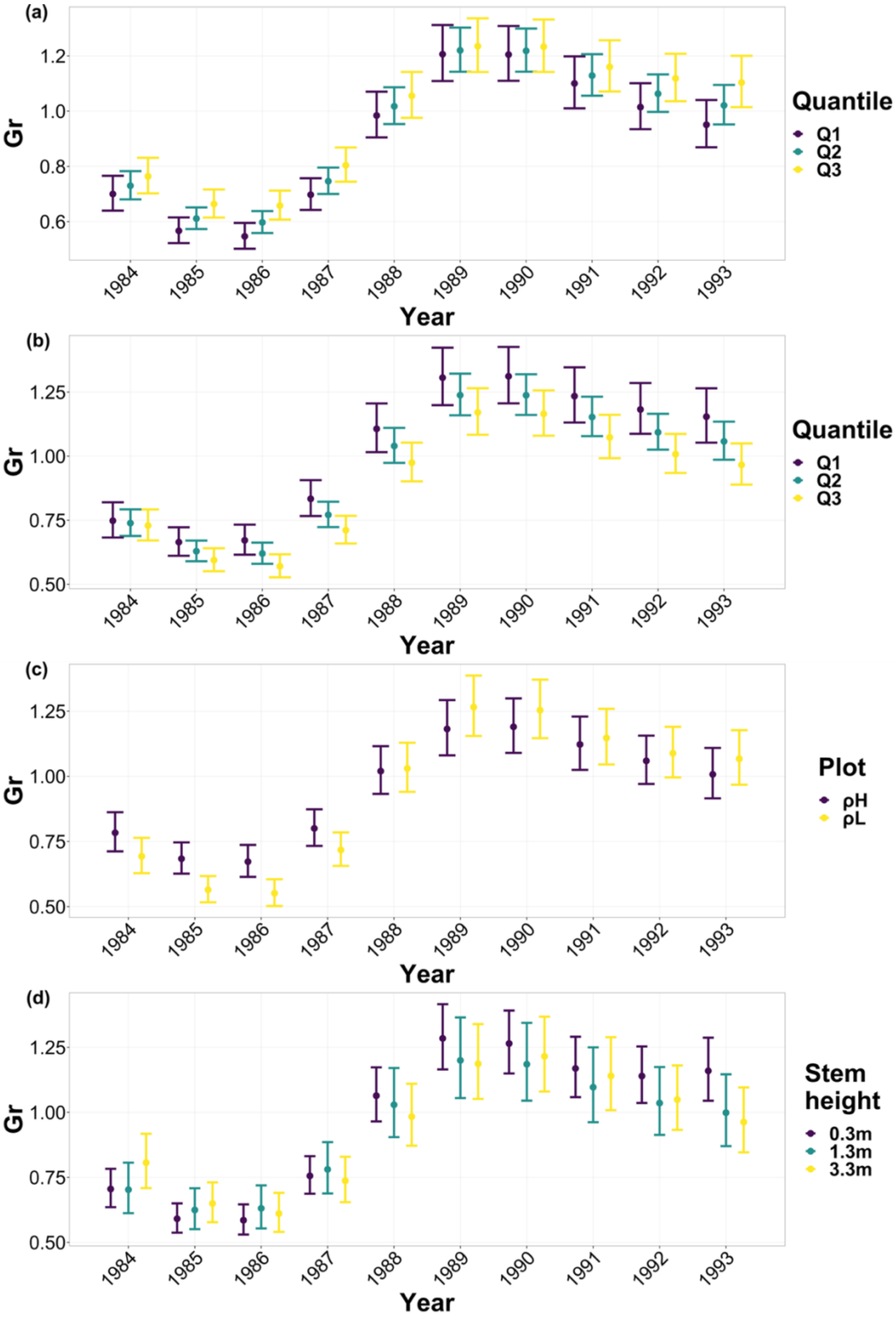

(a)
Gr
0.6
0.8
1.0
1.2
1984
1985
1986
1987
1988
1989
1990
1991
1992
1993
Year
Quantile
Q1
Q2
Q3
(b)
Gr
0.50
0.75
1.00
1.25
1984
1985
1986
1987
1988
1989
1990
1991
1992
1993
Year
Quantile
Q1
Q2
Q3
(c)
Gr
0.50
0.75
1.00
1.25
1984
1985
1986
1987
1988
1989
1990
1991
1992
1993
Year
Plot
ρH
ρL
(d)
Gr
0.50
0.75
1.00
1.25
1984
1985
1986
1987
1988
1989
1990
1991
1992
1993
Year
Stem height
0.3m
1.3m
3.3m

Figure S2.8 *- Emmeans comparison of the interactions between (a)* BAI_{1983} *(b)* BA_{1983}*, (c) high (*ρ_H*) and low (*ρ_L*) tree density and (d) stem height with year for growth resilience (Gr) from the mixed-model analysis to illustrate the temporal dependency of their importance. As* BAI_{1983} *and* BA_{1983} *are continuous variables, comparisons were made using quantiles of the data with thresholds set at 0.25, 0.5 and 0.75. Gr was back transformed and displayed here on the original scale. Error bars represent 95% unadjusted confidence intervals.*

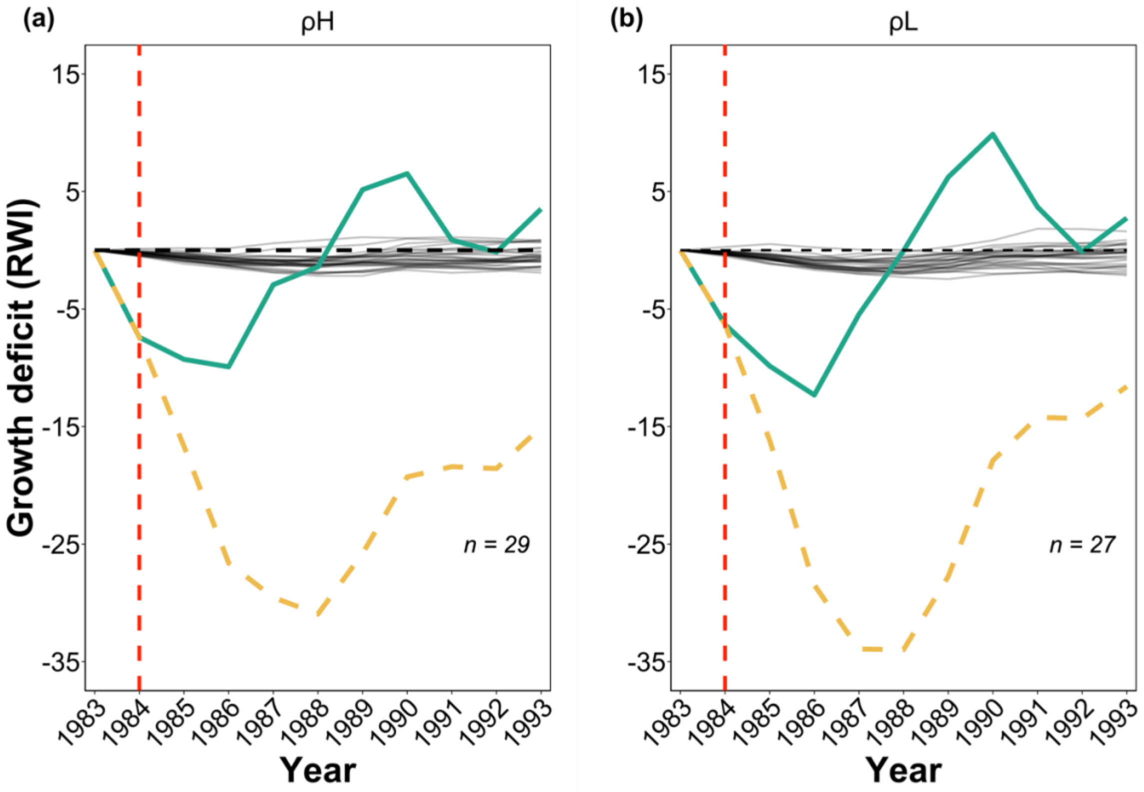


Figure S2.9 *- Growth deficit derived from the difference between observed and forecasted growth for tree ring chronologies that were detrended using a cubic smoothing spline with a 30-year cut-off, expressed in terms of a Ring-width Index (RWI). Individual dynamic regression models were fit to each chronology following the same methods outlined in the main text. Individual tree cumulative growth deficit (grey lines), stand annual deficit calculated by summing annual growth deficit for all chronologies in a given year (solid green line) and the cumulative stand growth deficit calculated annually by summing the annual stand deficit over time (dashed yellow line) in the high density (*ρ_H*) and low density (*ρ_L*) stands at a stem height of 0.3m. Annual values were calculated for the drought year in 1984 (vertical dotted red line) and the subsequent 9 years (1985-1993) while n= the sample size for each stem height in the respective density treatment.*

Table S2.1 *- Cumulative observed and forecasted growth and growth deficits calculated annually as the difference between forecasted and observed values for the high (*ρH*) and low (*ρL*) density stands for all three stem heights (0.3m, 1.3m and 3.3m).*

ρ_L 0.3m, $n = 27$

Year	Cumulative actual growth (cm^2)	Cumulative growth forecast (cm^2)	Annual growth deficit (cm^2 year^{-1})	Cumulative growth deficit (cm^2)
1983	9508	9508	0	0
1984	9711	9788	-77	-77
1985	9884	10075	-114	-191
1986	10027	10341	-123	-314
1987	10267	10634	-53	-367
1988	10565	10935	-3	-370
1989	10935	11235	70	-300
1990	11348	11530	117	-182
1991	11700	11838	44	-138
1992	12015	12132	21	-117
1993	12346	12402	60	-56

ρ_L 1.3m, $n = 14$

Year	Cumulative actual growth (cm^2)	Cumulative growth forecast (cm^2)	Annual growth deficit (cm^2 year^{-1})	Cumulative growth deficit (cm^2)
1983	3718	3718	0	0
1984	3785	3817	-32	-32
1985	3848	3924	-45	-77
1986	3901	4021	-44	-120
1987	3990	4127	-17	-138
1988	4104	4232	10	-128
1989	4229	4334	24	-104
1990	4365	4430	39	-65
1991	4490	4533	22	-43
1992	4596	4631	7	-36
1993	4699	4728	7	-29

ρ_L 3.3m, *n = 17*

Year	Cumulative actual growth (cm^2)	Cumulative growth forecast (cm^2)	Annual growth deficit (cm^2 $year^{-1}$)	Cumulative growth deficit (cm^2)
1983	4060	4060	0	0
1984	4146	4180	-34	-34
1985	4228	4312	-51	-85
1986	4293	4437	-59	-143
1987	4405	4577	-28	-172
1988	4541	4717	-4	-176
1989	4700	4852	24	-152
1990	4874	4985	41	-111
1991	5030	5124	17	-94
1992	5162	5256	-1	-95
1993	5298	5382	11	-83

ρ_H 0.3m, *n = 29*

Year	Cumulative actual growth (cm^2)	Cumulative growth forecast (cm^2)	Annual growth deficit (cm^2 $year^{-1}$)	Cumulative growth deficit (cm^2)
1983	9288	9288	0	0
1984	9488	9550	-62	-62
1985	9670	9816	-84	-145
1986	9820	10054	-89	-235
1987	10060	10319	-25	-260
1988	10335	10607	-12	-271
1989	10674	10890	56	-215
1990	11046	11190	72	-144
1991	11370	11483	31	-112
1992	11680	11768	24	-88
1993	11996	12021	63	-25

ρ_H 1.3m, *n = 15*

Year	Cumulative actual growth (cm^2)	Cumulative growth forecast(cm^2)	Annual growth deficit ($cm^2 year^{-1}$)	Cumulative growth deficit(cm^2)
1983	3651	3651	0	0
1984	3726	3751	-24	-24
1985	3802	3847	-21	-46
1986	3867	3940	-27	-73
1987	3958	4039	-8	-81
1988	4066	4141	6	-75
1989	4178	4244	8	-67
1990	4302	4344	25	-42
1991	4425	4449	17	-24
1992	4521	4552	-6	-31
1993	4623	4648	6	-25

ρ_H 3.3m, *n = 18*

Year	Cumulative actual growth (cm^2)	Cumulative growth forecast(cm^2)	Annual growth deficit ($cm^2 year^{-1}$)	Cumulative growth deficit (cm^2)
1983	4002	4002	0	0
1984	4090	4110	-20	-20
1985	4168	4219	-31	-51
1986	4236	4327	-41	-92
1987	4329	4441	-21	-112
1988	4438	4552	-3	-115
1989	4560	4665	10	-104
1990	4699	4770	33	-71
1991	4834	4884	21	-50
1992	4946	4994	2	-48
1993	5051	5104	-4	-52

CHAPTER 3 - Threshold response to extreme drought shifts inter-tree growth dominance in Pinus

Published in the journal Frontiers in Forests and Global Change:

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https://doi.org/10.3389/ffgc.2021.737342

3.1. Abstract

Many studies quantify short-term drought impact on tree growth relative to pre-drought growth averages. However, fewer studies examine the extent to which droughts of differing severity differentially impact tree growth or shape stand dynamics. Focusing on three droughts in high and low density stands of *Pinus sylvestris* in Scotland, we calculated pre-drought growth averages using climatically standardised antecedent growth years to assess tree level drought and post-drought growth performance as percentage growth change (PGC). We then used mixed-effects models to understand how droughts of differing severity impact tree growth and calculated indices of growth dominance (G_d), size inequality (S_i) and size asymmetry (S_a) to detect changes in stand structure. Mixed-effects model results indicate that the magnitude and duration of the growth reduction during and following the more extreme drought was significantly larger compared to less severe droughts, for which we found limited evidence of drought impact. While no changes in S_i or S_a were noted following any drought, we found evidence of a difference in G_d after the most extreme drought in both stand densities indicative of a threshold response, with smaller trees contributing proportionally more to stand growth relative to their size. Under less severe droughts, inter-tree variability may have partially buffered against stand-level growth change, however a small increase in drought severity was associated with a significant reduction in average tree growth, an increase in the number of trees growing at > 2SD

below pre-drought levels and a shift in G_d towards smaller trees, indicating that a drought severity threshold in *P. sylvestris* may have been exceeded.

3.2. Introduction

Climate change is expected to increase the frequency, intensity and duration of extreme drought events globally (Shukla et al., 2019). This predicted increase has resulted in growing concerns regarding the impacts of a hotter climate upon forest ecosystems (Allen et al., 2010, 2015; Anderegg et al., 2013) including negative impacts on tree growth (Anderegg et al., 2015), shifts in community composition (Suarez & Kitzberger, 2008) and the potential for large scale tree mortality (van Mantgem et al. 2009; Anderegg et al. 2019). As a result, recent work assessing forest vulnerability to drought and its association with particular functional traits (Anderegg et al., 2018; Greenwood et al., 2017; Li et al., 2020) and previous drought performance (Anderegg et al., 2020; DeSoto et al., 2020) has greatly improved our understanding of forest drought susceptibility.

Despite progress in identifying attributes that promote forest resistance and resilience to drought, the impact of drought on stand attributes has been less well documented. Recent evidence indicates that droughts can induce shifts in competitive dominance between species (Cavin et al., 2013), cause persistent shifts in species composition (Martínez-Vilalta & Lloret, 2016; Suarez & Kitzberger, 2008) and will likely lead to changes in forest dynamics under global change (McDowell et al., 2020). Similarly, increases in environmental stressors such as drought may potentially reshape species interactions away from competitive, towards more facilitative processes (He et al., 2013). These changes, coupled with the existence of non-linear threshold-type responses to increasing drought severity (Cavin et al. 2013; Bartlett et al. 2016; Adams et al. 2017, Stuart-Haëntjens et al. 2015) means that understanding how and when drought alters forest structure and function (Haber et al., 2020) is increasingly important. Equally, if we are to implement successful forest management to promote stand-level drought resilience (Sohn et al., 2016), it is essential that we understand the interplay between increasing drought severity, patterns in forest response and the location of thresholds across a range of species, environments and scales (Anderegg et al., 2015; Choat et al., 2012; Huang et al., 2015).

Assessments of short-term drought impacts indicate larger trees are commonly more susceptible to drought-induced growth decline (Bennett et al., 2015; Ding et al., 2017; Martínez-Vilalta et al., 2012) including in *P. sylvestris* (Merlin et al., 2015). However, this pattern is not universal, with basal area having been found to be positively associated with the drought resistance in Norway spruce (*Picea abies*) and silver fir (*Abie alba*) (Zang et al., 2014), while the importance of tree sizes on drought recovery can vary depending on the stage of recovery being considered (Ovenden et al., 2021). Similarly, exposure to historic drought may increase future tree vulnerability to extreme drought (Bose et al., 2020), particularly in *Pinaceae* (Anderegg et al., 2020) while lower historic drought resilience can increase future mortality risk (DeSoto et al., 2020). If larger, older trees do suffer more under drought, this may interact with successional processes, gap dynamics and growth release (Rubio-Cuadrado et al., 2018) to shift forests towards younger, smaller stands (McDowell et al., 2020) by favouring particular tree attributes (small, slow growing and younger trees) that confer drought resilience.

Characterising tree response to drought requires an understanding of the influence of pre-drought growth in priming drought year performance (Bose et al., 2020; Gessler et al., 2020; Hilker et al., 2016). While many indices of resistance and resilience exist in the literature (Ingrisch & Bahn, 2018), those introduced by Lloret et al. (2011), where pre-drought and post-drought growth averages are calculated over a pre-defined period (Gazol et al., 2018; Granda et al., 2018), have been widely applied in the forest sciences. While this approach has been instrumental in improving our understanding of the radial growth of trees both during and following drought, the *a priori* assumption that average growth, calculated from the years immediately preceding a drought accurately represents a ‘normal’ growth rate to which a tree should be expected to return risks omitting some of the climatic context within which a drought is occurring (Anderegg et al., 2015; Kannenberg et al., 2020; Ovenden et al., 2021).

The Standardised Precipitation Evapotranspiration Index (SPEI) (Vicente-Serrano et al., 2010) is widely used to identify drought events in the climate record (DeSoto et al., 2020; Gazol et al., 2018; Huang et al., 2015). Here, we use the SPEI to define a climatically-constrained pre-drought growth average. We then use this growth average to calculate the annual percentage growth change (PGC) during and after three droughts of differing severity for individual *Pinus sylvestris* trees growing at two different stand densities and quantify how many trees show a significant growth impact following each drought. Indices of growth dominance, size inequality and size asymmetry are then calculated annually to characterise stand behaviour before, during and after drought and combined with change point analysis to identify any drought-associated shifts in stand dynamics. This assessment enables us to address the following questions: (a) How are increases in drought severity associated with differences in growth response at the tree and stand levels? (b) Is drought associated with detectable and lasting changes in growth dominance and stand dynamics?

3.3. Materials and methods

3.3.1. Study site, sampling design and dendrochronological data

The present study was conducted with samples taken from a monospecific spacing experiment of *Pinus sylvestris* L., established in 1935 and situated in the north-east of Scotland (57° 36′ 23″ N, 4° 16′ 50″ W) at 170m a.s.l and two spacing (density) treatments were selected for use: high density (ρ_H) and low density (ρ_L).

Sample plots were randomly established so that ten 0.02ha plots were present in both ρ_H and ρ_L. Measurements of tree diameter at breast height (DBH – 1.3m) were collected for all trees within the sample plots. Sample trees were then selected from within these sample plots using the diameter distribution of measured trees to represent three dominance classes (Dominant, Co-dominant and Sub-dominant). Dominant trees were selected as those closest to, but above the upper quartile diameter value, co-dominant trees were selected as those closest to, but above the median diameter value and sub-dominant trees were those closest to, but above the lower quartile diameter value across all trees in the ten sample plots in both ρ_H and ρ_L where present. This approach meant 14 dominant, 14 co-dominant and 6 sub-dominant trees in each treatment were felled in the winters of 2002 and 2003, resulting in 34 sample trees from both ρ_H and ρ_L. Cross sectional discs were taken from the base of each tree at 0.3m ± 30cm and scanned, resulting in 29 (ρ_H) and 27 (ρ_L) usable discs images for analysis (**Table 3.1**). Mortality assessments had been conducted in these plots approximately every five years from 1955 - 1990 (**Table S3.1**).

Table 3.1 *- Stand characteristics at the time of sampling for felled Dominant (Dom), Co-dominant (Co-dom) and Sub-dominant (Sub-dom) P. sylvestris trees in both the high density (ρ_H) and low density (ρ_L) treatments. Error for mean diameter at breast height (DBH), basal area (BA) and mean top height represents standard error.*

	ρ_H			ρ_L		
	Dom	Co-dom	Sub-dom	Dom	Co-dom	Sub-dom
Mean DBH (cm^2)	29.2 ± 0.2	25.8 ± 0.3	19.7 ± 0.3	33.4 ± 1.0	26.9 ± 0.3	22.3 ± 0.1
Mean BA (cm^2)	671.8 ± 9.7	524.5 ± 11.8	305.6 ± 9.1	882.8 ± 53.7	571.0 ± 13.3	389.3 ± 3.0
Mean Top height (m)	21.1 ± 0.6	20.8 ± 0.5	19.8 ± 0.6	20.3 ± 0.6	18.8 ± 0.5	17.7 ± 0.5
Number of trees	13	11	5	9	12	6

Individual tree annual basal area increments (BAI) were calculated from raw ring width data following **Eq. 3.1** where *R* is the radius of the tree in years *t* and *t-1* using the *dplR* package (Bunn et al., 2019) in R version 3.6.1 (R Core Team, 2019). See Ovenden et al., (2021) for further details of the site and dendroecological methods used to process the collected samples.

Eq. 3.1

$$BAI = \pi(R_t^2 - R_{t-1}^2)$$

3.3.2. Drought year identification

To identify notable drought years, we used interpolated climate data at 1 km resolution, obtained from the Climate Hydrology and Ecology Research Support System (CHESS) meteorology dataset for Great Britain (Robinson et al., 2017) for the study period (1961 – 2002) to calculate monthly values for both the Standardised Precipitation Evapotranspiration Index (SPEI) (Vicente-Serrano et al., 2010) and the Climatic Water Deficit (CWD). SPEI was calculated for August using the five previous months data (i.e. using a six month integration period of March - August) ($\text{SPEI}_{\text{Aug6}}$) across the study period using the *SPEI* package in R (Beguería et al., 2014). Increasingly negative SPEI values indicate increasingly severe drought conditions. Huang et al., (2015) identified an SPEI threshold of – 1.64 in other species of pine (*Pinus edulis* and *Pinus ponderosa*), below which drought was linked to significant growth decline. As such, –1.64 was the thresholds adopted here for defining a drought event using the SPEI (**Figure 3.1**).

CWD was calculated for the site at monthly time steps between 1961 and 2002 following Lutz et al., (2010) using R code developed by Redmond (2019). The approach used by Lutz et al., (2010) to calculating CWD applies a Thornthwaite-type water-balance model (Thornthwaite, 1948) which is considered most appropriate when climatic data are limited (e.g. when data on historic wind speed, humidity and net radiation are absent). As such, CWD was calculated here using slope (degrees), latitude (decimal degrees), folded aspect (degrees) (McCune & Keon, 2002), monthly total precipitation (mm), mean monthly temperature (°C) and the soil available water capacity (mm) in the top 200 cm of the soil. Soil available water capacity for the study site of 143.63 mm was obtained from the James Hutton Institute's Available Water Capacity (AWC) dataset (Gagkas et al., 2019). Monthly CWD values between March and August were then summed annually to give a single annual CWD value for each year during the study period (**Figure 3.1**).

Only years that showed a clear drought signal in the calculations of both SPEI and CWD were selected for analysis, resulting in the identification of three drought events in 1976 ($SPEI_{Aug6}$ of – 1.8, CWD of 60.2 mm), 1984 ($SPEI_{Aug6}$ of –2.0, CWD of 66.0 mm) and 1995 ($SPEI_{Aug6}$ of – 1.9, CWD of 58.5 mm), meaning that both SPEI and CWD indicate that 1984 was the most severe drought in the study period (**Figure 3.1**).

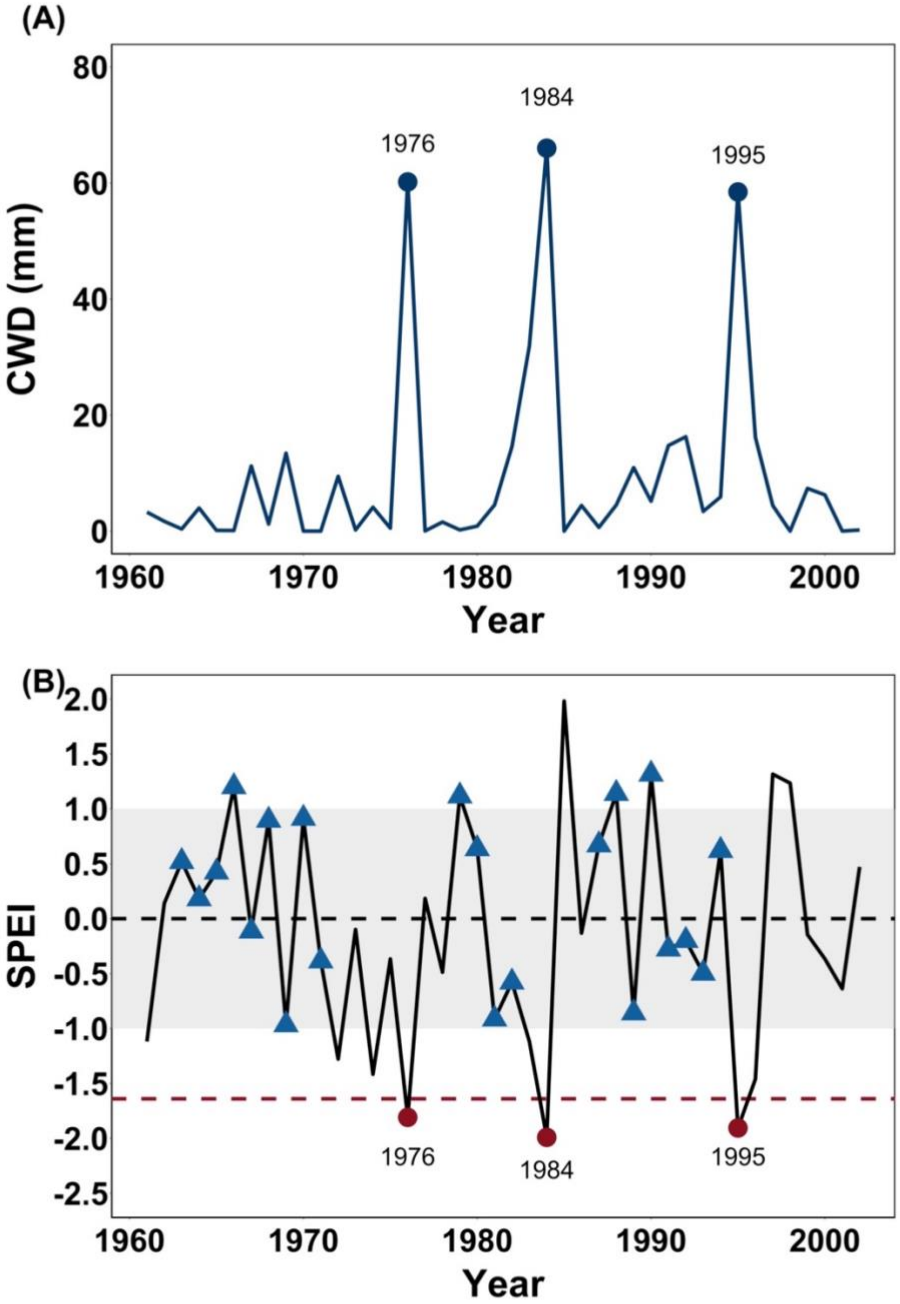

Figure 3.1 - ***(A)*** *Annual climatic water defect (CWD in mm) summed over 6 months (Mar – Aug) for each year during the study period (1961 – 2002).* ***(B)*** *Annual Standardized Precipitation Evapotranspiration Index (SPEI) values calculated over the same study period (1961-2002). The grey band indicates typical climate years (<1 and >-1). The horizontal red dashed line at an SPEI of -1.64 reflects the threshold for drought linked growth decline in pine species proposed by Huang et al. (2015). The three droughts (1976, 1984 and 1995) considered in this study are indicated by red filled circles and annotated in both* ***(A)*** *and* ***(B)*** *while blue triangles indicate the years used to calculate the pre-drought growth averages.*

3.3.3. SPEI-constrained pre-drought growth average

We applied a set of exclusion criteria to $\text{SPEI}_{\text{Aug6}}$ values for the study site across all years preceding each of the three drought events to remove years that indicated unusually dry conditions or potential drought recovery years. This was necessary to ensure that only BAI values from non-drought years or drought recovery years were used to calculate pre-drought growth averages, against which drought responses would be subsequently compared. We then used the corresponding BAI values for the retained SPEI- constrained years to calculate a cumulative moving average (CMA) BAI value at an annual time step (BAI_{con}). In this way, BAI_{con} changes over time as additional SPEI-constrained growth years are included in the average. Initially, we identified all years during the study period (1961 – 2002) where the $\text{SPEI}_{\text{Aug6}}$ values were between –1 and 1 (**Figure 3.1**). This threshold is commonly used in drought studies to indicate non-drought conditions (Bose et al., 2020; Hoffmann et al., 2018; Slette et al., 2019; Vanhellemont et al., 2018). In order to avoid including BAI values that might represent growth during a recovery year (*i.e.* the year(s) after SPEI values < –1) in the calculation of an SPEI-constrained growth average, we applied thresholds for data exclusion by omitting 1 year of BAI after an observed SPEI value of ≤ –1 but > –1.5, 2 years after a SPEI value ≤ –1.5 but > –2.0 and 3 years if the SPEI value was ≤ –2, reflecting commonly used thresholds of drought severity (Hoffmann et al., 2018; Vanhellemont et al., 2018). This approach was designed to be conservative (by excluding growth years that may themselves be a recovery year) and reflect the fact that higher stress levels may be more likely to result in physical damage such as hydraulic failure (Adams et al., 2017) and potentially slower recovery (Gessler et al., 2020). Thus, BAI_{con} was calculated annually from the CMA of all prior years that had not been excluded using one of the above criteria. In this way, SPEI-constrained growth years were defined as having an $\text{SPEI}_{\text{Aug6}}$ value of > –1, with CMA BAI calculations also omitting any BAI values where growth was potentially recovering from a previous dry year. This approach meant that for each tree separately, the $\text{BAI1976}_{\text{con}}$ for the 1976 drought was calculated using nine prior annual growth records, the $\text{BAI1984}_{\text{con}}$ for the 1984 drought was calculated using 13 prior growth records and the $\text{BAI1995}_{\text{con}}$ for the

1995 drought was calculated using 21 prior growth records from the study period (**Figure 3.1**).

3.3.4. Resistance and percentage growth change

Resistance (*Rt*) is a measure of the immediate impact of drought on tree radial growth relative to a pre-drought growth average calculated over a pre-defined period, often between two and five years before drought (Lloret et al., 2011). As a result, *Rt* is calculated following **Eq. 3.2**,

Eq. 3.2

$$Resistance\ (Rt) = \frac{Dr}{PreDr}$$

where *PreDr* is average pre-drought growth and *Dr* is growth during the drought year, providing a measure of drought impact as the ratio of drought year growth performance relative to a pre-drought growth average. We made a simple modification to **Eq. 3.2** which allowed us to express *Rt* as percentage growth change (PGC) following **Eq. 3.3**,

Eq. 3.3

$$PGC = \left(\frac{BAI_t}{BAI_{con}} - 1\right) \times 100$$

where the pre-drought growth average in the *Rt* calculation is replaced with individual tree BAI_{con} values ($\text{BAI1976}_{\text{con}}$, $\text{BAI1984}_{\text{con}}$ and $\text{BAI1995}_{\text{con}}$) and *Dr* is replaced with BAI_t which represents the observed BAI in any year (during or after drought). The use of **Eq. 3.3** over **Eq. 3.2** enabled us to assess BAI_t annually against an SPEI-constrained pre-drought growth average for individual drought episodes. The use of **Eq. 3.3** also allowed an assessment of recovery, with an annual PGC value of 0% indicating growth rates have returned to $\text{BAI1976}_{\text{con}}$, $\text{BAI1984}_{\text{con}}$ or $\text{BAI1995}_{\text{con}}$ levels. We calculated PGC the three drought years and for the four years following each drought but could not calculate PGC for the years immediately preceding each drought event due to the inclusion of some of these years in the calculations of the pre-drought growth averages ($BAI1976_{con}$, $BAI1984_{con}$ and $BAI1995_{con}$) (**Figure 3.1**). We also calculated PGC annually over the same period for all three drought events using ring-width data that had been detrended using a cubic smoothing spline with a 30-year cut-off to ensure our results derived from BAI data were robust.

3.3.5. Growth response to drought severity

We fit a mixed-effects model using the *nlme* package in R (Pinheiro et al., 2020) following **Eq. 3.4** to investigate at an annual resolution whether *P. sylvestris* trees show differences in growth (indexed by BAI) after droughts of differing severity, at different stand densities and to ascertain how long any differences might persist post-drought.

Eq. 3.4

$$BAI_{ij} = X_{ij}\beta + b0_i + \varepsilon_{ij}$$

In **Eq. 3.4**, BAI_{ij} is the *j*th measure (representing measurement at each *j* year) of BAI for the *i*th tree, X is an *n* x *p* matrix of fixed effect variables, where *n* = the number of observations and *p* = the fixed effect variables, including drought event, stand density and timepoint (year), with an interaction between drought event and timepoint (year), β is a *p* x *1* column vector of regression estimates, $b0_i$ represents the random effect of *tree*, where b0i ~ $N(0,\sigma^2_0)$ and ε represents the residual error term, where $\varepsilon_{ij} \sim N(0, \sigma^2)$ (where the error terms are assumed to be normally distributed with a mean of 0 and standard deviation σ^2).

BAI values were square root transformed prior to analysis to improve model fit. In order to compare the three drought events, the year of the drought was assigned timepoint ‘0’ (1976, 1984 or 1995). The next four recovery years were then described as years 1-4. Timepoint (year) (zero to four, where zero is the drought year and one to four are the post-drought years) was fitted using third order orthogonal polynomials to accommodate for non-linearities in BAI over time, with the optimal degree of polynomials selected by minimising AIC values. Tree ID was fitted as a random effect and interaction terms between drought event and year were included. To correct for temporal autocorrelation, the correlation structure was modelled using a corARMA correlation structure of p=2, q=0 and year as a time covariate, which also served to detrend the BAI data.

We subsequently compared the association between BAI and the three drought events over time using estimate marginal means calculated using the *'emtrends'* function in the *'emmeans'* R package and used the Tukey HSD method to correct for multiple comparisons (Lenth, 2020). Estimated marginal means are the mean response for each factor, averaged across the other variables in the model. When the adjusted marginal means were extracted from the model, the estimates were back-transformed to the original scale and these are the values presented in **Figure 3.2**. Adjusted marginal means and unadjusted 95% confidence intervals were also obtained using '*emmeans'* for each year and drought event. All calculations were performed using R version 3.6.1 (R Core Team 2019).

We then used a generalized linear mixed model using the '*lme4*' package to test whether the proportion of trees growing at > 2SD below their pre-drought growth average was different during and following the 1976, 1984 and 1995 droughts. Drought event and year were fit as fixed effects along with an interaction between these two variables, while tree ID was fit as a random effect. A two-degree polynomial was applied to Year. Adjusted marginal means were extracted from the model using the '*emmeans*' package and the proportions of trees with reduced growth compared at each year. A Bonferroni correction was applied to adjust for multiple comparisons.

3.3.6. Growth and size dominance, asymmetry, and inequality

To assess the extent to which drought induces shifts in stand structure, we calculated three complementary indices annually for each treatment using all BAI records; growth dominance (G_d), size inequality (S_i) and size asymmetry (S_a). G_d was calculated manually in R following Method 3 outlined in (West, 2018) by plotting cumulative proportional tree basal area (BA) (χ) against the corresponding cumulative proportional tree BAI (γ) and then fitting multiple polynomial functions using ordinary least squared regression and calculating the area under the fitted curve. We selected the best fitting polynomial function using the lowest AIC value with a maximum polynomial order of eight for each year.

G_d measures the degree to which larger or smaller trees are contributing to overall stand growth relative to their size and ranges from –1 to 1, with a hypothetical value of 0 indicating no size class is dominating growth and all trees are growing at rates directly proportional to their size (West, 2018). The closer G_d is to 1, the more larger sized trees are dominating total stand growth, while the closer G_d is to –1, the more smaller trees are dominating total stand growth (West, 2014, 2018).

Size inequality (S_i) reflects the variability in tree sizes and ranges from 0 to 1, with inequality being zero (i.e., total equality) if all trees are identical in size. S_a is intimately linked to S_i, with values ranging from 0 to 2. S_a measures how much larger trees (S_a values ranging from 1 to 2) or smaller trees (S_a values ranging from 0 to 1) in the population contribute to the observed levels of S_i. Both S_i and S_a were calculated using the Gini coefficient and the Lorenz asymmetry coefficient respectively in the *ineq* package in R (Zeileis & Kleiber, 2014) by plotting cumulative proportional tree size (BA) against cumulative proportional tree frequency.

To identify whether changes in G_d following drought were indicative of a threshold-type response, we initially tested for structural change in G_d over time (separately for high (ρ_H) and low (ρ_L) density stands) using the *efp* function in the *strucchange* package in R (Zeileis et al. 2002) and specifying "OLS-CUSUM" which runs an empirical fluctuation process of OLS residuals to tests whether the null hypothesis of no structural change over time is supported. For G_d in both ρ_L and ρ_H the null hypothesis was rejected, indicating the presence of significant structural change at some point(s) in both G_d timeseries ($p < 0.05$ for G_d in both ρ_H and ρ_L). We subsequently used change point analysis (where the term 'change point' is synonymous with the term 'threshold' (Andersen et al., 2009)) to identify the number and temporal location of any thresholds for G_d in both ρ_H and ρ_L. This method has been previously used to assess abrupt decreases in tree growth linked to drought (Vanoni et al., 2016b, 2016a) and does not require the number of potential thresholds to be pre-determined. Similarly, this method can detect both positive (abrupt increases in G_d) or negative (abrupt decreases in G_d) change points. The optimum number of change points was simultaneously estimated using the Bayesian Information Criterion (BIC) and the location of each change points along with their 95% CI were estimated as calendar years using the *breakpoints* function from the *strucchange* package in R (Zeileis et al., 2002). G_d values for ρ_H were also compared to ρ_L in all three drought years (1976, 1984 and 1995) by permuting the difference between values 10,000 times and using the distribution of these G_d differences to determine the probability of observing a particular value by chance.

3.4. Results

3.4.1. Drought impact linked to drought severity

During the 1976 drought year, mean percentage growth change (PGC) was positive in both the high density (ρ_H) (+21%) and low density (ρ_L) (+5%) stands but slightly negative in the 1995 drought year for both ρ_H (-3%) and ρ_L (-1%) (**Figure 3.3**). In contrast, mean PGC was -23% in ρ_H and -25% in ρ_L in 1984 (**Figure 3.3**) and continued to decline in both stand densities in the two years following the 1984 drought, so that by 1986, mean PGC was -43% and -46% in ρ_H and ρ_L respectively, meaning that average tree BAI was 43% and 46% lower than $BAI1984_{con}$ in 1986. While the impact of all three drought events was more pronounced for spline detrended ring width data, the general patterns in PGC were the same as those derived from the BAI analysis (**Figure S3.1).** The annual pairwise comparison between droughts showed that the 1984 drought year was associated with significantly more trees growing at > 2SD below average than in the 1995 drought year and in all three post-drought years after both the 1976 and 1995 droughts ($p < 0.05$ in all cases **Table S3.4**). By 1986, 16 trees in ρ_L (55%) and 13 trees in ρ_H (48%) were growing at rates >2SD below $BAI1984_{con}$ levels (**Table S3.5**). Following 1986, the pattern of continued growth decline reversed and mean PGC became positive in 1988 in both ρ_L and ρ_H (**Figure 3.3**) and the number of trees with BAI > 2SD below BAI1976$_{con}$, BAI1984$_{con}$ or BAI1995$_{con}$ levels was not statistically different between all three drought events ($p > 0.9$ in all cases) (**Table S3.4**).

Mixed-effects model analysis showed a significant difference in BAI among drought events, but this difference changed over time ($p < 0.001$) (**Figure 3.2** and **Table 3.2**). Post-hoc analyses of estimated marginal means for BAI were used to compare differences between droughts at an annual resolution (**Figure 3.2**). BAI differed significantly after the 1984 drought compared to the 1976 and 1995 droughts for 3 years following the event ($p < 0.0001$ in all cases, **Figure 3.2** and **Table S3.3**). However, differences in BAI between the 1976 and 1995 drought were only significant ($p < 0.05$) in the first post-drought year ($p = 0.014$), but not in the drought year itself or any other post-drought years ($p > 0.06$ in all cases) (**Figure 3.2** and **Table S3.3**). As a result, the slightly more extreme drought of 1984 was associated with a greater absolute change in BAI in the drought year and in the following three years relative to the less severe 1976 or 1995 droughts.

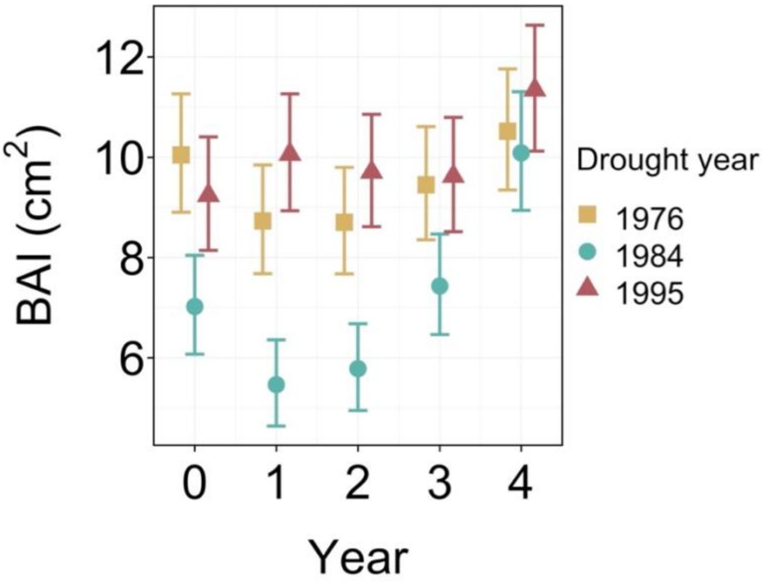

Figure 3.2 *- BAI adjusted marginal means (averaged over high (ρ_H) and low (ρ_L) density stands) for the 1976, 1984 and 1995 drought years. Year = 0 represents the drought year while years 1-4 indicate the four years post-drought, while error bars represent 95% unadjusted confidence intervals.*

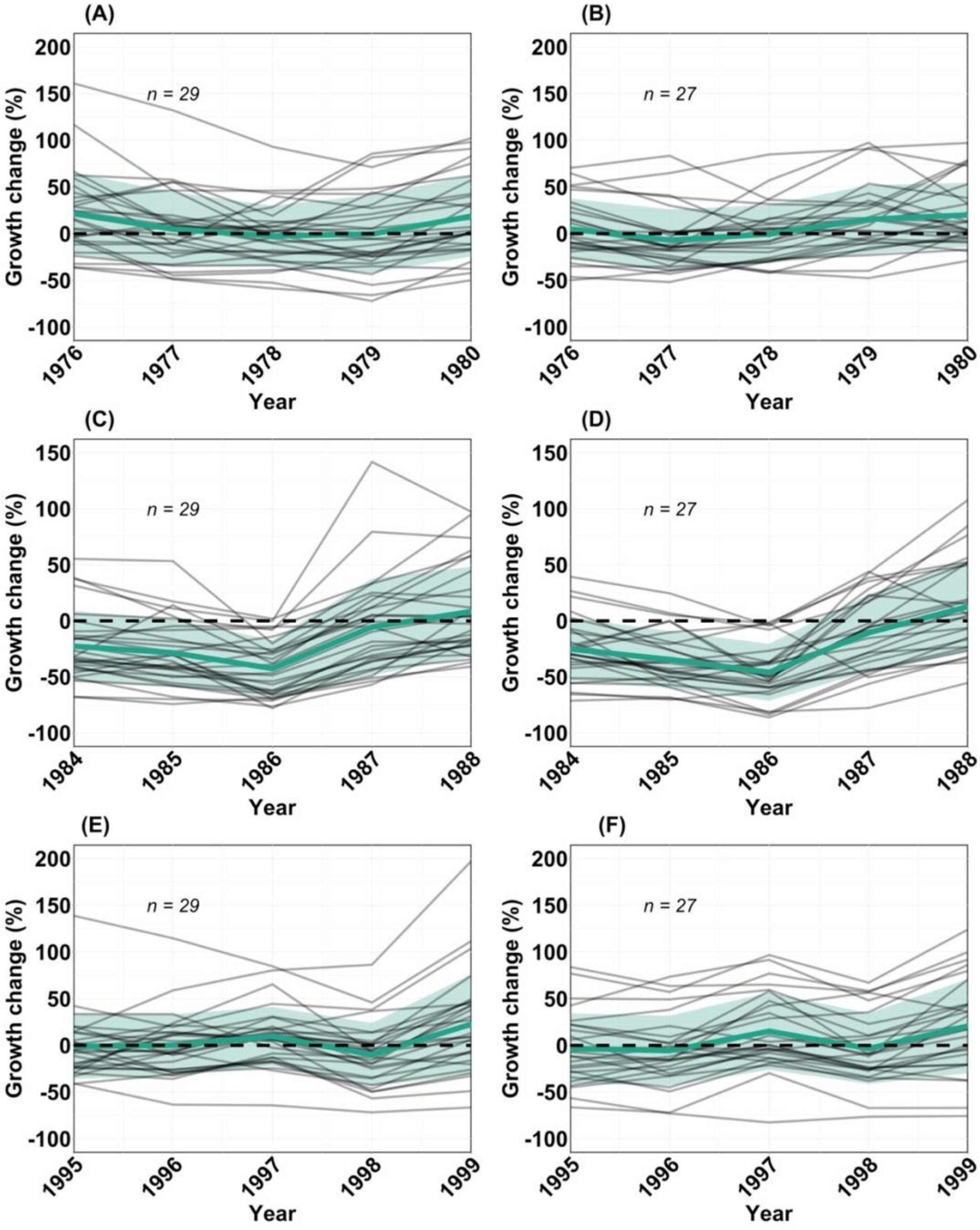

Figure 3.3 *- Individual tree (grey lines) and mean (solid green lines) ±1 SD (green shaded areas) percentage growth change across all trees at a given density relative to* $BAI1976_{con}$*,* $BAI1984_{con}$ *or* $BAI1995_{con}$ *values for the 1976* ***(A, B)****, 1984* ***(C, D)*** *and 1995* ***(E, F)*** *droughts respectively, calculated annually for both high density* ***(***ρ_H ***– A, C, E; n = 29)*** *and low density* ***(***ρ_L ***– B, D, F; n = 27)*** *stands. The horizontal black dashed lines indicate no detectable difference between a given year's growth and* BAI_{con} *(growth rates recovered to climatically constrained pre-drought average levels).*

Table 3.2 *- ANOVA table for the mixed-effects model of BAI, where numDF = numerator degrees of freedom, denDF = denominator degrees of freedom, interactions are denoted by a × and significant effects (p < 0.05) are highlighted in bold. Stand density was either high (ρ_H) or low (ρ_L) while Drought year represents the 1976, 1984 or 1995 drought years. Time point (Year) (0 being the drought year and 1-4 being post-drought years) was fit using third order orthogonal polynomials and represents the time since drought.*

Fixed-effect	***numDF***	***denDF***	**F-value**	***p-value***
(Intercept)	**1**	**773**	**1491**	**<0.001**
Stand density	1	54	0.5	0.471
Drought event	**2**	**773**	**38**	**<0.001**
Time point (Year)	**3**	**773**	**75**	**<0.001**
Drought event × Time point (Year)	**6**	**773**	**18**	**<0.001**

3.4.2. Growth and size dominance, asymmetry, and inequality

Interannual variability in G_d was higher in ρ_H than ρ_L across the study period (**Figure 3.4a**). Between 1961 and 1973, G_d in ρ_H indicates that smaller trees were dominating stand growth (small trees were contributing more to total BAI than the same trees were contributing to total BA), but by 1975 larger trees began to dominate growth (larger trees started growing at rates disproportionately fast for their size) (**Figure 3.4a**). During the 1976 drought year in ρ_H, all trees were growing at rates roughly proportional to their size (G_d), however in the years following 1976 larger trees contributed proportionately more to total stand BAI than their BA contributed to total stand BA (**Figure 3.4a**). In contrast, for ρ_L, G_d remained relatively stable, oscillating around 0 from 1961 – 1985, indicating that all trees were growing at rates roughly proportional to their size (**Figure 3.4a**).

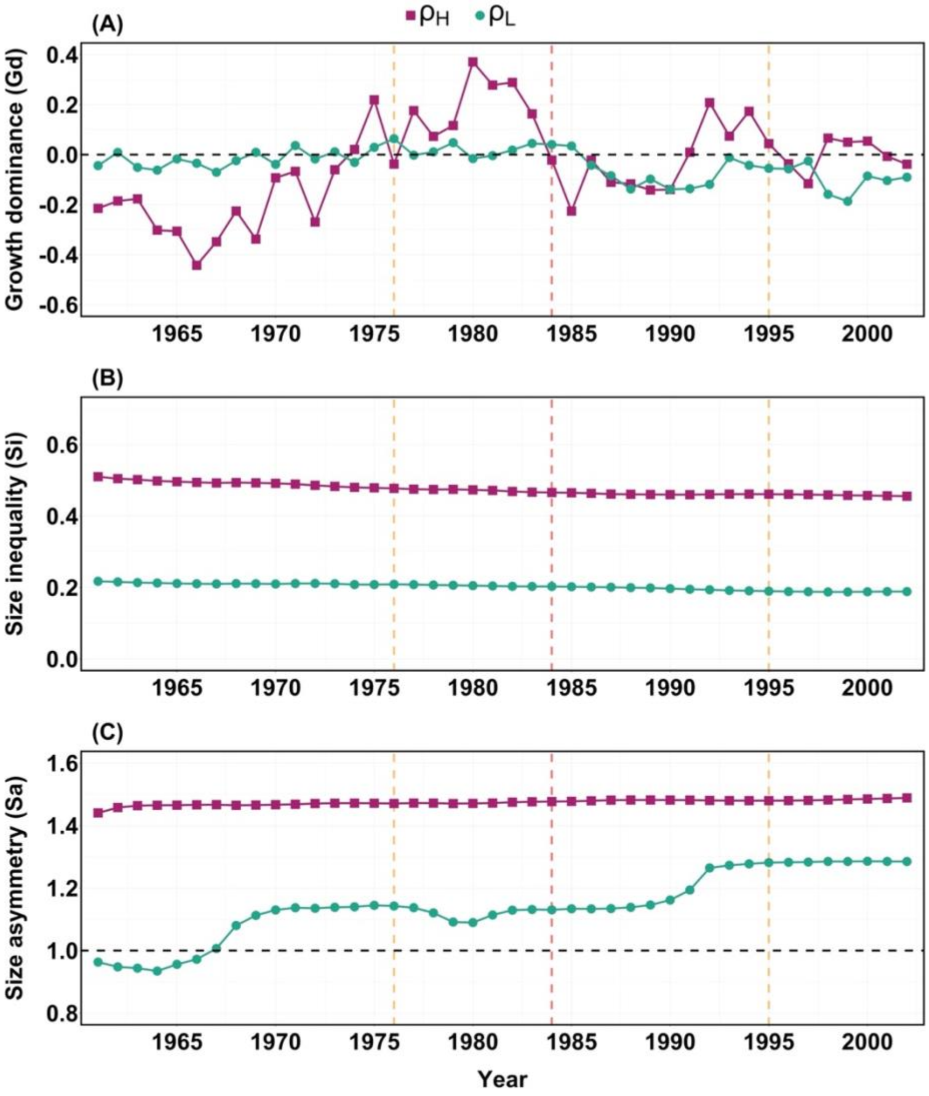

Figure 3.4 *- Annual values for (A) Growth dominance (Gd), (B) Size inequality (Si) and (C) Size asymmetry (Sa) calculated annually for both high (ρH) and low (ρL) density treatments. The horizontal black line in (A) indicates that all trees are growing at rates directly proportional to their size, positive values indicate larger trees are dominating growth relative to their size while negative values indicate smaller trees are dominating growth relative to their size in a given year. The dashed horizontal line in (C) indicates both large and small trees are contributing equally to tree size inequality while values >1 or <1 indicate larger or smaller sized trees are contributing more to size inequality respectively. Orange vertical dashed lines indicate the 1976 and 1995 droughts, while the red vertical dashed line indicates the 1984 drought. Purple squares represent ρH (high density) n = 29, while green circles represent ρL (low density) n = 27.*

In 1984 G_d shifted away from larger trees towards smaller trees in ρ_H, meaning all trees contributed to total stand BAI at rates roughly proportional to their BA. This directional shift in G_d continued into 1985 as smaller trees showed increased growth dominance, contributing proportionally more to stand level BAI than they did to total stand BA (**Figure 3.4a**). G_d briefly returned to roughly zero (all trees were again growing at rates proportional to their size) in 1986, however in contrast to values of G_d prior to 1984, smaller trees contributed proportionally more to stand level growth from 1987 – 1991. Larger trees again began to dominate growth from 1992 in ρ_H, a pattern that appeared to temporarily reverse following 1995, where smaller trees dominated growth until 1998. In ρ_L, G_d became consistently negative from 1986 until 1993 when G_d returned to roughly zero, though G_d never became positive again after 1986 in ρ_L (**Figure 3.4a**). Despite these shifts in G_d, the ten largest trees for all three years prior to the 1984 drought were still the same ten largest trees in 1988.

Across the study period (1961 – 2002), *Si* was consistently higher for all years in the higher density (ρ_H) than the lower density (ρ_L) treatment (**Figure 3.4b**) meaning that there was a greater range of tree diameters in the higher density stand. There was also a slight decrease in S_i in both ρ_H and ρ_L across the study period but no discernible change in S_i during or after any of the three drought events (**Figure 3.4b**).

In general, S_a remained stable throughout the study period in ρ_H, while ρ_L showed a brief depression in S_a between 1978-1981, indicating larger trees were temporarily contributing less to S_i than before 1978 (**Figure 3.4c**). However, S_a returned to pre-1978 levels in ρ_L by 1982. No immediate change in S_a followed the 1984 drought in either ρ_H or ρ_L, however between 1990-1993, S_a shifted to a higher and stable level in ρ_L, indicating that from 1990 onwards in this lower density stand, larger trees were consistently contributing more to size inequality than previously (**Figure 3.4c**).

Change point analysis of G_d revealed three change points (i.e., thresholds) for ρ_H (1973, 1983 and 1990) and two change points for ρ_L (1970 and 1985) (**Figure S3.2**). Since the date assigned to each breakpoint is allocated to the last year of the previous period (i.e., 1 year before a change to a lower or higher G_d level) a change point in 1983 indicates a change occurred in 1984. As a result, the extreme drought event of 1984 aligns with a threshold change in G_d in the same year in ρ_H, while a threshold change in G_d for ρ_L occurred two years later in 1986 (**Figure S3.2**). Neither the severe drought of 1976 or 1995 fell within the 95% CI of any of the other G_d thresholds identified in either ρ_H or ρ_L (**Figure 3.4a** and **Figure S3.2**). Change point analysis was not conducted for S_i or S_a due to apparent insensitivity of these indices around all three drought years (**Figure 3.4**) and no significant differences in G_d were noted between ρ_H and ρ_L in either 1976, 1984 or 1995 ($p > 0.613$ in all cases).

3.5. Discussion

In this study we developed a standardised method for calculating tree-level pre-drought growth averages using SPEI-constrained growth years, against which drought and post-drought growth performance was assessed for three droughts of differing severity. We then used mixed-effects models, stand level indices of growth dominance (G_d), size inequality (S_i) and size asymmetry (S_a) calculated annually and change point analysis to investigate whether droughts of differing severity were associated with significantly different growth responses in both absolute (BAI) and relative (PGC) terms, changes in stand dynamics or the magnitude and duration of any drought legacies.

We provide evidence of a threshold response to the most extreme drought (1984) in the study period (1961 – 2002) which was associated with a large and sustained post-drought growth reduction in both density treatments. In contrast, we found no evidence of a significant impact on average tree growth following the two less severe droughts in 1976 and 1995. This result was mirrored at the stand level with a significant shift in G_d towards smaller trees in both high and low density stands following the most extreme drought in 1984, but neither of the less severe droughts in 1976 or 1995. Collectively, the impact on average tree growth, the proportion of trees impacted and the shift in G_d indicate that a drought severity threshold for *P. sylvestris* may have been crossed at this site following the 1984 drought.

3.5.1. Threshold growth response and shifts in growth dominance

Many studies calculate resistance, recovery and resilience relative to a pre-drought growth average derived from the years immediately preceding a drought event (Gazol et al., 2017, 2018; Zang et al., 2014). However, recent work has shown that the subjective choice of the number of years to include when calculating these pre-drought growth averages can bias estimates of drought resilience (Ovenden et al., 2021; Schwarz et al., 2020). Here we developed an approach which uses the SPEI to climatically standardize the selection of these pre-drought years to avoid the need for this subjective selection and minimise the risk of including pre-drought year BAI values that may themselves be the product of an abnormally dry year in the calculation of pre-drought average growth.

Using these climatically constrained pre-drought growth averages to address our first objective, we show that the extreme drought of 1984 was associated with a protracted period of low growth and changes in growth dominance at the stand level, consistent with a threshold-type drought response noted in other pine species (Asbjornsen et al., 2021; Huang et al., 2015). However, we did not find any evidence of a similar response following the lower severity droughts on 1976 and 1995, nor did we document any significant differences between the high or low density stands (**Table 3.2**), the latter result being in keeping with other recent work on the growth response of *P. sylvestris* to drought which also documented no effect of tree density in this species (Bello et al., 2019). As such, we found that a small increase in drought severity (measured in both absolute (CWD) and relative (SPEI) terms) in 1984 compared to the 1976 and 1995 droughts was associated with a significant decrease in average tree BAI and a significant increase in the number of trees growing a > 2SD below their pre-drought average for up to three post-drought years (**Figure 3.2, Table S3.3** and **S3.4**). These results reflect other studies that have documented multi-year legacies on tree growth following extreme drought (Anderegg et al., 2015; Wu et al., 2018). Huang et al. (2015) reported an SPEI threshold of -1.64 for *Pinus edulis* and *Pinus ponderosa*, after which progressively more negative SPEI values cause significant declines in forest growth. This value reported by Huang et al. (2015) is slightly less negative than the SPEI recorded for all three droughts in this present study (1976 $\text{SPEI}_{\text{Aug6}}$ of – 1.8, 1984 $\text{SPEI}_{\text{Aug6}}$ of –2.0 and a 1995 $\text{SPEI}_{\text{Aug6}}$ of – 1.9) (**Figure 3.1**). As such, our results support other recent work that suggests that thresholds of drought severity likely vary among species (Cavin et al., 2013; Gazol et al., 2020; Kolb, 2015) but also highlights how setting generic, climatologically defined drought thresholds too low can risk including events that may not have been strong enough to elicit an organismal or systemic response (Smith, 2011), potentially clouding our understanding of how different species respond to extreme events. Similarly, the characterisation of drought purely in terms of severity using indices (e.g., SPEI or CWD) may also be obscure important differences between droughts stemming from the inherent multi-dimensionality of these events (e.g., timing, duration, and intensity). Due to the limited number of drought events in the climate data at this study site, it was not possible to ascertain whether the timing, duration, or intensity of drought at this site were linked to patterns in tree growth response. While none of the post-drought years in this study appeared to be abnormally dry (**Figure 3.1**), we acknowledge that post-drought climate likely plays an important role in regulating forest recovery dynamics but was not explicitly considered in this study, however where possible future studies should on forest resilience to drought should aim to included post-drought climate to ensure a more complete understanding of drought recovery.

At the stand level, mean PGC in both the high and low density stands remained relatively constant during and following both the 1976 and 1995 droughts with some trees showing reductions in radial growth while others showed radial growth increases. The net effect of this inter-tree variability may have partly buffered against stand-level changes in BAI during these two less severe droughts. While individual tree growth variability is negatively linked to individual drought resilience (Bose et al., 2020), inter-tree variability in pre-drought growth may act as a form of response diversity (Mori et al., 2013) and reflects other recent studies that highlight the potential for intraspecific differences to partly buffer against the impacts of climate change (Moran et al., 2016; Oney et al., 2013; Taeger et al., 2015). In contrast, after the 1984 drought stand growth reduced to levels substantially below $\text{BAI1984}_{\text{con}}$ (**Figure 3.3**), temporarily reduced inter-tree growth variability (**Figure 3.3**) and shifted growth dominance (*Gd*) towards smaller trees (**Figure 3.4**), indicating that a threshold for intraspecific variability to buffer against stand level growth loss may have been exceeded.

The drought severity required to cross such thresholds is likely to be linked to the ecophysiological limits of a species hydraulic system to drought stress (Adams et al., 2017; Choat et al., 2012) and pre-drought conditions, which can lead to phenomenon such as structural overshoot (Jump et al., 2017). While it is possible that observed shifts in growth dominance (*Gd*) in this study are partly the result of the death of neighbouring trees, assessments of both the high density (ρ_H) and low density (ρ_L) treatments in 1985 and 1990 (1 and 6 years after the 1984 extreme drought) show mortality was not abnormally high during these post-drought periods (**Table S3.1**). While we acknowledge that in some cases mortality might be delayed for many years following drought (Bigler et al., 2007), we show that the crossing of drought thresholds does not necessarily need to result in widespread or elevated tree mortality to be associated with detectable changes in growth dominance and stand dynamics (Batllori et al., 2020; Stuart-Haëntjens et al., 2015), addressing our second research question. Persistent, interspecific shifts in competitive dominance have been documented following extreme drought in other species (Cavin et al., 2013), but such shifts at the population level were not observed in a much larger scale study of *P. sylvestris* (Martínez-Vilalta et al., 2012).

Collectively, our results demonstrate how small increases in drought severity can be associated with changes in tree growth at different tree densities and may influence stand dynamics to a degree that is not observed under less severe drought conditions. While we did not detect any large changes in size inequality (*Si*) or size asymmetry (*Sa*) in response to drought, this study exclusively looked at even aged, monospecific stands of *P. sylvestris*. Future work should investigate whether drought induces changes in *Si*, *Sa* and *Gd* in more structurally diverse, species rich stands of variable age classes to further our understanding of the role of drought in driving novel developmental trajectories and structuring community composition. Similarly, understanding which combinations of drought intensity, timing, duration, and frequency are associated with differences in forest growth and stand development will be key.

3.6. Conclusion

Here we demonstrate how extreme drought is associated with a threshold response in *Pinus sylvestris* trees growing in Scotland at different stand densities. Once crossed, this threshold was associated with decreased BAI which persisted for up to 2 years after drought, a significant increase in the number of trees growing below average and shifts in growth dominance from larger trees to smaller trees in both stand densities. These results suggests that tree level variability may provide some stand level resilience to drought, but also demonstrates how small increases in drought severity may exceed this compensatory mechanism and result in stand level changes that are not manifest under slightly less severe drought conditions.

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3.8. Supplementary Material

Table S3.1 *- Periodic assessments of previously unrecorded tree mortality in the both the high density (ρH) and low density (ρL) plots and scaled up to a hectare (ha).*

Year	No. trees (ha)	No. trees (plot)	Mortality (ha)	Mortality (ha)	Stand
1955	3805	400	30	12	ρ_H
1969	3241	341	154	16	ρ_H
1974	2823	297	413	43	ρ_H
1980	2471	260	351	37	ρ_H
1985	2148	226	323	34	ρ_H
1990	1929	203	218	23	ρ_H
1955	1258	152	27	11	ρ_L
1969	1240	150	16	2	ρ_L
1974	1215	147	24	3	ρ_L
1980	1157	140	53	6	ρ_L
1985	1074	130	82	10	ρ_L
1990	1008	122	66	8	ρ_L

Table S3.2 *- Results of the pairwise comparison of slopes between the three drought years. Df = degrees of freedom, SE = standard error.*

Drought year comparison	Estimate	SE	***df***	***t.ratio***	***p.value***
1976 - 1984	-0.142	0.051	773	-2.809	0.014
1976 - 1995	0.148	0.050	773	2.951	0.009
1984 - 1995	0.290	0.050	773	5.763	<0.001

Table S3.3 - *Post-hoc analyses of estimated marginal means for BAI between the three drought events (1976, 1984 and 1995) in the drought year (Year 0) and four post-drought years (Years 1-4). Significant values ($p < 0.05$) are highlighted in bold.*

		Year 0			
Contrast	**Estimate**	**SE**	***df***	***t.ratio***	***p.value***
1976 - 1984	**0.52**	**0.0761**	**773**	**6.826**	**< 0.0001**
1976 - 1995	0.13	0.0804	773	1.62	0.2379
1984 - 1995	**-0.39**	**0.0786**	**773**	**-4.956**	**<0.0001**
		Year 1			
1976 - 1984	**0.617**	**0.073**	**773**	**8.447**	**< 0.0001**
1976 - 1995	**-0.218**	**0.0775**	**773**	**-2.811**	**0.014**
1984 - 1995	**-0.835**	**0.0756**	**773**	**-11.041**	**< 0.0001**
		Year 2			
1976 - 1984	**0.545**	**0.0682**	**773**	**7.991**	**< 0.0001**
1976 - 1995	-0.165	0.073	773	-2.257	0.0626
1984 - 1995	**-0.71**	**0.071**	**773**	**-10.002**	**< 0.0001**
		Year 3			
1976 - 1984	**0.3477**	**0.73**	**773**	**4.76**	**< 0.0001**
1976 - 1995	-0.0279	0.0775	773	-0.36	0.9309
1984 - 1995	**-0.3756**	**0.0756**	**773**	**-4.968**	**< 0.0001**
		Year 4			
1976 - 1984	0.0669	0.0761	773	0.879	0.6537
1976 - 1995	-0.01248	0.0804	773	-1.553	0.267
1984 - 1995	**-0.1917**	**0.0786**	**773**	**-2.439**	**0.0396**

Table S3.4 *- Post-hoc pairwise comparison of estimated marginal means for the proportion of trees growing at < 2 SD of the SPEI-constrained pre-drought growth averages ($BAI1976_{con}$, $BAI1984_{con}$, $BAI1995_{con}$) for all three drought events (1976, 1984 and 1995). Pairwise comparisons were conducted annually between all three droughts for events (Year = 0) and in the four post-drought years (Year = 1, 2, 3 and 4). Significant results are highlighted in bold, and p-values were adjusted using a Bonferroni correction to adjust for multiple tests and SE = standard error.*

Year 0

Contrast	**Odds ratio**	**SE**	**z.ratio**	***p.value***
1976 - 1984	0.167	0.116	-2.568	0.153
1976 - 1995	2.825	2.99	0.981	1
1984 - 1995	**16.96**	**16.315**	**2.943**	**0.049**
Year 1				
1976 - 1984	**0.066**	**0.029**	**-6.151**	**<0.001**
1976 - 1995	4.208	2.661	2.273	0.346
1984 - 1995	**64.141**	**39.166**	**6.814**	**<0.001**
Year 2				
1976 - 1984	**0.067**	**0.032**	**-5.608**	**<0.001**
1976 - 1995	3.716	2.575	1.894	0.874
1984 - 1995	**55.155**	**36.455**	**6.067**	**<0.001**
Year 3				
1976 - 1984	**0.18**	**0.09**	**-3.418**	**0.009**
1976 - 1995	1.945	1.232	1.05	1
1984 - 1995	**10.784**	**6.351**	**4.038**	**<0.001**
Year 4				
1976 - 1984	1.258	1.364	0.212	1
1976 - 1995	0.603	0.648	-0.47	1
1984 - 1995	0.479	0.49	-0.719	1

Table S3.5 *- The number of trees (n) growing at <2SD of the pre-drought growth averages (BAI1976$_{con}$, BAI1984$_{con}$, BAI1995$_{con}$) in all three drought years (1976, 1984 and 1995) and four post-drought years in both the low (ρ_L – 29 trees) and high (ρ_H – 27 trees) density stands.*

ρL

Year	***n***	**Year**	***n***	**Year**	***n***
1976	3	1984	6	1995	1
1977	3	1985	13	1996	2
1978	1	1986	16	1997	1
1979	1	1987	3	1998	1
1980	0	1988	2	1999	2

ρH

1976	0	1984	5	1995	0
1977	2	1985	8	1996	0
1978	3	1986	13	1997	0
1979	3	1987	2	1998	1
1980	1	1988	1	1999	0

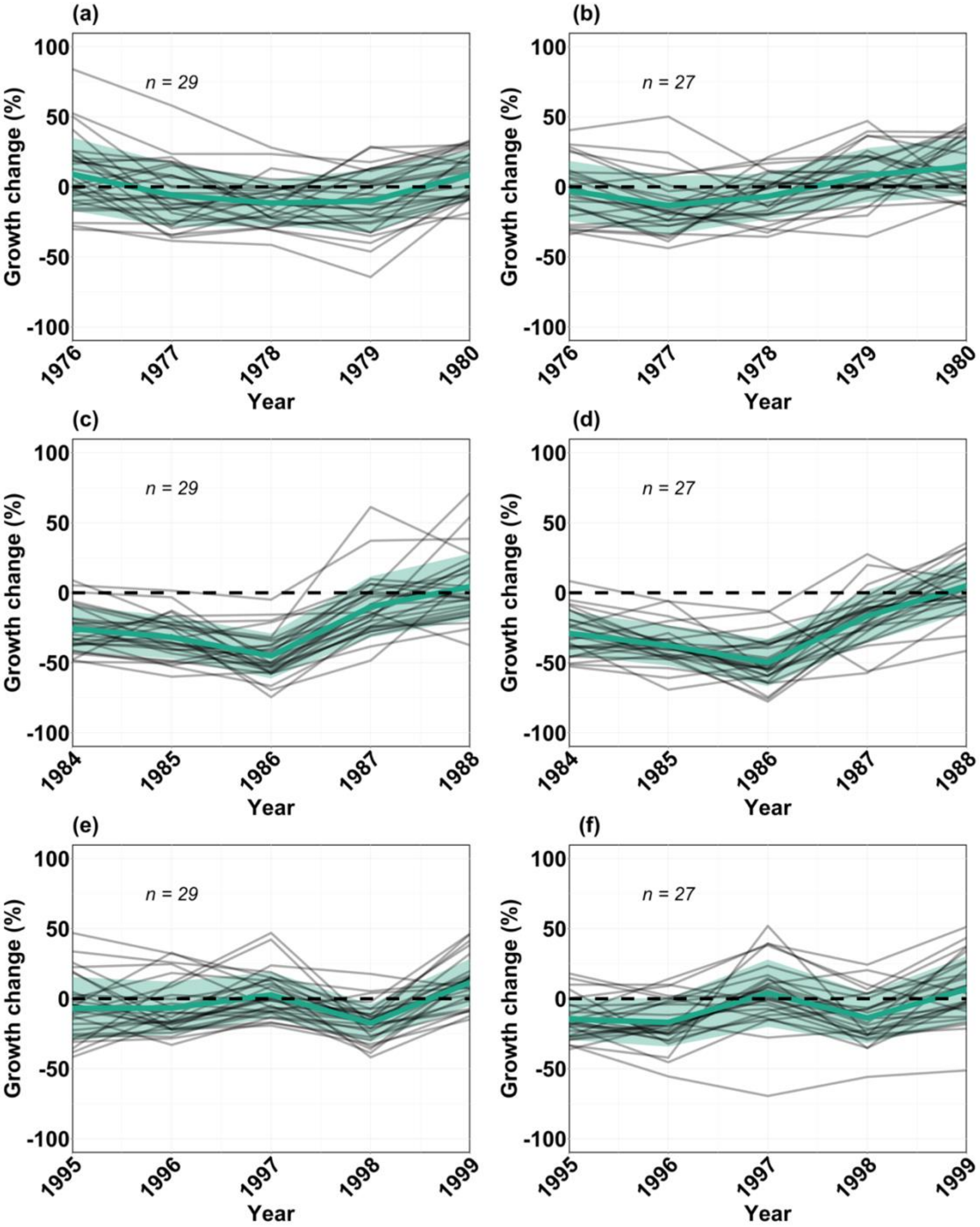
(a)
(b)
(c)
(d)
(e)
(f)
n = 29
n = 27
n = 29
n = 27
n = 29
n = 27
Growth change (%)
100
50
0
-50
-100
Year
1976
1977
1978
1979
1980
1984
1985
1986
1987
1988
1995
1996
1997
1998
1999

Figure S3.1 *Individual tree and mean percentage growth change relative to* $RWI1976_{con}$*,* $RWI1984_{con}$ *or* $RWI1995_{con}$ *values for the 1976 (a, b), 1984 (c, d) and 1995 (e, f) droughts respectively, calculated annually for both high density (*ρ_H *– a, c, d) and low density (*ρ_L *– b, d, f) stands.* RWI_{con} *values represent the pre-drought growth averages calculated using the same approach as for BAI in the main text but form ring width data detrended using a cubic smoothing spline with a 30-year cut off. Grey lines are individual trees, while solid green lines and green shaded area are the annual mean ± 1SD across all trees at a given density. Solid horizontal dashed black lines indicate no detectable difference between a given years growth and* RWI_{con} *(growth rates have recovered to* RWI_{con} *levels for each drought). High density (*$\rho_{H,}$ *n = 29) and low density (*$\rho_{L,}$ *n = 27).*

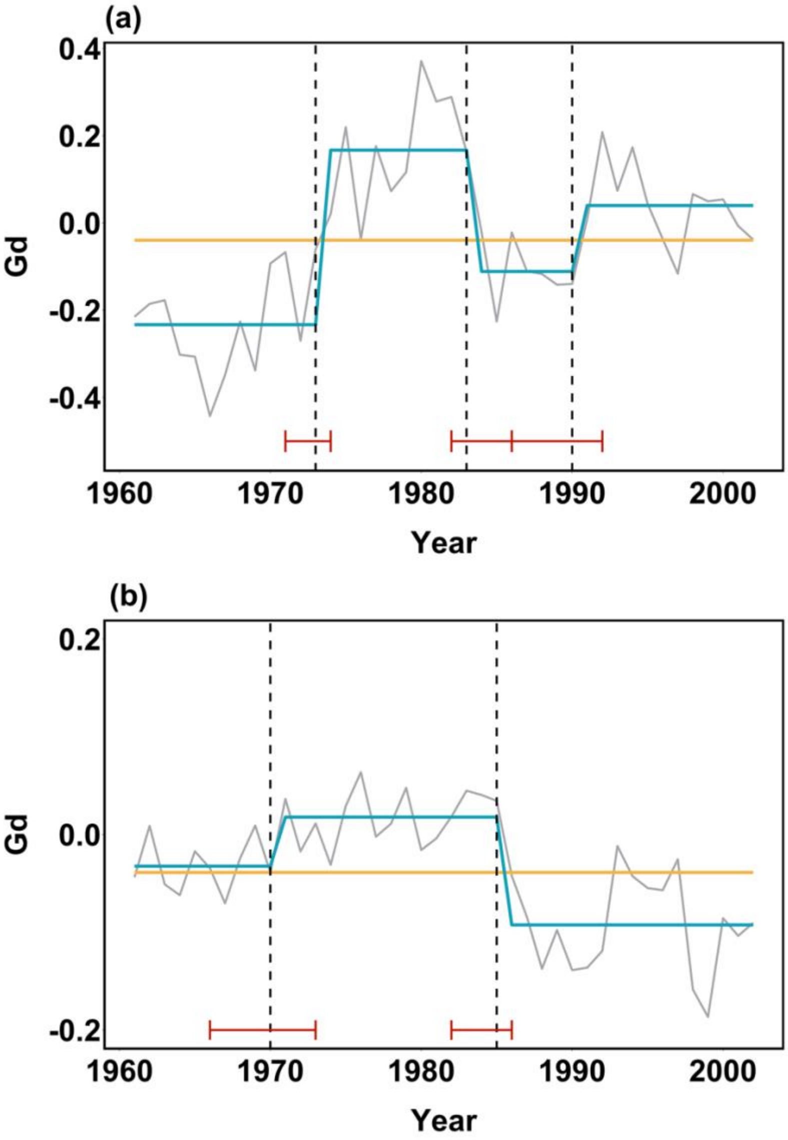

Figure S3.2 *- Change point analysis showing the years where abrupt changes (e.g. thresholds - vertical black dashed lines) in growth dominance (G_d) (grey lines) were detected for (a) the high (ρ_H – 1973, 1983 and 1990) and (b) low (ρ_L – 1970 and 1985) density treatments along with the corresponding 95% confidence intervals (red error bars). Horizontal yellow lines indicate the null model (linear regression line with no change points) and blue lines represent fitted regression lines of linear models with break points. Note the year indicated by each change point is the last year of the previous period (i.e., 1 year before a change to a lower or higher G_d level, so a change point in 1983 would indicate a change occurred in 1984).*

CHAPTER 4 - Intimate mixtures of Scots pine and Sitka spruce do not increase resilience to spring drought

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4.1. Abstract

Understanding how we can increase the resilience of forest systems to future extreme drought events is increasingly important as these events become more frequent and intense. Diversifying production forests using intimate mixtures of trees with complementary functional traits is considered as one promising silvicultural approach that may increase drought resilience. However, the direction and magnitude of the drought response of mixed-species stands relative to monospecific stands of the same species can vary with species identity, relative abundance, and levels of competition in a focal tree's immediate neighbourhood. Using a long-term experiment where tree-level mortality and the neighbourhood composition of each tree was known, we assessed the radial growth response of 24-year-old Scots pine (*Pinus sylvestris*) and Sitka spruce (*Picea sitchensis*) trees in intimately mixed and monospecific stands to a short-duration, high-intensity spring drought in Scotland. Mixing proportions included 25:75, 50:50 and 75:25 of *P. sylvestris* and *P. sitchensis*. At the species level, Scots pine was more drought resistant and resilient than Sitka spruce, while Sitka spruce showed higher recovery. Surprisingly, neither pre-drought tree size nor neighbourhood competition were significantly associated with resistance or resilience to drought, and trees of both species within monospecific stands showed higher recovery and resilience than trees growing in mixed stands. Our study suggests intimate mixtures of these two species may not be an effective way to mitigate the negative impacts of

future extreme spring drought events. Given that these two species comprise almost 70% of coniferous forests in the UK, our results highlight the pressing need to better understand their vulnerability to drought and the conditions under which intimate mixtures of these species could be beneficial or detrimental. Such knowledge is essential if we are to enable forest managers to effectively plan how to adapt these forests to the challenges of a changing climate.

4.2. Introduction

With the intensity, duration and frequency of extreme drought events expected to increase in the coming decades across many parts of the world (Dai, 2013; McDowell et al., 2018; Trenberth et al., 2014), understanding how forest managers can increase the resilience of forest systems to future extreme drought events is critically important (Field et al., 2020; Sohn et al., 2016). Diversifying species composition at a range of scales has been proposed as a promising approach to increase the drought resilience of planted forests (Bauhus et al., 2017; Messier et al., 2021) and reduce drought-linked losses in biomass accumulation. This approach includes the use of intimate mixtures, where the term ‘intimate’ indicates that some or all of a given tree’s immediate neighbours are of a different species. However, a growing body of evidence is highlighting that the existence and nature of any mixing effects on both forest growth and drought resilience are both species and context-dependent (Gillerot et al., 2021; Grossiord et al., 2014; Grossiord, 2019; Jactel et al., 2017; Van de Peer et al., 2018). For example, Muñoz-Gálvez et al. (2020) demonstrated higher growth for *Pinus sylvestris* in mixtures with *Quercus pyrenaica* under drought conditions compared to monospecific stands, but also observed a resistance/recovery trade-off in both these species. Such trade-offs between the different components of tree resilience (Lloret et al., 2011) have now been documented across gymnosperm species both spatially (Gazol et al., 2017) and temporally (Li et al., 2020) in some of the most abundant and economically important tree species in Europe (Vitasse et al., 2019), possibly reflecting different ecophysiological strategies for dealing with drought (Gazol et al., 2020; Li et al., 2020).

The ecological theory proposing better performance of mixed-species forests under drought relative to monospecific stands of the same species relates in part to processes such as niche differentiation or facilitation, collectively referred to as 'complementarity' (Loreau & Hector, 2001). Niche differentiation can occur when differences in the physiological or morphological traits of admixed species increases access to, or exploitation of available resources, potentially acting to reduce direct tree-to-tree competition under stressful conditions (Bauhus et al., 2017). Niche differentiation can result from variability in tree architecture above and below ground and vary over time. Stratification of the canopy can lead to greater total light capture and create favourable microclimates (De Frenne et al., 2021), while differences in rooting depth can increase access to water in mixed-species stands compared to monospecific stands of the same species. Facilitative processes such as hydraulic redistribution (where water is moved from deeper, moister soil layers to dryer surface soils via plant roots) has also been shown to mitigate against the negative effects of drought on individual trees (Neumann et al., 2012; Pickles & Simard, 2017).

Studies that look at the composition of individual tree neighbourhoods to understand the relationship between species diversity, competition and forest productivity highlight the importance of interactions between species and individual trees at fine spatial scales (Fichtner et al., 2017, 2018, 2020). Vitali et al. (2018) demonstrated that the drought response of Norway spruce (*Picea abies*) in mixtures could be positive or negative depending on the identity of the species in a tree's immediate neighbourhood, while Jourdan et al. (2020) showed that the proportion of heterospecific neighbours could have a positive, negative or neutral effect on drought resilience depending on the identity of the focal species. Furthermore, Fichtner et al. (2020) provided evidence that the functional traits of the species occupying a tree's immediate neighbourhood play a dominant role in mediating individual tree drought response, with drought sensitive species benefiting from more functionally diverse neighbourhoods. Specifically, Fichtner et al. (2020) highlighted how species with low cavitation resistance particularly stand to benefit from growing in diverse neighbourhoods. In addition to the functional characteristics of admixed species, individual tree size can be a strong predictor of tree growth response to drought, with larger trees commonly reported to be more susceptible to drought (Bennett et al., 2015; Martínez-Vilalta et al., 2012; Ovenden et al., 2021). This pattern has been found to be particularly evident in *P. sylvestris* (Merlin et al., 2015) and is likely associated with, but not limited to differences in stomatal control on photosynthesis (Zang et al., 2012) and the fact that larger trees are often exposed to higher solar radiation and leaf-to-air vapour pressure deficit than sub-canopy trees (Bennett et al., 2015).

How processes at the level of individual trees and their neighbourhoods interact and scale up to patterns of drought resistance and resilience at the stand level is an equally important but under-explored aspect of forest drought studies, often due to sampling designs that fail to record the full range of tree sizes or capture the influence of tree mortality (Bottero et al., 2021). However, understanding how different species, trees growing in different species mixtures, mixing proportions or pre-drought tree and stand characteristics influence drought response is particularly important for informing forest management decisions targeted at increasing the drought resilience of both economically and ecologically important tree species (Thurm et al., 2016).

In the UK, Sitka spruce (*Picea sitchensis* Bong. Carr.) and Scots pine (*Pinus sylvestris* L.) are the two most economically important timber species, collectively making up >68% of all coniferous forest area, with *P. sitchensis* alone comprising 51% (Forest Research, 2020). *P. sitchensis* is considered to be a drought-susceptible species (Grant et al., 2018; Green et al., 2008; Huang et al., 2017) and often has a shallow rooting architecture in Scotland on upland sites (Coutts & Philipson, 1987), sometimes due to planting on seasonally waterlogged soils (Quine & Gardiner, 2007). In contrast, *P. sylvestris* is a widely distributed (Matías & Jump, 2012), more drought resistant species due to its ability to root deeper and access deeper water sources (Faulkner & Malcolm, 1972; Mickovski & Ennos, 2002), its higher cavitation resistance than *P. sitchensis* (Jackson et al., 1995) and ability to increase both fine root biomass of absorptive fine roots in mixed- relative to monospecific stands (Wambsganss et al., 2021). Similarly, differences in growth rates and the nutritional requirements of *P. sylvestris* and *P. sitchensis* has meant that these two species are sometimes planted in nursing mixtures where the pine facilitates the growth of the spruce through improved nitrogen availability on nutrient poor soils (Mason et al., 2021; Mason & Connolly, 2018). This in turn means that intimate mixtures of these two species likely result in structural variability, canopy stratification and differences in site microclimate (e.g., through shading). Consequently, these two species potentially express complementary functional traits that may also act to reduce drought stress when planted in intimate mixtures. However, little is known about the radial growth response of mature trees of either species to drought and to our knowledge, no study has yet compared the relative performance of these two species under drought conditions in both monospecific and mixed-species stands.

In this study, we set out to determine whether *P. sitchensis* and *P. sylvestris* differed in their resistance, recovery, and resilience to an extreme spring drought event in 2012 using an experimental forest of these two species containing both mixed and monospecific stands. We examined whether pre-drought tree size modulated individual drought response and how patterns at the tree level change depending on the species, neighbourhood composition at establishment and proportion of each species in intimate mixtures. Specifically, we aimed to test the following hypotheses:

1. *P. sitchensis* will exhibit lower resistance but higher recovery and resilience than *P. sylvestris* to a commonly experienced extreme drought event, reflecting the greater drought susceptibility of *P. sitchensis* and the observed trade-off in the components of tree resilience noted in other gymnosperms.
2. As more drought-susceptible species have been shown to benefit from the presence of more drought adapted species (Fichtner et al., 2020), *P. sitchensis* resistance and resilience will increase with the numbers of *P. sylvestris* trees in their immediate neighbourhood. In turn, this difference is expected to result in the highest drought resistance and resilience in those mixtures with the highest pine-to-spruce ratio.
3. Larger trees will show lower resistance and resilience to drought than smaller trees, reflecting the findings of other recent work across a range of species (Bennett et al., 2015).

4.3. Materials and Methods

4.3.1. Site description and management history

Our study site was established in 1988 as a nursing experiment to investigate the long-term differences in growth and yield between intimate mixtures of *Pinus sylvestris* and *Picea sitchensis.* Trees were planted in different proportions alongside monospecific stands of the same two species (**Figure 4.1** and **Table 4.1**) (Mason et al., 2021). The experiment is located in the north of Scotland (57°47'05.0"N, 4°08'53.5"W) at an elevation of 213m a.s.l. with the soil classified as a podzolic ironpan with a peaty surface horizon (i.e., a peaty layer of 15-45cm across much of the site). The site was cultivated to 60cm with a double mould-board plough and tine to break the ironpan at the time of establishment. The planting scheme resulted in monospecific stands of *Pinus sylvestris* and *Picea sitchensis* and five intimate mixtures of the two species (mixed in 25:75, 33:66, 50:50, 66:33 and 75:25 proportions), so that the eight trees immediately surrounding each focal tree characterised its neighbourhood (**Figure 4.1).** In this present study, we focused on the monospecific stands and the 25:75, 50:50 and 75:25 mixtures only. Four replicate plots of each treatment were established in a randomised block design, with each plot consisting of 100 trees in a 10x10 tree grid at 1.9 - 2.0m spacing (**Figure 4.1**) surrounded by a two- to three-deep tree buffer on all sides (buffer trees are not shown in **Figure 4.1**). A small amount of post-planting mortality was replaced with the original species across the experiment in 1989 and 1990 to ensure all plots were fully stocked. No fertilisers were applied to the treatments used in this study, but the site was known to be nitrogen deficient (Mason et al., 2021). No thinning had been conducted in the stand since it was established and no windthrow has been recorded historically or at the time of sampling. An experiment-wide mortality assessment was conducted visually between October and December 2018, during which the status of each tree (dead or alive) (**Figure 4.1** and **Table 4.2**) and its diameter at breast height (DBH – 1.3m) was recorded. While all mixtures had > 99% survival in 2000 (Mason et al., 2021), a considerable amount of mortality (predominantly *P. sylvestris*) was present across many of the treatments by 2018. We quantified neighbourhood composition based on planted species proportions, not post-mortality species proportions, because the former did not require additional assumptions to calculate, they represent a large proportion of the lifetime of the experiment (prior to the 2012 drought) and managers are less likely to modify tree neighbourhoods (e.g. due to economic constraints of selective thinning in short-rotation forestry), making the planted species proportions the treatment of more interest in this study. For a more detailed description of the site and tree establishment, see Mason et al. (2021).

4.3.2. Dendrochronological data

In November 2019, internal 6x6 tree plots were established centrally in each of the wider 10x10 tree plots, within which dendrochronological samples were collected for the following mixing proportions: SP, SS, SS25, SS50 and SS75 (**Figure 4.1** and **Table 4.1**). Two cores were collected using 5.15mm Haglöf increment borers from each live tree in the north and south direction (parallel with the direction of the plough lines) at 1.3m high in each of the four replicates of each mixture. In the pure *P. sitchensis* and *P. sylvestris* plots, 10 trees of each species were randomly selected for coring from each of the four replicates. This sampling design resulted in 706 useable cores (a small number of cores were damaged) from 353 sample trees. Additionally, the DBH at 1.3m high of all live trees from inside each internal 6x6 tree sample plot was measured. No samples were collected from dead trees. Sampling these mixing proportions produced a mirrored design, meaning that both *P. sitchensis* and *P. sylvestris* were represented by individual trees for which the eight-tree neighbourhood at establishment consisted of one, two, five, seven or eight conspecific and corresponding seven, six, three, one and zero heterospecific neighbours.

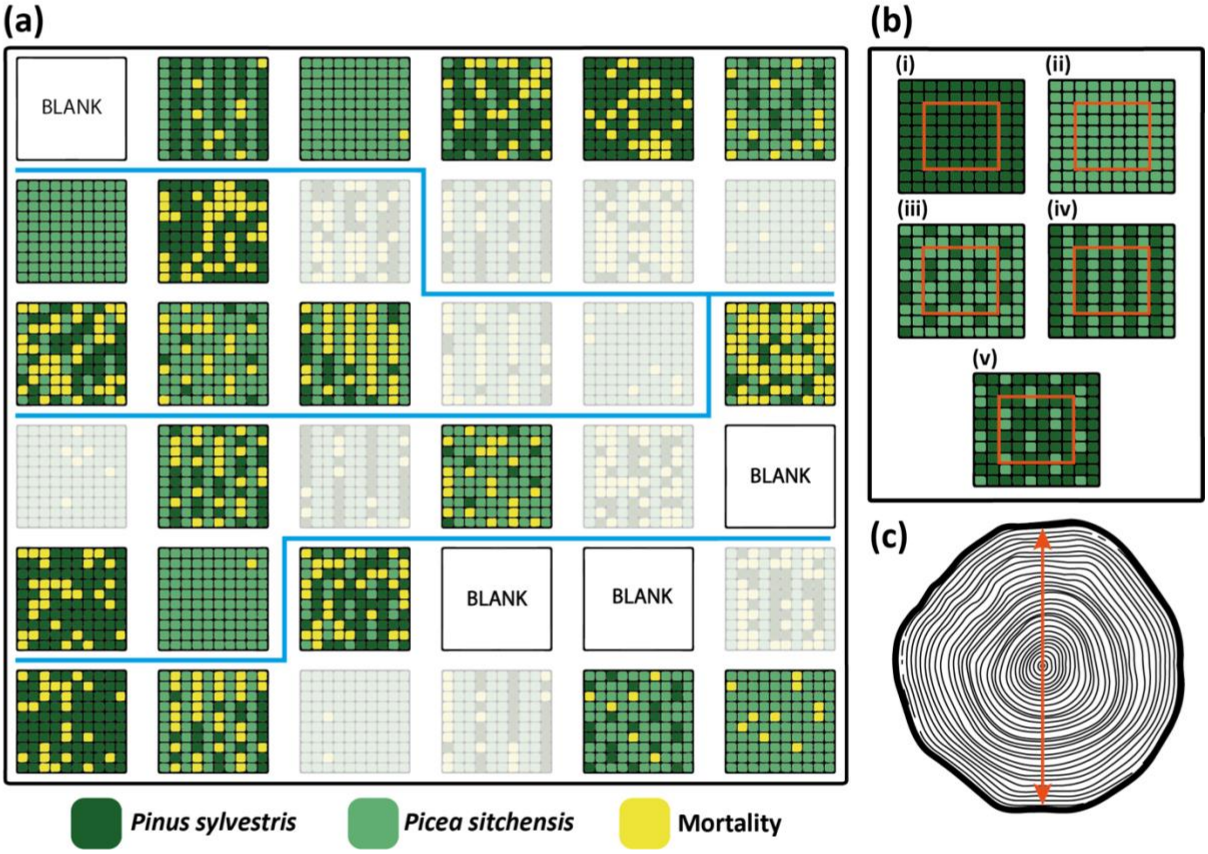

Figure 4.1 *- Experimental layout depicting the location of every tree and whether each tree was dead or alive in 2018. (a) Dark and light green squares indicate live P. sylvestris (SP) and P. sitchensis (SS) trees respectively, yellow squares indicate trees recorded as 'dead' during the 2018 survey and blue lines delineate the four blocks of the randomised block design. Plots labelled as "Blank" indicate filler plots with non-experimental trees established at the same time, while translucent plots are additional treatments which were not included in the present study. (b) Indicates the mixing proportions at establishment and resultant tree neighbourhoods used in the present study, with (i) = pure SP, (ii) = pure SS, (iii) = 75% SS with 25% SP, (iv) = 50% SS and 50% SP and (v) = 25% SS with 75% SP. Orange squares in (b) indicate the internal 6x6 sample plots from which dendrochronological data were collected from all live trees. (c) Indicates the north/south direction that tree-cores were collected.*

***Table 4.1** - Proportions of P. sylvestris (SP) and P. sitchensis (SS) in the three intimate mixtures (SS25, SS50 and SS75) used in this study along with a description of the conspecific and heterospecific neighbourhoods produced by each mixture (or monoculture – SP and SS).*

Treatment code	**Treatment details**	**Neighbourhoods**
SP	Pure SP	Each SP neighboured by 8 other SP
SS	Pure SS	Each SS neighboured by 8 other SS
SS75	A 75:25 SS and SP mixture. Mixture created by a pattern of one row of pure SS followed by one row with alternating pairs of SS and SP.	SS surrounded by 5 other SS and 3 SP SS surrounded by 7 other SS and 1 SP SP surrounded by 7 SS and 1 other SP
SS50	A 50:50 SS and SP mixture. Mixture created by a pattern of alternate rows of each species	SS surrounded by 2 other SS and 6 SP SP surrounded by 2 other SP and 6 SS
SS25	A 25:75 SS and SP mixture. Mixture created by a pattern of one row of pure SP followed by one row with alternating pairs of SS and SP.	SP surrounded by 5 other SP and 3 SS SP surrounded by 7 other SP and 1 SS SS surrounded by 7 SP and 1 other SS

Parts of this table have been modified with permission from Mason et al. (2021).

Table 4.2 *- Total number of trees noted as dead during the 2018 mortality assessment for each species (SP = P. sylvestris and SS = P. sitchensis) in pure (SP and SS) and mixed (SS25, SS50 and SS75) stands, summed across all four replicates in the wider 10x10 tree plots (Total mortality) and within the internal 6x6 tree sample plots (Total sample plot mortality). The Total number of sample trees refers to the number trees from which undamaged dendrochronological samples were used in the analysis. Values in parentheses indicate the percentage mortality of each species in each treatment across the wider experiment and in the sample plots.*

Mixture	**Species**	**Total mortality**	**Total sample plot mortality**	**Total number of sample trees**
SP	SP	113 (28%)	36 (25%)	40
SS	SS	12 (3%)	4 (3%)	40
SS25	SP	153 (51%)	49 (45%)	50
SS25	SS	0 (0%)	0 (0%)	27
SS50	SP	96 (48%)	41 (57%)	31
SS50	SS	0 (0%)	0 (0%)	72
SS75	SP	54 (54%)	20 (56%)	15
SS75	SS	7 (2%)	3 (3%)	78
		435	153	353

Each tree core was mounted, sanded with progressively finer sandpaper to ensure each ring boundary could be readily identified and then scanned at a resolution of 1600dpi. The width of each ring was subsequently calculated for each tree core using WinDENDRO image analysis software (Regents Instruments, Quebec). Each core was then crossdated, both visually and using the *dplR* package in R version 3.6.1 (R Core Team, 2019), resulting in 321 confidently dated trees (of the original 353 useable samples). These 321 trees were then detrended using an autoregressive detrending method using the *dplR* package to produce a Ring Width Index (RWI) (Bunn et al., 2019) (**Figure S4.1**). We used an autoregressive detrending method over other methods such as cubic smoothing splines as the use of splines did not adequately remove age related trends in our data, likely linked to the young age of our samples. We also calculated annual tree growth rate in terms of basal area increments (BAI) following **Eq. 4.1**,

Eq. 4.1

$$BAI = \pi(R_t^2 - R_{t-1}^2)$$

where *R* is the radius of the tree in year t. Tree size in terms of basal area (BA) was subsequently calculated for each year by summing annual BAI over time for each tree (**Table S4.1**).

4.3.3. Pointer year detection and climate analysis

We used the Standardised Growth Change (SGC) method to identify negative pointer years (PYs) in the tree-ring record (representing years of abnormally low growth) as this method has been shown to outperform other common PY detection methods (Buras et al., 2020). PY analysis was conducted using detrended RWI values for all trees across the common overlap period (2001 – 2019) and considered extreme if they lie outside the 95% confidence interval*,* meaning that only abnormally low growth episodes with a probability of occurring less than 0.025 are considered as negative Pys (Buras et al., 2020).

To identify any short term (monthly), seasonal (3 months), or multi-seasonal (6 months) droughts in the climate record, we calculated the Standardised Precipitation Evapotranspiration Index (SPEI) (Vicente-Serrano et al., 2010) using the *SPEI* package in R (Begueria & Vicente-Serrano, 2017). The SPEI uses a standardised climatic water balance calculated as the difference between precipitation and evapotranspiration over different timescales to give a relative measure of drought severity (Beguería et al., 2014; Vicente-Serrano et al., 2010). We calculated the SPEI for every month and year, integrated over one, two, three and six months from 1988 – 2019, reflecting the dates of tree establishment and sampling. The SPEI was calculated using interpolated climate data at 1 km resolution, obtained from the Climate Hydrology and Ecology

Research Support System (CHESS) meteorology dataset for Great Britain (Robinson et al., 2017). Only 2012 was identified as an extreme drought year between 1988 – 2019 (see section *4.4.1 – Drought year detection*) in both the climate and tree-ring record (when the experiment was 24 years old) and so this year became the focus of our analysis.

4.3.4. Neighbourhood competition

To assess the influence of neighbourhood competition on tree-level drought response, we calculated a distance-dependent index of neighbourhood competition in the year before drought (2011) following **Eq. 4.2,**

Eq. 4.2

$$TotNID_i = \sum_{j=1}^{8} \frac{BA_j}{distance_{ij}}$$

where $TotNID_i$ is the neighbourhood index for each tree (i), with eight neighbours (j), BA is the basal area of the jth competitor (cm) and *distance* is the distance between tree i and the jth neighbour (m) (Forrester et al., 2013; Vitali et al., 2018). Due to the sampling design and the way in which $TotNID_i$ is calculated (requiring the BA of all eight trees in each tree's immediate neighbourhood), $TotNID_i$ could only be calculated for live trees forming the central 4x4 trees inside the 6x6 tree sample plots. Any trees noted as dead during an experiment-wide mortality assessment carried out by Forest Research Technical Support Staff in 2018 were also considered to have been dead or exerting no competitive influence in 2011 and so had their BA set to zero for the purposes of calculating the $TotNID_i$ for live trees in the year before drought. Any sample trees that could not be confidently crossdated were excluded from this analysis, as were any trees for which an undatable tree would have formed part of the immediate eight tree neighbourhood (as the presence of an undatable tree in a focal tree's neighbourhood meant $TotNID_i$ could not be derived), resulting in 108 trees for which $TotNID_i$ in 2011 was calculated (34% of the crossdated trees).

4.3.5. Resistance, recovery, and resilience

To quantify the impact of the 2012 drought, we calculated the Resistance (*Rt*), Recovery (*Rc*) and Resilience (*Rs*) indices proposed by (Lloret et al., 2011) for each tree using RWI values. Resistance is commonly calculated as the ratio of growth in the drought year relative to a pre-drought growth average (Dr/PreDr), recovery as the ratio of a post-drought growth average to growth in the drought year (PostDr/Dr), and resilience as the ratio of a post-drought growth average to a pre-drought growth average (PostDr/PreDr). For these calculations, Dr, PreDr and PostDr are growth in the drought year and the pre- and post-drought growth averages respectively. Pre- and post-drought growth averages are normally calculated using between two- and four-years growth before and after the drought year (Rubio-Cuadrado et al., 2018; Steckel et al., 2020; Vitasse et al., 2019), however recent work has demonstrated how the choice of the number of years over which growth averages are calculated can influence estimates of these indices (Ovenden et al., 2021; Schwarz et al., 2020). To check our results were robust to the choice of pre- and post-drought period, we calculated multiple values of *Rt* for each tree using pre-drought growth averages derived from two, three and four years before the 2012 drought and calculated *Rc* for each tree one, two, three and four years after drought, instead of using a post-drought growth average. Calculating *Rc* in this way (as opposed to using post-drought growth averages) allowed recovery to be assessed annually throughout the post-drought period (where climate likely varied from year to year). We calculated *Rs* for each tree in the first, second, third and fourth years after drought using pre-drought growth averages derived from two, three and four years before drought, resulting in 12 estimates of *Rs* for each tree.

4.3.6. Statistical analysis

We initially fit three separate linear mixed-effects models using the *lme4* package in R (Bates et al., 2015) following **Eq. 4.3** to assess whether Resistance (*Rt*), Recovery (*Rc*) or Resilience (*Rs*) to the 2012 drought differed between species, neighbourhood composition and tree size in the year before drought (BA_{2011}). These models also allowed us to test whether our results were sensitive to the timescales used to calculate each index using all 321 confidently dated sample trees. *Rt*, *Rc* and *Rs* (response variables) were log-transformed prior to analysis to satisfy assumptions of normally distributed residuals.

Eq. 4.3

$$Index_{ij} = X_{ij}\beta + b0_{ij} + \varepsilon_{ij}$$

In **Eq. 4.3**, $Index_{ij}$ refers to either Resistance (*Rt*), Recovery (*Rc*) or Resilience (*Rs*) for the *j*th tree in the *i*th plot, X is an *n* x *p* matrix of *p* fixed effect variables (including *Species, Conspecific Neighbourhood, Index calculation* and BA_{2011} fixed effects) across the *n* measured trees, β is a *p* x *1* column vector of regression estimates, $b0_{ij}$ represents the random effect of $TreeID_{i}j$, where b_i ~ N(0, σ^2_{b0}) and ε_{ij} represents error term, where ε_{ij} ~ N(0, σ^2_ε). Σ^2_{b0} and σ^2_ε are estimates of variance of random effects and residual error, respectively. *Conspecific Neighbourhood* stands for the number of conspecifics in a focal tree's immediate neighbourhood of eight surrounding trees at establishment, with five treatment levels (one, two, five, seven and eight). *Index calculation* stands for the different combinations of the pre-drought and post-drought period lengths used to define the three indices. BA_{2011} was globally standardised across all trees (by subtracting the mean and dividing by the standard deviation) and represents tree size in the year before drought. Two-way interactions between *Species* × *Neighbourhood*, *Neighbourhood* × *Index calculation* and *Species* × *Index calculation* were included in all models.

We subsequently re-fit the same three mixed-effects models for *Rt*, *Rc* and *Rs* detailed in **Eq. 4.3** with the restricted dataset of 108 trees for which the 2011 neighbourhood competition index ($TotNID_i$) could be calculated but including $TotNID_i$ as an additional predictor variable to test for the influence of neighbourhood competition on *Rt*, *Rc* and *Rs*. No significant interactions between *Species* ×*TotNIDi* and *Neighbourhood* × $TotNID_i$ were found for any of the three models and so these interactions were dropped from the final models that included $TotNID_i$.

Finally, we fit three mixed effect models, again following **Eq. 4.3,** to investigate the differences in all three indices between the different mixtures (SS, SP, SS25, SS50 and SS75, **Table 4.1, Figure 4.1**), rather than between neighbourhoods. In this case, each index (*Rt*, *Rc* and *Rs*) was the response variable and *Species, Mixture, Index calculation* and BA_{2011} were fixed effects and *Tree ID* was a random effect. For all models, we checked for multicollinearity between predictor variables using the Variance Inflation Factor (VIF < 3 in all cases). We subsequently used the *emmeans* package in R (Lenth, 2016) to conduct post-hoc pairwise comparisons on all fitted mixed-effects models, and corrected for multiple comparisons using the Tukey method.

4.4. Results

4.4.1. Drought year detection

Standardised Growth Change analysis identified a single negative pointer year in the tree-ring record in 2012 ($p = 0.015$) and so this year became the focus of our analysis. The 1-month (SPEI of –2.22) and 2-month (SPEI of – 2.41) SPEI analysis showed that March 2012 corresponded to an extreme drought event (where extreme is defined as an SPEI < –2 (Hoffmann et al., 2018; Potop et al., 2014)). In contrast, SPEI values for April with a one-, two-, three- or six-month integration period in 2012 ranged from – 0.63 to 1.96, suggesting that drought conditions did not persist into April 2012. These SPEI values indicate that the extreme drought of 2012 at our study site can be characterised as a short duration, high intensity event in early spring. This assessment is reflected in the raw climate data which shows a combination of both abnormally low precipitation and abnormally high temperatures in March 2012, which in turn corresponds to the start of the growing season for the two study species in Scotland (Adams, 2014; Grace & Norton, 1990). March 2012 precipitation was > 2SD below the 1988 – 2011 average while the mean monthly temperature in March 2012 was > 2SD above the 1988 – 2011 average. In contrast, January 2012 was relatively wet with above average precipitation (2012 = 130mm compared with a 1988 – 2011 mean of 82 ± 43mm (1SD)) and average temperatures (2012 = 2.5°C compared with a 1988 – 2011 mean of 3 ± 1.3°C (1SD)) while both November and December 2011 were not abnormally dry (within 2SD of the 1988 – 2010 average). Collectively, this analysis suggests that it is unlikely that any growth depression in 2012 was due to an abnormally dry winter of 2011/12. Similarly, mean daily temperatures did not drop below zero during March, April, or May 2012, suggesting there were no late spring frosts in 2012 at this site that might have impacted tree growth.

4.4.2. Resistance, recovery, and resilience

Results from the mixed-effects modelling and *post-hoc* analysis using estimated marginal means revealed a significant difference in resistance (*Rt)*, recovery (*Rc*) and resilience (*Rs*) between *P. sitchensis* and *P. sylvestris* in response to the 2012 drought event (**Figure 4.2** and **Table 4.3**). *Pinus sylvestris* displayed significantly higher *Rt* (*P. sylvestris* = 0.924 ± 0.032 (1SE), *P. sitchensis* = 0.687 ± 0.020 (1SE), $p < 0.001$; **Figure 4.2a**), while *P. sitchensis* displayed higher *Rc* (*P. sylvestris* = 1.06 ± 0.034 (1SE), *P. sitchensis* = 1.32 ± 0.036 (1SE), $p < 0.001$; Fig 2b) regardless of the years used to calculate each index (**Figure 4.2b**), though the existence of significant interactions between *Species* and *Index calculation* (**Table 4.3**) indicated that the relationships between *Species* and *Rt*, *Rc* and *Rs* varied depending on the method used to calculate these indices. The interaction between *Species* and the *Index calculation* was more complex for *Rs.* The significant differences in resilience observed between *P. sylvestris* and *P. sitchensis* were dependent on the number of years used to calculate the pre-growth average (**Figure 4.2c**). For example, when using a two-year pre-drought growth average to calculate *Rs*, we found evidence that *P. sylvestris* had significantly higher *Rs* than *P. sitchensis* in the first, second, third and fourth years after the 2012 drought (**Figure 4.2c**). However, if pre-drought growth averages were calculated using four pre-drought years rather than two pre-drought years, *P. sylvestris* was only significantly more resilient than *P. sitchensis* in the second year after drought. We found no evidence that *P. sitchensis* was ever more resilient to drought than *P. sylvestris,* regardless of the approach to calculating *Rs* (**Figure 4.2c**).

Estimated marginal means indicated that monospecific stands (eight conspecific neighbours) had significantly higher *Rc* ($p < 0.04$) than neighbourhoods consisting of one or five conspecifics in the second year after drought only (**Figure 4.3b**), but these differences between neighbourhoods were not significant in the first or third year after drought. No other pairwise comparisons between other neighbourhood combinations were significant for *Rc* (**Figure 4.3b**). No significant interaction between *Species* and *Neighbourhood* was documented for *Rc, Rt or Rs* ($p > 0.07$ *in all cases)* (**Table 4.3**). Comparing estimated marginal means between neighbourhoods for each species separately showed that the only significant differences in *Rs* for both *P. sylvestris* and *P. sitchensis* were between the monospecific neighbourhoods and other neighbourhood types considered. Monospecific neighbourhoods were always associated with higher *Rs* compared to all other conspecific neighbourhoods or mixtures for *P. sitchensis* (**Figure 4.3c** and **Figure 4.4c**). In addition, *P. sylvestris* had significantly higher *Rs* than *P. sitchensis* when focal tree neighbourhoods contained one or two conspecifics ($p= < 0.005$ in both cases), but *P. sitchensis* never displayed higher *Rs* than *P. sylvestris* in any of the considered neighbourhood compositions. No other significant differences in *Rs* between species based on neighbourhood composition were detected.

Significant two-way interactions were identified between the approach used to calculate all three indices (*Index calculation*) and the conspecific *Neighbourhood* (**Table 4.3** and **Figure 4.3**), indicating that the relationship between neighbourhood composition and all three indices varied depending on the post-drought year and/or the number of years used to calculate each index. *Post-hoc* analysis using estimated marginal means found no significant differences in *Rt* between different neighbourhood compositions, regardless of the number of years used to calculate pre-drought growth averages and *Rt* (**Figure 4.3a**). Significant differences within neighbourhoods for *Rc* were only detected between methods that used two and four post-drought years to calculate post-drought growth averages in neighbourhoods consisting of one or two conspecifics, with a similar pattern found for *Rs*.

When considering average tree response in the different mixtures, a similar pattern emerged. No significant differences in *Rt* were found between any combinations of pure or mixed stands (**Table 4.4** and **Figure 4.4a**) but significant differences between monospecific and mixed stands were detected for both *Rc* and *Rs* ($p < 0.002$ in both cases, **Table 4.4,** and **Figures 4.4b** and **4.4c**). For *Rc*, pairwise comparisons of estimated marginal means show that monospecific stands of *P. sylvestris* and *P. sitchensis* were not significantly different from one another (p = 0.246, **Table 4.4**) and pure stands of *P. sylvestris* did not display significantly different values for *Rc* than any of the other mixtures (SS25, SS50 and SS75, p > 0.417 in all three cases). However, pure stands of *P. sitchensis* displayed significantly higher *Rc* than all three mixed stands (p < 0.006 in all three cases) (**Figure 4.4b**). Pairwise comparisons also showed that monospecific stands of both *P. sitchensis* and *P. sylvestris* displayed significantly higher *Rs* than all three mixed stands (p < 0.006 in all cases) but were not significantly different from each other (p = 0.204) (**Figure 4.4c**).

Finally, pre-drought tree size (BA_{2011}) was not a significant predictor of *Rt* or *Rs* (but marginally significant for *Rc*) (**Table 4.3**) and neither was $TotNID_i$ (**Tables S4.2**, $p > 0.21$ in all cases), indicating that neither tree size nor neighbourhood competition were likely associated with differences in the resistance or resilience of the trees in this experiment to the spring drought of 2012.

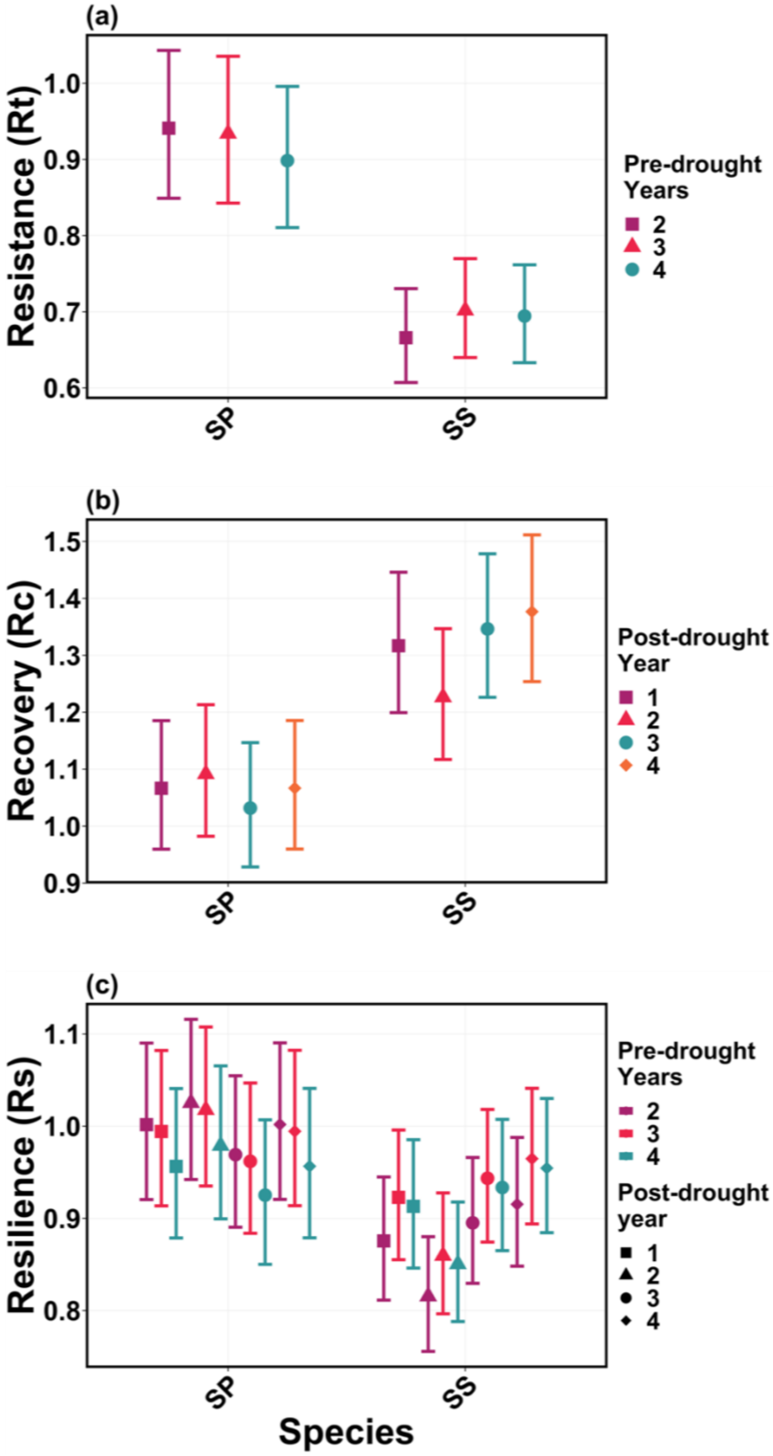

Figure 4.2 *- Differences in Resistance (a), Recovery (b) and Resilience (c) between P. sylvestris (SP) and P. sitchensis (SS) to the 2012 drought averaged across all conspecific neighbourhoods. Pre- or post-drought year(s) reflect the number of years used to calculate each index. Error bars represent 95% unadjusted confidence intervals and values were back-transformed onto the original scale.*

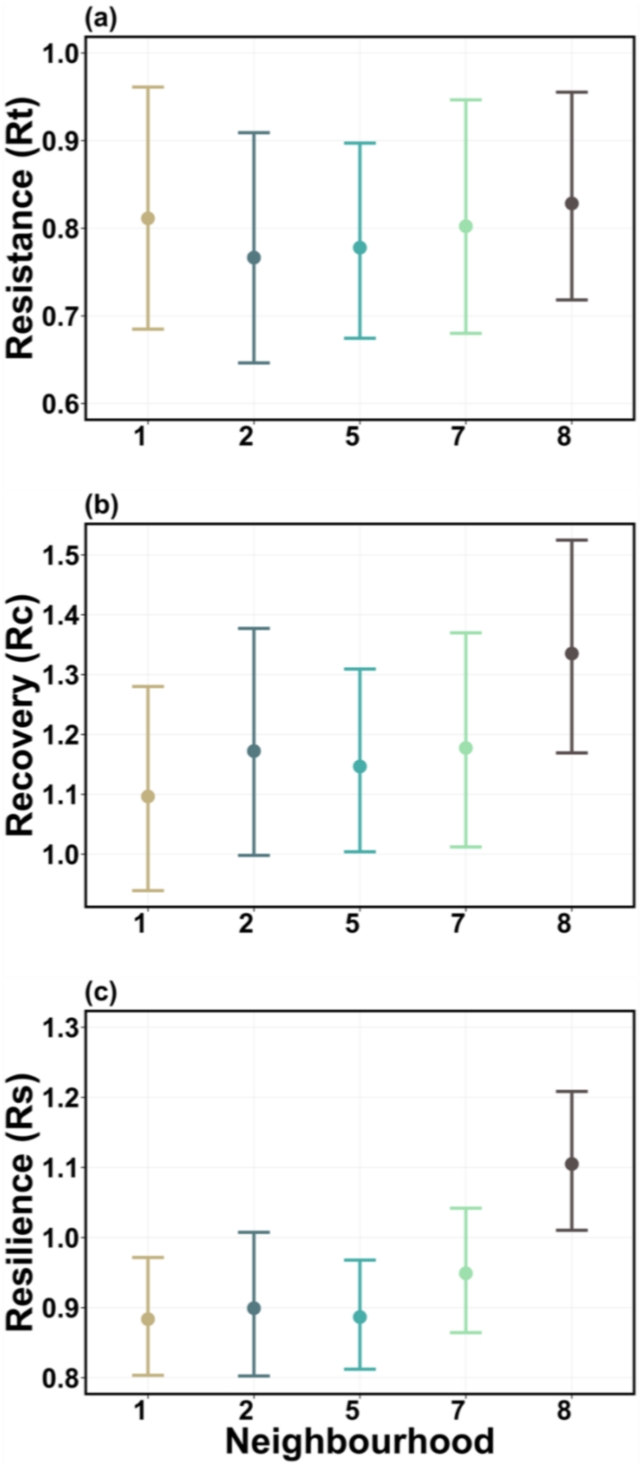

Figure 4.3 *- Differences in Resistance (a), Recovery (b) and Resilience (c) between conspecific neighbourhoods (one, two, five, seven or eight conspecifics) to the 2012 drought, averaged across species (P. sylvestris and P. sitchensis) and the number of years used to calculate each index. Error bars represent 95% unadjusted confidence intervals.*

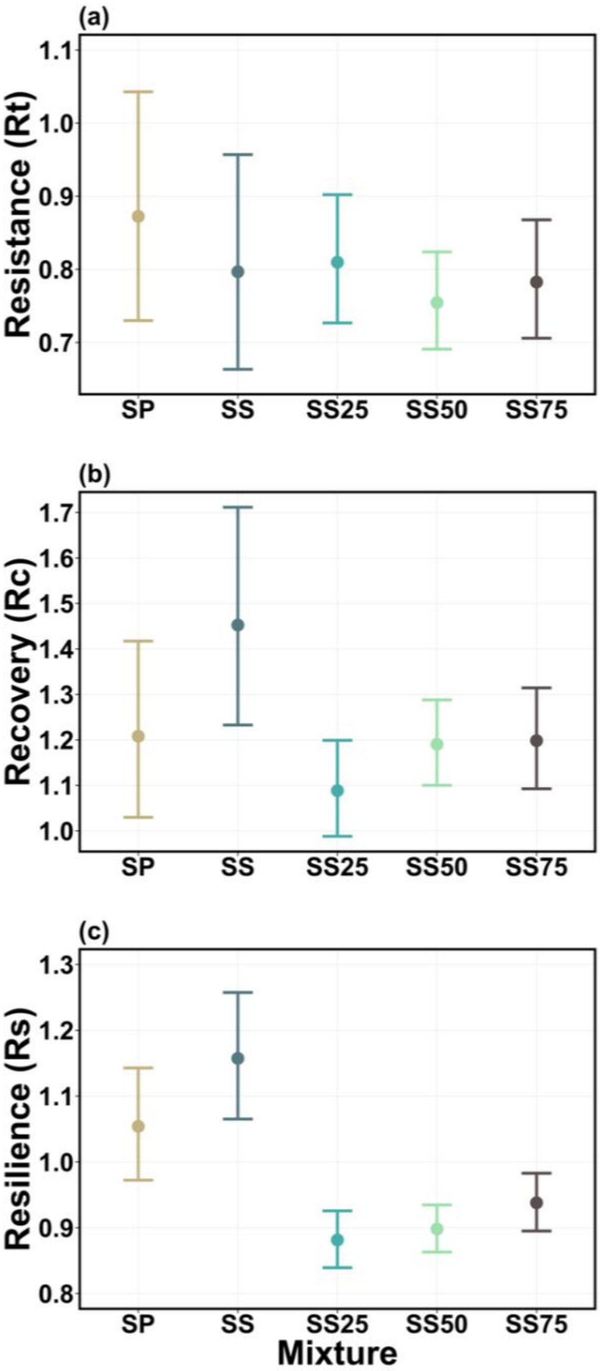

Figure 4.4 *- Differences in Resistance (a), Recovery (b) and Resilience (c) between the different monospecific and mixed species stands (SP = pure P. sylvestris, SS = pure P. sitchensis, SS25 = 25% P. sitchensis and 75% P. sylvestris, SS50 = 50% P. sitchensis and 50% P. sylvestris and SS75 = 75% P. sitchensis and 25% P. sylvestris, see* ***Figure 4.1*** *and* ***Table 4.1*** *for a more detailed description) to the 2012 drought, averaged across Species and Index calculation. Error bars represent 95% unadjusted confidence intervals.*

Table 4.3 *- Type 2 ANOVA for the mixed-effects models of Resistance (Rt), Recovery (Rc) and Resilience (Rs) for all 321 sample trees. Df = degrees of freedom, interactions are denoted by a × and significant effects ($p < 0.05$) are highlighted in bold. Species was either P. sitchensis or P. sylvestris while Neighbourhood indicates the number of conspecifics (one, two, five, seven or eight) in the immediate eight tree neighbourhood of every tree while BA$_{2011}$ represents tree size (basal area) in the pre-drought year (2011).*

Resistance (*Rt*)

	Chisq	*df*	*p-value*
Species	**64.033**	**1**	**<0.001**
Neighbourhood	2.821	4	0.588
Index calculation	**65.632**	**2**	**<0.001**
BA$_{2011}$	1.140	1	0.286
Species × Neighbourhood	2.071	4	0.722
Species × Index calculation	**100.929**	**2**	**<0.001**
Neighbourhood × Index calculation	**32.452**	**8**	**<0.001**

Recovery (*Rc*)

	Chisq	*df*	*p-value*
Species	**42.558**	**1**	**<0.001**
Neighbourhood	**10.304**	**4**	**0.356**
Index calculation	**25.181**	**3**	**<0.001**
BA$_{2011}$	**4.297**	**1**	**0.038**
Species × Neighbourhood	**6.300**	4	0.178
Species × Index calculation	**32.443**	**3**	**<0.001**
Neighbourhood × Index calculation	**25.411**	**12**	**0.013**

Resilience (*Rs*)

	Chisq	*df*	*p-value*
Species	**22.992**	**1**	**<0.001**
Neighbourhood	**44.464**	**4**	**<0.001**
Index calculation	**113.030**	**11**	**<0.001**
BA_{2011}	3.355	1	0.670
Species × Neighbourhood	8.526	4	0.074
Species × Index calculation	**152.565**	**11**	**<0.001**
Neighbourhood × Index calculation	**99.749**	**44**	**<0.001**

Table 4.4 *- Type 2 ANOVA for the mixed-effects models of Resistance (Rt), Recovery (Rc) and Resilience (Rs) for all 321 sample trees in the different mixtures. Df = degrees of freedom, Species was either P. sitchensis (SS) or P. sylvestris (SP), Mixture indicates the mixing proportions of the two species (SP, SS, SS25, SS50 and SS75) while* BA_{2011} *represents tree size (basal area) in the pre-drought year (2011). Significant results (*$p < 0.05$*) are highlighted in bold.*

Resistance (*Rt*)

	Chisq	df	*p-value*
Species	**32.39**	**1**	**<0.001**
Mixture	5.43	4	0.246
Index calculation	**54.60**	**2**	**<0.001**
BA_{2011}	0.58	1	0.448

Recovery (*Rc*)

	Chisq	df	*p-value*
Species	**14.49**	**1**	**<0.001**
Mixture	**19.37**	**4**	**0.001**
Index calculation	**24.01**	**3**	**<0.001**
BA_{2011}	2.37	1	0.124

Resilience (*Rs*)

	Chisq	df	*p-value*
Species	**25.43**	**1**	**<0.001**
Mixture	**118.86**	**4**	**<0.001**
Index calculation	**106.57**	**11**	**<0.001**
BA_{2011}	1.87	1	0.172

4.5. Discussion

In this study, we investigated whether the number of conspecifics in a focal tree's immediate neighbourhood, the degree of neighbourhood competition or species identity was associated with differences in the resistance (*Rt*), recovery (*Rc*) or resilience (*Rs*) of *P. sylvestris* and *P. sitchensis* to a short-duration, but high-intensity spring drought. Additionally, we investigated whether any relationship between neighbourhood composition and these three indices varied between the two species or with pre-drought tree size, whether any trade-off between these indices existed and how average tree response varied based on the mixing proportions at establishment. We found evidence that *P. sylvestris* was significantly more resistant and resilient to spring drought than *P. sitchensis*, but *P. sitchensis* exhibited greater recovery. In contrast to our expectations, monospecific neighbourhoods of both species displayed higher recovery and resilience than other neighbourhood compositions we considered. Pure stands of both species were also associated with greater levels of resilience than all mixed species stands, and pre-drought tree size and neighbourhood competition had little effect on drought resistance or resilience.

In support of our first hypothesis, we found evidence for a trade-off between resistance and resilience with recovery in *P. sitchensis* and *P. sylvestris* (**Figure 4.2**). Resistance (*Rt*) values for *P. sylvestris* were consistently higher than *P. sitchensis* across all neighbourhoods, reflecting the relatively greater drought resistance of *P. sylvestris*. In contrast to *Rt* and as expected, *P. sitchensis* displayed higher recovery (*Rc*) than *P. sylvestris* in each of the four post-drought years considered (**Figure 4.2**), in keeping with our first hypothesis and the trade-off reported by Gazol et al. (2017). However, in contrast to Gazol et al. (2017) and the analysis of gymnosperm responses to wet season droughts by Li et al. (2020), we did not find evidence of a resistance (*Rt*)/resilience (*Rs*) trade-off between the two species, as *P. sylvestris* was both more resistant and resilient than *P. sitchensis*. It is worth noting that trade-offs between resistance and recovery might be expected due to the way in which these indices are calculated. Resistance is a measure of growth reduction in the drought year relative to a pre-drought growth average, but recovery is a measure of post-drought growth relative to growth in the drought year. As a result, trees that show the greatest growth reductions in the drought year (i.e., least resistance) might also be expected to display the highest recovery values when recovery is rapid, resulting in an apparent trade-off while actually reflecting differences in initial drought resistance.

The high *Rt* of *P. sylvestris* to the early spring drought of March 2012 is in keeping with the findings of Merlin et al. (2015) who also found high resistance in this species to spring drought. However, Castagneri et al. (2015) found that successive periods of low precipitation in late spring (May) were associated with multi-year growth declines in *P. sylvestris* growing in north-western Italy. While the multidimensionality of drought (timing, duration, intensity, frequency, etc.) and other site factors (e.g. soil type) complicates the direct comparison of tree response to different events in different locations, a growing body of work is highlighting how species-specific vulnerabilities to drought are intimately linked to the timing of a given event (D’Orangeville et al., 2018; Forner et al., 2018; Huang et al., 2018; Kannenberg et al., 2019; Vanhellemont et al., 2018). This differential response of *P. sylvestris* to early and late spring droughts might indicate that the drought susceptibility of *P. sylvestris* is more temporally specific than previously thought, implying the need to explore drought vulnerability at an intra-seasonal resolution.

Despite its importance as a commercial timber species, very little research has assessed the growth response of *P. sitchensis* to drought using the resilience framework of Lloret et al. (2011) employed here. Huang et al. (2017) also noted *P. sitchensis* as having relatively low drought resilience but slightly higher drought resistance than found in our study, however Huang et al. (2017) focused on summer drought and did not consider the influence of neighbourhood composition. In a study of five major European tree species, Vitasse et al. (2019) found low resistance to extreme spring drought events in Norway spruce (*Picea abies* (L.)), a similarly drought-susceptible spruce species to *P. sitchensis*. However, Vitali et al. (2017) showed that the impact of drought on *P. abies* in Germany differed between drought events, being least resistant and resilient to the summer drought of 2003. Collectively, this evidence demonstrates the pressing need to understand the historic drought response of *P. sitchensis* under a range of both drought and site conditions and highlights the need to consider the interactions between the various dimensions of drought when making cross-study comparisons. Understanding these interactions will be key to ensuring forest managers can make informed decisions on how to increase the resilience of this commercially important species under global change.

While the between-species comparison of all three indices (*Rt*, *Rc* and *Rs*) in our study was often robust to the number of years used in the calculation (e.g., *P. sylvestris* consistently had higher *Rt* than *P. sitchensis*, regardless of the method used to calculate *Rt*), in many cases the absolute value for each index changed significantly depending on the pre- or post-drought period considered. Significant two-way interactions were observed for both *Neighbourhood* and *Species* with *Index calculation* for all three indices (**Table 4.3**) and through post-hoc comparisons using estimated marginal means (**Figure 4.2**). These findings echo other recent studies which demonstrate the risks of the often subjective *a priori* selection of a single pre- and post-drought period over which growth is averaged and these indices calculated (Ovenden et al., 2021b; Schwarz et al., 2020), whilst also highlighting how the lack of consistency in the choice of these periods seriously hampers cross-study comparability. In turn, these issues mean that we should be cautious in the use of meta-analytical approaches that attempt to synthesise studies on forest resilience (Castagneri et al., 2021), as the values for these indices may not be directly comparable where different approaches to calculating them have been used.

In contrast to our second hypothesis, we found that monospecific neighbourhoods exhibited both higher *Rc* than individuals with one or five conspecifics in their immediate neighbourhood (in the second year after drought only) and higher *Rs* than all other considered neighbourhoods, while no differences in *Rt* were detected between any of the neighbourhoods (**Figure 4.3**). Similarly, average tree response in monospecific plots of both species was consistently more resilient than any of the mixed-species plots we considered, while none of these mixtures were significantly different from one another for any of the three indices (**Figure 4.4**). We therefore found no evidence that increasing the proportion of *P. sylvestris* in the neighbourhood of *P. sitchensis* increased the resistance, recovery, or resilience of *P. sitchensis* to spring drought (or *vice versa*). Whilst we cannot rule out that some *P. sylvestris* mortality occurred due to drought, the relatively small impact of the 2012 drought on sampled *P. sylvestris* trees compared to *P. sitchensis* suggests this is unlikely. Similarly, we did not find any evidence that mixed-species stands of these two species displayed higher *Rt*, *Rc* or *Rs* than pure stands under drought, reflecting findings of no positive mixing effect for the *Rc* or *Rs* of *P. abies* to drought in similar studies (Gillerot et al., 2021; Vitali et al., 2018). Our findings appear to contrast with the proposal by Fichtner et al. (2020), that drought sensitive species with lower cavitation resistance (e.g. *P. sitchensis*) may benefit from more diverse neighbourhoods that include less drought sensitive species (e.g. *P. sylvestris*). However, our study was limited to comparisons of only one and two species mixtures and only considered the radial growth under a short but intense spring drought. Similarly, we acknowledge that while our study focused on the relative response to spring drought between these two species, the absolute impact on tree growth was small for *P. sylvestris*, suggesting the 2012 drought conditions may not have been severe enough to cross any threshold in this species (Ovenden et al., 2021a). Future research should investigate how intimate mixtures of these two species respond to different types of drought (i.e., differences in timing, duration, or intensity) across a range of sites to build a more comprehensive understanding of the conditions under which these mixtures might be beneficial or detrimental.

That monospecific stands were more resilient to drought than intimate mixtures of two species which potentially exhibit complementary functional traits (e.g. rooting depths) reflects other recent work showing negligible neighbourhood diversity effects on drought resilience (Gillerot et al., 2021). While our results agree with Bello et al. (2019), who documented faster growth in *P. sylvestris* monocultures than when mixed with *Quercus petraea*, they contrast with our second and third hypotheses as well as other work on both *P. sylvestris* (Merlin et al., 2015; Steckel et al., 2020) and other spruce species (*P. abies*) (Ding et al., 2017). This difference between studies is unlikely to be linked to differences in tree age, as both Ding et al. (2017) and Merlin et al. (2015) examined the drought response of *P. sylvestris* and *P. abies* trees that were of a similar age to those used in this present study when drought occurred.

At the stand level, the lowest total stand basal area observed in the year before the 2012 drought was in the pure stands of *P. sitchensis,* with the second lowest total basal area being in the pure stands of *P. sylvestris*. These results reflect the findings of Mason et al. (2021), who present evidence of significant overyielding in all mixtures relative to the monocultures at this same site both 15 and 30 years after they were planted in 1988. Mason et al. (2021) suggest that the overyielding of these mixtures is due to the initial facilitation of spruce growth due to the nutritional benefits of being mixed with pine on nitrogen deficient soils. As the canopy closes, Mason et al. (2021) suggests that these facilitative mechanisms then give way to intense competition, with the faster-growing spruce outcompeting the light-demanding pine, causing pine mortality and subsequently a reduction in inter-tree competition. Neighbourhood competition was not a significant predictor of *Rt*, *Rc* or *Rs*, suggesting that these stands might have been in a developmental phase where facilitative processes rather than competitive ones were still dominant when the 2012 drought occurred, or that sufficient pine mortality had already occurred for inter-tree competition to be of minimal importance for regulating tree drought response. While it is possible that neighbourhood composition and competition were confounded in our analysis, VIF values <3 suggested low multicollinearity between predictor variables.

In our study, the SS25 and SS50 mixtures (**Table 4.1**) had both the lowest mean resilience values (**Figure 4.4c**) and the highest levels of mortality (all of which was *P. sylvestris*) in both the internal 6x6 tree sample plots and the wider 10x10 tree plots (**Figure 4.1** and **Table 4.2**). As we calculated neighbourhood competition using only those eight trees in a focal tree's immediate neighbourhood, such high levels of *P. sylvestris* mortality would likely result in an index of low neighbourhood competition but need not necessarily be reflected by a low stand basal area, as those remaining live trees grow larger due to competitive release following the mortality (or heavy suppression) of their neighbours. Indeed, when the experiment was 30 years old, Mason et al. (2021) estimated the largest mean *P. sitchensis* DBH (28.7cm) to be in the mixture with the lowest proportion of *P. sitchensis* (SS25). These results may indicate that, while individual tree basal area or estimates of competition derived from the basal area of local neighbourhoods were not significant predictors of any of *Rt*, *Rc* or *Rs*, higher total stand basal area might influence recovery and resilience at both the tree and stand level, reflecting the hypothesis that mixtures may require more resources to sustain above-ground productivity (Wambsganss et al., 2021). This result is particularly interesting as tree size itself was not a significant predictor of tree level resistance or resilience, highlighting the need to consider the influence of tree mortality and facilitative/competitive processes at both the tree and stand scales when assessing forest drought response (Bottero et al., 2021).

Collectively, our results demonstrate the importance of inter-species differences in drought tolerance and how intimate two-species mixtures do not automatically confer greater drought resistance or resilience. Instead, our findings suggest there is a need to more precisely understand the drought conditions, species composition, tree age and developmental stage at which species mixtures might become beneficial if we are to increase forest resilience to drought.

4.6. Conclusion

Understanding how to adapt our planted forests to deal with the challenges of a changing climate is of critical importance if we are to ensure the continuity of these habitats and the products and services we derive from them. Despite the call by Messier et al. (2021) to diversify the species composition of our planted forests to increase their resilience, these authors also suggest that the strength of evidence regarding the susceptibility of monospecific vs mixed-species plantations to drought is low. In our study, we found that monospecific neighbourhoods of both *P. sitchensis* and *P. sylvestris* were more resilient to spring drought than any of the intimate mixtures we considered, highlighting the need to better understand the complexity of diversity-resilience relationships.

To our knowledge, this is the first study to assess both the historic drought response of *P. sitchensis* in the UK and the first study to evaluate the relative drought response of intimate mixtures of key commercial UK species. Considering the economic and ecological importance of these two species alongside the overyielding in these species mixtures reported by Mason et al. (2021), developing a more comprehensive understanding of how these (and other) species have responded to a range of historic drought conditions in both mixed and monospecific stands will be essential if we are to inform effective management decisions that balance a range of objectives.

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4.8. Supplementary Material

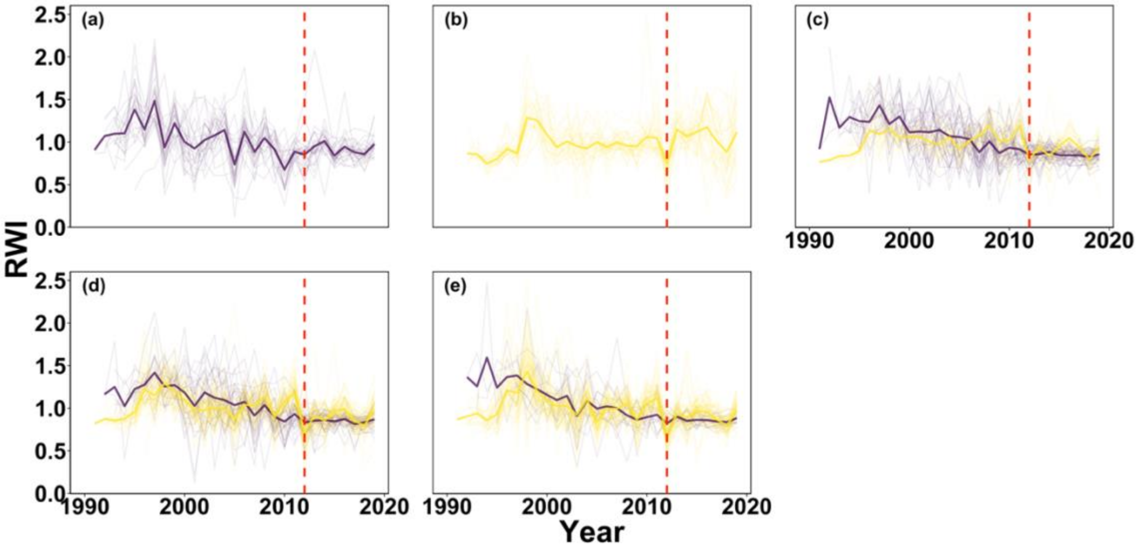

Figure S4.1 *- Annual ring width index (RWI) values for dendrochronologically sampled P. sylvestris (SP - purple lines) and P. sitchensis (SS - yellow lines) trees in (a) pure SP, (b) pure SS, (c) 25:75 SS:SP mixture, (d) 50:50 SS:SP mixture and (e) 75:25 SS:SP mixture. Thicker lines of the same colours indicate mean annual RWI values, and the vertical red dashed lined indicates the spring drought of 2012.*

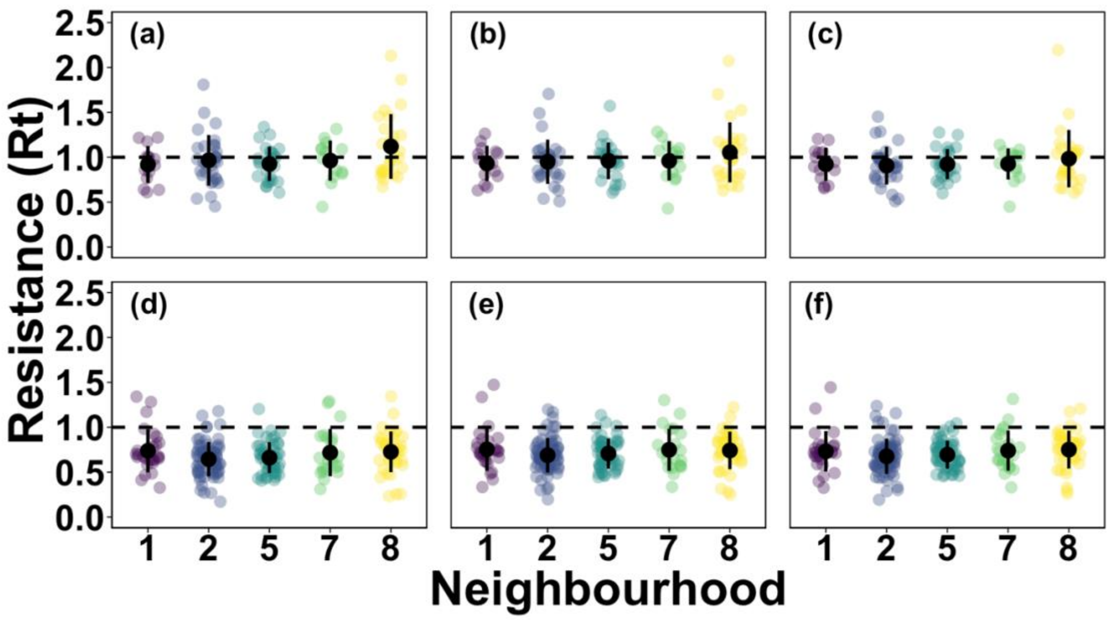

Figure S4.2 *- Differences in resistance (Rt) for P. sylvestris (a, b and c) and P. sitchensis (d, e and f) to the 2012 extreme drought event based on the number of conspecifics in the immediate eight tree neighbourhood (x-axis) using different numbers of pre-drought years to calculate the pre-drought growth average. Resistance was calculated using a two-year pre-drought growth average (a and d), three-year pre-drought growth average (b and e) and four-year pre-drought growth average (c and f). Coloured dots represent individual trees while black dots and error bars represent the mean ± 1SD.*

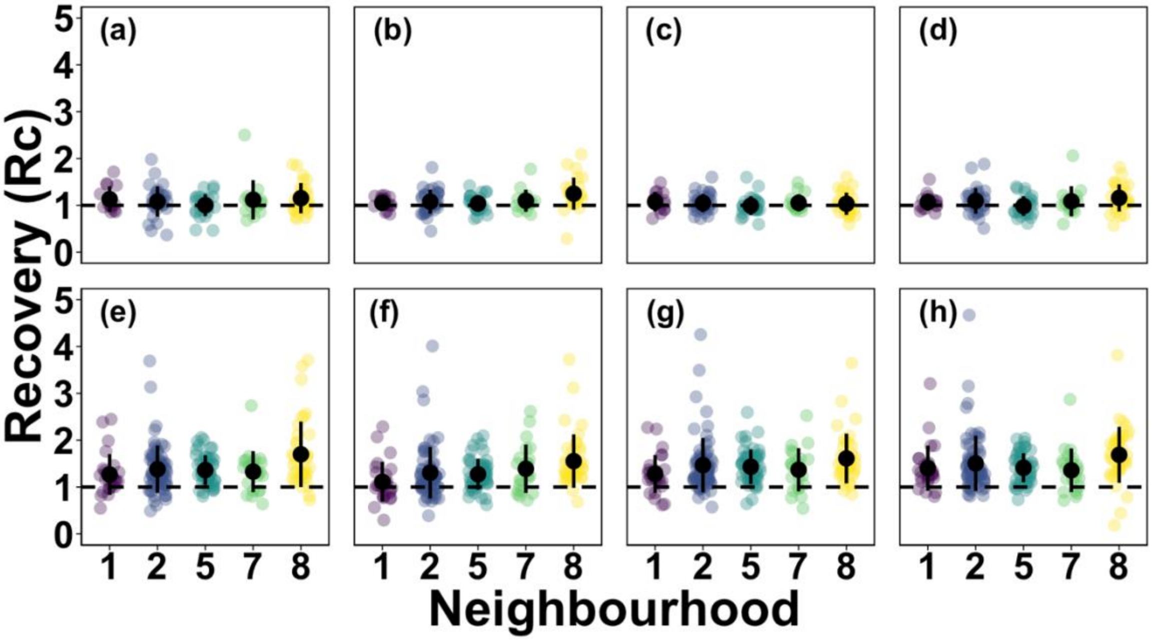

Figure S4.3 *- Differences in recovery (Rc) for P. sylvestris (a, b, c and d) and P. sitchensis (e, f, g and h) following the 2012 extreme drought event based on the number of conspecifics in the immediate eight tree neighbourhood (x-axis). Recovery was calculated for the first (a and e), second (b and f), third (c and g) and fourth (d and h) year after drought. Coloured dots represent individual trees while black dots and error bars represent the mean ± 1SD.*

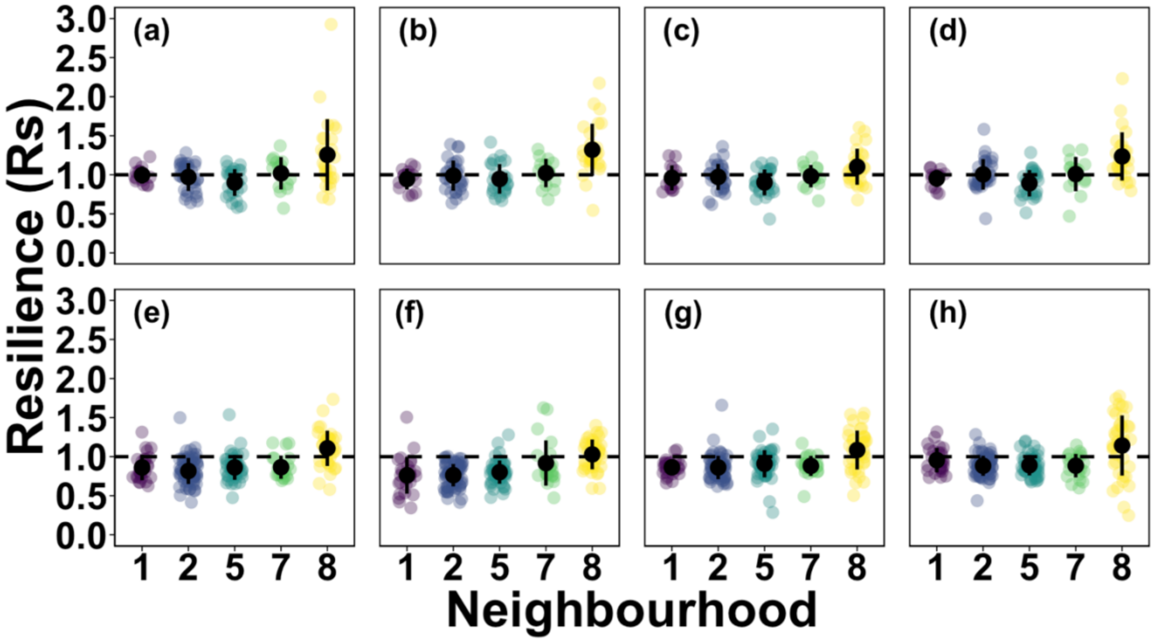

Figure S4.4 *- Differences in resilience (Rs) for P. sylvestris (a, b, c and d) and P. sitchensis (e, f, g and h) following the 2012 extreme drought event based on the number of conspecifics in the immediate eight tree neighbourhood (x-axis). Resilience was calculated for the first (a and e), second (b and f), third (c and g) and fourth (d and h) year after drought using a two-year pre-drought growth average. Coloured dots represent individual trees while black dots and error bars represent the mean ± 1SD.*

Table S4.1 *- Summary of mean (±1SD) tree BAI (basal area increment) and BA (basal area) for each combination of species and neighbourhood composition in 2011 (the year before drought) for 321 sample trees whose dendrochronological data were collected and could be accurately dated. n = sample size.*

Species	**Neighbourhood**	**BAI (cm^2)**	**BA (cm^2)**	***n***
P. sylvestris	1 SP, 7 SS	5 (3)	147 (46)	14
P. sylvestris	2 SP, 6 SS	5 (2)	142 (45)	31
P. sylvestris	5 SP, 3 SS	6 (2)	151 (55)	26
P. sylvestris	7 SP, 1 SS	4 (2)	141 (47)	15
P. sylvestris	8 SP	6 (4)	213 (100)	27
P. sitchensis	1 SS, 7 SP	35 (15)	456 (166)	27
P. sitchensis	2 SS, 6 SP	19 (10)	282 (114)	70
P. sitchensis	5 SS, 3 SP	15 (8)	263 (102)	50
P. sitchensis	7 SS, 1 SP	12 (7)	210 (89)	22
P. sitchensis	8 SS	6 (4)	85 (63)	39

***Table S4.2** - Type 2 ANOVA for the mixed-effects models of resistance (Rt), recovery (Rc) and resilience (Rs) for the restricted sample of 108 trees for which the neighbourhood competition index (TotNID) could be calculated. Df = degrees of freedom, interactions are denoted by a × and significant effects ($p < 0.05$) are highlighted in bold. Species was either P. sitchensis or P. sylvestris while Neighbourhood indicates the number of conspecifics (one, two, five, seven or eight) in the immediate eight tree neighbourhood of every tree while BA_{2011} represents tree size (basal area) in the pre-drought year (2011).*

Resistance (*Rt*)

	Chisq	*df*	*p-value*
Species	**22.521**	**1**	**<0.001**
Neighbourhood	**9.933**	**4**	**0.042**
Index calculation	**17.031**	**2**	**<0.001**
BA_{2011}	0.240	1	0.624
TotNID	0.667	1	0.414
Species x Neighbourhood	2.442	4	0.655
Species x Index calculation	**27.007**	**2**	**<0.001**
Neighbourhood x Index calculation	14.600	8	0.067

Recovery (*Rc*)

	Chisq	*df*	*p-value*
Species	**23.644**	**1**	**<0.001**
Neighbourhood	4.448	4	0.349
Index calculation	**39.801**	**3**	**<0.001**
BA_{2011}	0.176	1	0.675
TotNID	0.086	1	0.770
Species x Neighbourhood	3.223	4	0.521
Species x Index calculation	**25.904**	**3**	**<0.001**
Neighbourhood x Index calculation	**29.984**	**12**	**0.003**

Resilience (*Rs*)

	Chisq	*df*	*p-value*
Species	1.714	1	0.190
Neighbourhood	**45.696**	**4**	**<0.001**
Index calculation	**139.272**	**11**	**<0.001**
BA_{2011}	0.120	1	0.729
TotNID	1.604	1	0.205
Species x Neighbourhood	4.473	4	0.346
Species x Index calculation	**105.703**	**11**	**<0.001**
Neighbourhood x Index calculation	**113.099**	**44**	**<0.001**

CHAPTER 5 - Identifying and characterising the multi-dimensionality of extreme drought using the Standardised Precipitation Evapotranspiration Index

The chapter is currently being prepared for submission to the Journal *Agricultural and Forest Meteorology*

5.1. Abstract

The predicted increase in drought frequency and severity across many parts of the world in the coming decades is intensifying the need to accurately identify and characterise historic drought events and their impact. The Standardised Precipitation Evapotranspiration Index (SPEI) has rapidly become the most widely used approach to characterising drought severity, particularly in the forest sciences. The SPEI is a powerful tool for estimating the relative severity of historic drought events, yet the efficacy of this index and the interpretations derived from it are intimately linked to the choice of focal month and integration timescale over which it is calculated. We demonstrate how small differences in the selected values of these two parameters changes whether we consider a given year to be a drought event, limits our ability to detect events in different seasons and potentially obscures our understanding of important drought characteristics such as timing, duration, and intensity. We show how the complementary use of the Climatic Water Deficit and basic climate analysis can enable a more informed selection of the candidate month and integration timescales over which the SPEI is calculated, and drought severity derived. This approach builds on the strengths of the SPEI to enable a more robust understanding of the multidimensionality of drought and facilitates cross-study comparison of organismal and systemic responses to drought events.

5.2. Introduction

Extreme drought events are expected to increase in frequency and severity across many parts of the world in the coming decades as our climate continues to warm (McDowell et al., 2018; Xu et al., 2019). The threat of these events to ecosystem stability and the continuity of ecosystem services has seen a surge in studies that attempt to quantify the impact of historic drought events, particularly in forest ecosystems (Nikinmaa et al., 2020), and understand the response dynamics of these systems (Anderegg et al., 2015; Kannenberg et al., 2020; Kannenberg et al., 2019; Lloret et al., 2011; Ovenden et al., 2021b; Peltier & Ogle, 2020). Consequently, there is a critical need for us to accurately identify drought events in the climate record, quantify their severity and characterise their intensity, timing, duration, and impact.

While many drought indices exist, the Standardised Precipitation Evapotranspiration Index (SPEI) (Vicente-Serrano et al., 2010) is the most commonly applied. Much of the success of the SPEI is due to its multi-scalar nature and the incorporation of water balance from *n* previous months (the integration period) with temperature, which allows it to outperform other drought indices such as the self-calibrated Palmer Drought Severity Index (sc-PDSI) and the SPEI's predecessor, the Standardised Precipitation Index (SPI) (Gurrapu et al., 2014; Vicente-Serrano et al., 2010, 2013). While some have called for the widespread adoption of the SPEI as a standardised approach to quantifying drought severity (Slette et al., 2019), others have raised concerns about the over reliance on the SPEI as a single drought metric, advocating its use in combination with complementary indices such as the Climatic Water Deficit (CWD) (Zang et al., 2019). In part, these concerns stem from the fact that the SPEI can misclassify a year as a drought, particularly in moist climates where a negative SPEI need not necessarily indicate a water deficit (Vicente-Serrano et al., 2013; Zang et al., 2019). The consequence of such misclassification can range from assessing the impact of drought events that never occurred, through to underestimating the severity of events that did occur, both of which risk clouding our understanding of drought impact.

Here we highlight that whilst the use of complementary metrics can improve the identification of a drought event, an informed selection of the SPEI parameters (focal month (f_m) and integration period (t_i)) is essential to ensure different types of drought are not missed or miss-characterised, particularly those of a shorter duration which are known to be of particular importance across biomes (Vicente-Serrano et al., 2013). We demonstrate how any *a-priori* choice of focal month and integration period when calculating the SPEI can limit our ability to identify drought events, alter how we characterise their severity and miss crucial aspects needed to describe their multidimensionality, such as duration and seasonality. We conclude by suggesting approaches to SPEI parameter selection through the complementary use of the CWD and raw climate data to catalyse a more critical approach to drought identification and characterisation. In turn we believe this advance will provide much needed insight into the specific characteristics of a given drought whilst facilitating robust cross-study comparisons.

5.3. SPEI parameter selection and their implications

At the core of the calculation of the SPEI is the selection of a target month for which the index will be calculated and the length of an integration period (often between 1 – 24 months), which defines the number of months prior to the target month to be included in the calculation. The climatic water balance (CWB) for the target month and all of the months in the integration period are then summed to provide a deficit/surplus, adjusted to a log-logistic probability distribution and standardised so that SPEI values are presented as standard deviations of the mean for that target month and integration period combination (Vicente-Serrano et al., 2010).

Various approaches exist in the literature for selecting an integration period. One approach used in dendroecology calculates SPEI values for each month of each year over many different timescales, sometimes incorporating all combinations of between 1 and 24 historic months, and subsequently establishing which combination shows the highest correlation to observed tree-ring width chronologies (Camarero et al., 2018;

Vicente-Serrano et al., 2013) or basal area increments (Vanhellemont et al., 2018). Alternatively, biologically meaningful SPEI timescales are selected, for example a 12 month SPEI is calculated (Andivia et al., 2018), often starting with the month after the cessation of growth from the preceding growing season (Cavin et al., 2013). The timing and duration of the growing season itself is sometimes used (Merlin et al., 2015), however a range of other SPEI integration periods are found throughout the literature (Camarero et al., 2018; Príncipe et al., 2017; Sánchez-Salguero et al., 2018). The derived SPEI values are then assessed, droughts identified and severity classified, often using pre-defined thresholds of drought severity (Conte et al., 2018; Merlin et al., 2015; Vanhellemont et al., 2018). These thresholds commonly follow Potop et al., (2014) with SPEI values of ≤ –1 but > –1.5 indicating a drought (Bose et al., 2020), < –1.5 but > –2 indicating a severe drought (Gazol et al., 2020) and ≤ –2 indicating extreme drought (Hoffmann et al., 2018).

However, it is important to remember that the calculation of the SPEI for a given month and integration period is a *relative* measure of drought severity, and akin to asking the question:

"Taking into account χ previous months (the integration period), how bad was month γ relative to average conditions for that same month in previous years if we consider the same integration period?"

As a result, the *a priori* decision of which month and integration period to use to calculate the SPEI constrains the type of drought we can detect in terms of both its timing and duration and modulates our interpretation of drought severity. For example, an SPEI calculated for August with a six-month integration period cannot detect any drought event occurring in the northern hemisphere autumn and/or winter, since these months are not included in the calculation. Similarly, if this is the only focal month and integration period assessed, such a six-month integration period pre-supposes that all droughts in the climate record begin in March and conclude in August. However, should a drought have occurred between March and May but been followed by an unusually wet and mild June and July, the way in which the SPEI integrates the CWB over these six months for August may obscure the true severity of a northern-hemisphere spring drought. Alternatively, in this same example, if drought conditions persisted into September, our August example could not capture the totality of such a drought. Similarly, while correlating all possible month × integration period combinations with annual growth is methodologically attractive, the reduction of these combinations to a single focal month and integration period also assumes that all drought events in the climate record can be adequately captured and characterised by this single combination.

5.4. Exploring the constraints imposed by SPEI parameter selection

To demonstrate the importance of parameter selection when using the SPEI, we calculated the SPEI for every month using one, three, six and 12 month integration timescales for a site in the north of Scotland (57˚47′N and 4˚8′W) between 1989 and 2019 using the *SPEI* package (Vicente-Serrano et al., 2010) in *R* (R Core Team, 2021). We used interpolated climate data at 1 km resolution, obtained from the UK Met Office Centre for Environmental Data Analysis (Met Office et al., 2020). We then investigated how different focal months and integration periods altered the detection and characterisation of four drought events that are known to have occurred in the UK in 1995, 2003, 2012 and 2018 (Buras et al., 2020; Ciais et al., 2005; Fink et al., 2004; Hulme, 1997; Parry et al., 2013). For the purposes of demonstration, we restricted our analysis to ‘severe’ and ‘extreme’ droughts, defined according to the standard SPEI thresholds of drought severity where < -1.5 and > -2 indicates severe drought, and ≤ -2 indicates extreme drought (Potop et al., 2014). We also calculated mean monthly temperature and precipitation values along with monthly CWD values for each year at this site using code developed by Redmond (2019) which implements the approach detailed in Lutz et al. (2010).

5.5. The 2018 drought year

In 2018, the three and six-month SPEI integration periods with a July focal month both agree on an extreme drought event (**Figures 5.1b - 5.1c**). However, August, September, and October focal months with a six-month SPEI integration instead characterise 2018 as a severe drought, whilst a three-month SPEI integration period for August, September, and October indicates no drought occurred (**Figures 5.1b – 5.1c**). Similarly, no severe or extreme drought event is identified in 2018 in any month if a 12-month integration is used (**Figure 5.1d**). Analysis of monthly CWD in 2018 shows a very small deficit beginning in May, peaking in July, and followed by a rapid decline to low deficit values in August with no deficit in September, indicating four months of CWD in 2018 (**Figure 5.2**). This pattern in CWD is reflected in the precipitation and temperature data for 2018 which shows above average temperature in May, June and July and below average precipitation, predominantly in May and June and slightly below average in July and August (**Figure 5.3a**). As such, there is a climatological justification for a focal month of July or August with a three to four-month integration period, but average temperatures, above average precipitation and zero CWD indicate that at this site, any drought condition were likely alleviated by September 2018 (**Figures 5.2** and **5.3a**). Similarly, January and March precipitation in 2018 was above average whilst temperatures in January, February and March were all well below average (**Figure 5.3a**) suggesting that longer SPEI integration timescales may risk obscuring or reducing the 2018 drought signal by including months with a positive water balance in the calculation of SPEI.

5.6. The 2012 drought year

In 2012, a 1-month SPEI indicates March may have been an extreme month at the onset of spring, a critical time for plant growth. However, no other SPEI integration period identifies an event in 2012 (**Figures 5.1a – 5.1d**) and no CWD was detected during any month in 2012 (**Figure 5.2**). Analysis of the precipitation and temperature data does show that March temperatures were well above average and March precipitation was also extremely low (**Figure 5.3b**), indicating that while there was no detectable CWD in March, an SPEI with a 1-month integration timescale may be justified (**Figure 5.1a**) as monthly temperature and precipitation at this site was extremely high and low (respectively) relative to average March conditions.

5.7. The 2003 drought year

Both 6 and 12-month SPEI integration periods for July in 2003 identify a severe drought, however a three-month SPEI for July doesn't detect a drought year at all (**Figures 5.1b – 5.1d**). Similarly, while a 3, 6 and 12-month SPEI for August all identify a drought event in 2003, a 12-month SPEI integration period for August classifies 2003 as extreme, whereas both 3- and 6-month integration timescales classify it as severe (**Figures 5.1b – 5.1d**). Both 6 and 12-month SPEI integration timescales for November identify 2003 as extreme, while a 3-month SPEI in November doesn't detect a drought year at all (**Figures 5.1b – 5.1d**). Negative CWD values in 2003 start in June and peak in August (**Figure 5.2**), reflecting both the above average temperatures and below average precipitation for these three months (**Figure 5.3c**) and suggests a focal month of August but not July might be suitable, as the latter would fail to capture the entire drought event in 2003. While temperatures return to, or even fall below average values from September, precipitation in 2003 continues to remain below average into November (**Figure 5.3c**), and likely explains why an SPEI for November 2003 with a 6-month integration is classified as extreme (**Figure 5.1c**). Similarly, the classification of 2003 as extreme when August, November or December is the focal month with a 12-month integration period (**Figure 5.1d**) likely reflects the low precipitation in February and March and above average March temperatures which are captured by this longer integration period (**Figure 5.3c**). It is questionable whether a 12-month SPEI integration period, that incorporates February and March, is justified considering the observed above average precipitation in April and May, or whether these periods should be considered separately (**Figure 5.3c**). Equally, while below average rainfall may have persisted into November, it is likely that tree radial growth will have mostly ceased by this point (Jyske et al., 2014) and should also be considered when selecting appropriate month × integration period(s) to characterise a given drought event.

5.8. The 1995 drought year

While a 1-, 3- and 6-month SPEI for August 1995 agree a drought occurred, 1- and 6-month SPEI integration timescales for August suggest there was an extreme drought in 1995 while a 3-month integration classifies 1995 as a severe drought (**Figures 5.1a – 5.1c**). In contrast, a 12-month SPEI integration period for August 1995 indicates no drought occurred at all (**Figure 5.1d**). Similarly, if July or September were selected for any of the four integration periods presented here rather than August, we would conclude that no drought event occurred in 1995 (**Figures 5.1a – 5.1d**). Analysis of the CWD for 1995 indicates a similar pattern to that of 2003, with a small deficit appearing in June, peaking in August, and returning to zero by September, but a greater CWD than 2003 when summed across these months (**Figure 5.2**). This is, again, reflected in the climate data, with precipitation considerably below average from June to August, with July and August also experiencing above average temperatures, while September was extremely wet and temperatures returned to average (**Figure 5.3d**). The extremely wet September, coupled with the average climate in April and May (**Figure 5.3d**) and the high CWD values between June and August (**Figure 5.2**) suggest that any drought at this site in 1995 was a summer drought between June and August. As such, a focal month of August with a 3-month SPEI integration period might be appropriate to characterise the severity of this drought event (**Figure 5.1b**).

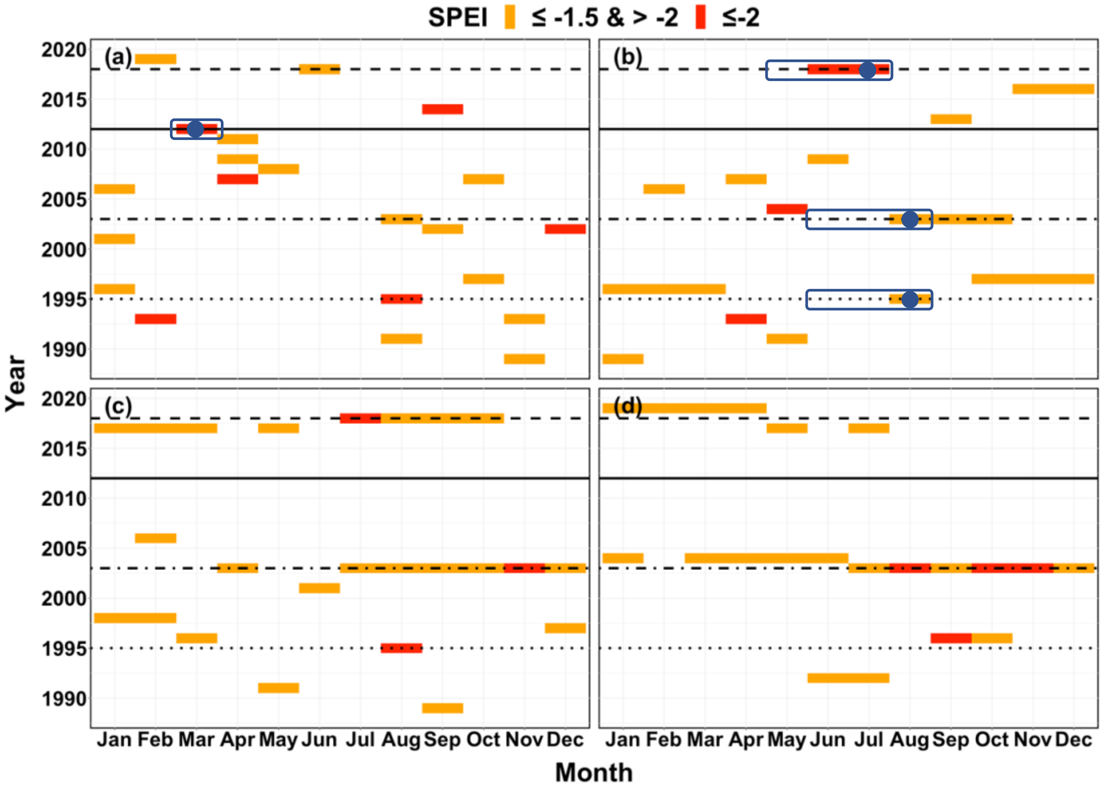

Figure 5.1 *- The Standardised Precipitation Evapotranspiration Index (SPEI) values qualifying as either severe drought (≤ –1.5 and > –2 SPEI, orange bars) or extreme drought (≤ –2 SPEI, red bars) calculated annually for each month using an integration period of (a) 1 month (b) 3 months (c), 6 months and (d) 12 months. The four horizontal lines indicate the four drought years of interest (2018, 2012, 2003 and 1995). Candidate focal months (blue dots) and integration periods (blue rectangles) derived from climate and CWD analysis (see main text) are indicated for each of the four drought events.*

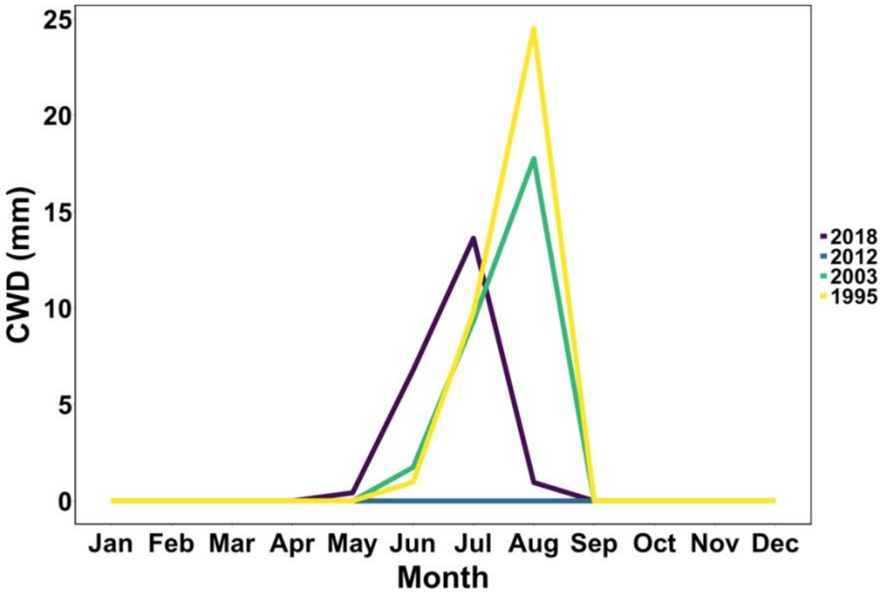

Figure 5.2 *- Climatic Water Deficit (CWD) values calculated monthly for each of the three drought years (1995, 2003, 2012 and 2018).*

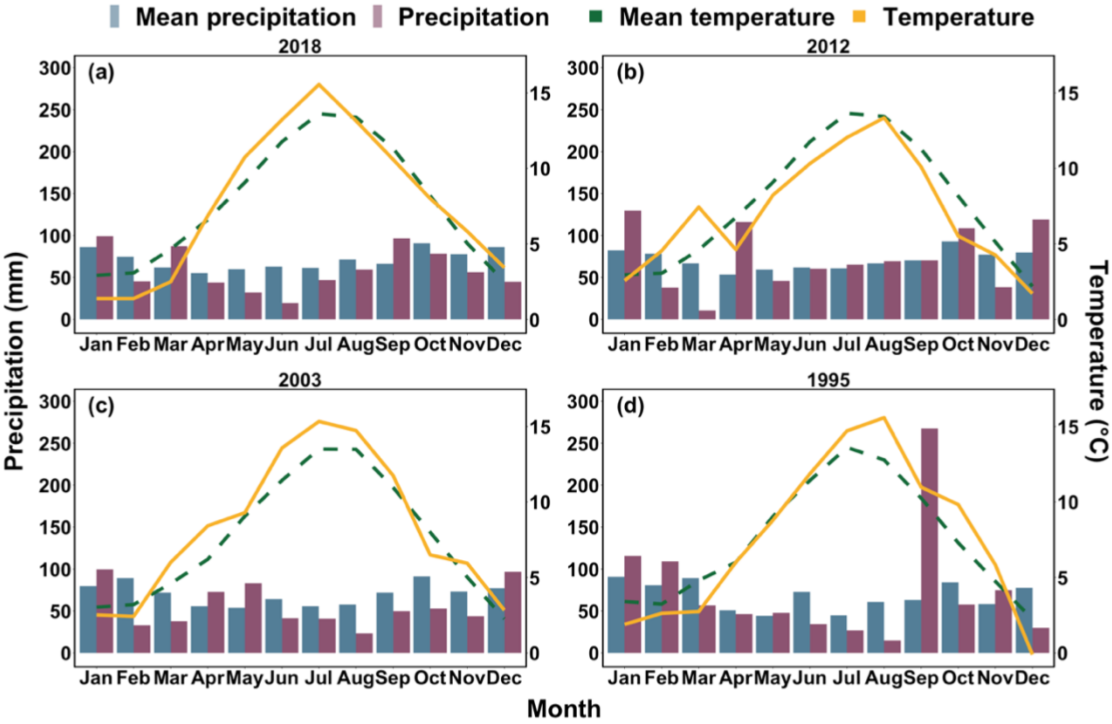

Figure 5.3 *- Climographs for the drought years (a) 2018, (b) 2012, (c) 2003, and (d) 1995 over the study period (1989 – 2019). Mean monthly precipitation is calculated using all years from 1989 up to the year prior to each drought year (blue bars) and monthly precipitation is calculated as total precipitation for each drought year (purple bars). Mean monthly temperature is calculated using all years from 1989 up to the year prior to each drought year (dashed green line) and mean monthly temperature is calculated during each drought year (solid yellow line). As such, blue bars and the green dashed lines indicate historic monthly means while purple bars and the yellow solid lines indicates drought year values.*

5.9. SPEI parameter selection – a way forward

Adapting to the challenges of a changing climate requires a detailed understanding of how ecological systems have responded to previous climate extremes across a range of scales, making the correct detection and accurate characterisation of these events particularly important. The results presented here demonstrate the sensitivity of the SPEI to the values of focal month (f_m) and integration timescale (t_i) used to parameterise it for drought detection, severity classification and our understanding of the timing and duration of an event. Consequently, the use of an *a-priori* selected single focal month and integration timescale to calculate the SPEI should be avoided as it risks overlooking events and mischaracterising the severity of those which are detected by assuming all events can be accurately captured by a single combination, an assumption we show to be unjustified.

Calculating the monthly CWD and summing these monthly deficit values annually provides a useful absolute measure of drought intensity and a starting point to identify obvious candidate drought years that warrant further investigation (Zang et al., 2019). Similarly, monthly CWD values for these candidate years also provide good estimates of drought onset, duration, and timing. Such estimates can then be used in conjunction with basic climate analyses such as those presented here, or the complementary use of other common indicators of drought intensity such as Vapour Pressure Deficit (VPD) (Eamus et al., 2013; Sanginés de Cárcer et al., 2018; Williams et al., 2013; Yuan et al., 2019) to further evidence suitable focal months and integration periods over which the SPEI can be calculated to also obtain a relative measure of drought severity. Firstly, this approach reduces the likelihood of incorporating months of positive water balance in SPEI calculations before or after the beginning or end of a particular event. Secondly, our suggested approach more comprehensively characterises the multi-dimensionality of a particular event by estimating values of intensity, duration, timing, and severity, which will enable more detailed cross study comparisons and will help provide much needed insight into how these dimensions interact to influence drought response across spatial and temporal scales.

In many cases, there may still be a range of focal months and integration timescales that CWD and climate analysis indicate are suitable for calculating the SPEI. In such cases we suggest that calculating and reporting this range of possibilities is an important step in contextualising the observed response and the uncertainty surrounding the characteristics of a particular event. The 2012 drought example presented here also demonstrates that short integration periods are worthy of further exploration, especially considering the importance of drought timing (D'Orangeville et al., 2018; Huang et al., 2018), the strong influence that pre-growing season drought has on tree growth (Gao et al., 2018) and recent work documenting the impact of short duration (one month) events on tree growth (Mood et al., 2021).

5.10. Conclusion

Understanding both organismal and systemic responses to drought is an increasingly important focus of global change research, but achieving such understanding depends on our ability to detect and characterise the timing, duration, intensity, and frequency of these events. We demonstrate the influence that SPEI parameter choice has on detection and characterisation of drought severity. We propose changes in the approach to SPEI parameter selection which uses absolute measures of water deficit and basic climate analysis to estimate the onset, duration and cessation of individual drought events which can then be used to define the target month(s) and integration period(s) for calculating the SPEI, whilst providing insights into the multidimensionality of these events. To compliment this improvement, the detection and use of species specific SPEI thresholds (Huang et al., 2015; Ovenden et al., 2021a) rather than ubiquitously applied thresholds (e.g. severe drought being ≤ –1.5 but > –2) will likely be a fruitful area of future research and allow a more precise understanding of how particular types of drought interact with different species.

5.11. References

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CHAPTER 6 - Accounting for the multidimensionality of drought and compensatory dynamics in understanding the resilience of Sitka spruce

The chapter is currently being prepared for submission to the Journal *Global Change Biology*

6.1. Abstract

As our climate warms, the intensity, frequency, and duration of extreme drought events is expected to increase across much of the world, but how the different dimensions of drought are associated with patterns of forest resilience, or how compensatory mechanisms might mitigate the negative impacts of drought remains mostly unexplored. In this study we used a 26-site dendrochronological network of Sitka spruce (*Picea sitchensis*) across the UK to investigate how soil type and the intensity, duration and severity of drought are associated with drought resistance, resilience, and recovery dynamics, including whether there was any evidence of post-drought compensatory growth. We documented compensatory growth throughout the recovery period in up to 12% of trees. By five years post-drought, 62% of trees had returned to a size similar to what would have been expected if no drought had occurred when observed growth was compared to point forecasts from dynamic regression models. Of the three drought characteristics tested, drought intensity was the strongest predictor of growth resilience and drought recovery time, with higher intensity droughts linked to lower growth resilience and longer recovery times. In contrast, the probability of compensatory growth occurring was not associated with either drought intensity, duration, or severity. The lowest growth resilience was documented on soils with an intermediate moisture content, while the highest growth resilience was on the driest and wettest soils, suggesting trees growing on dryer sites may be partially acclimated to drought while wetter sites might partially buffer against

drought impacts. These results provide a critical new understanding of the drought response of this productive and economically important timber species whilst demonstrating the importance of considering the different dimensions of drought alongside post-drought compensatory dynamics when quantifying forest resilience and above ground losses in forest productivity.

6.2. Introduction

Understanding how extreme drought events impact forest productivity is of critical importance if we are to develop adaptation strategies that effectively increase the resilience of our forests to these events. Across many parts of the world, the frequency of extreme drought events is anticipated to increase in the coming decades (Dai, 2013; McDowell et al., 2018; Trenberth et al., 2014), however the multidimensional and multiscale characteristics of drought make them particularly challenging to study (AghaKouchak et al., 2021; Chamorro et al., 2020). There is a growing recognition of the risks associated with both multivariate and temporally compound extreme events (Zscheischler et al., 2020) (e.g. two consecutive extreme droughts (Anderegg et al., 2020; Schnabel et al., 2022)) and the interactions between abiotic and biotic events (e.g. a drought followed by an outbreak of bark beetles (Thonfeld et al., 2022)). Similarly, it is likely that combinations of the various drought dimensions such as intensity (i.e. absolute water deficit), duration (i.e. number of months) and frequency (i.e. return interval) will produce a range of potential drought ‘types’ (Song et al., 2022). These drought types may in turn interact with species characteristics (e.g. cavitation thresholds (Brodribb et al., 2020)) and site- specific conditions (e.g. soil characteristics and stand level variables such as tree density) to produce a range of potential responses. As such, a particular type of drought may affect the same species in different locations in different ways.

In addition to differences in the intensity, duration, frequency and overall severity (i.e. how bad a drought is relative to average conditions at a given site) of an event, a growing body of work is highlighting how the impact of drought may also depend on its seasonal timing (D’Orangeville et al., 2018; Huang et al., 2018), tree age (Carnwath

& Nelson, 2017; Martínez-Vilalta et al., 2012) and the developmental stage of a forest (Halpin & Lorimer, 2016; Ibáñez et al., 2019). This complexity highlights the crucial importance of quantifying both the characteristics of a given event and understanding both its impact and the dynamics of any subsequent recovery. Despite this importance, recent work suggests that across the ecological drought literature, droughts are often insufficiently well characterised (Slette et al., 2019). To date, the vast majority of studies that investigate the impact of drought on tree growth use the Standardised Precipitation Evapotranspiration Index (SPEI) (Vicente-Serrano et al., 2010) to identify and quantify drought severity (D'Orangeville et al., 2018; Gazol et al., 2018; Huang et al., 2015; Vitasse et al., 2019). However, Zang et al., (2019) demonstrate that the reliance on the SPEI alone risks mischaracterising events under some conditions, particularly in wetter environments.

While useful, the SPEI by itself only provides a relative measure of drought severity for a specific, user-defined combination of focal month and integration period selected *a-priori*. In turn, this means that the SPEI alone cannot provide a measure of some of the other key drought dimensions, such as duration or intensity. To date, very few studies have attempted to disentangle the relative importance of drought timing, intensity, duration or severity in determining the impact of drought on tree growth or in modifying forest resilience and recovery dynamics (*c.f.* Song et al., 2022). In a recent study, Ovenden et al. (2021b) used dynamic regression to model tree growth in a scenario where no drought had occurred, then compared forecasted with observed growth to estimate the growth resilience of *Pinus sylvestris* to a single extreme drought event. This work identified a pattern of 'compensatory growth' in a post-recovery phase, that is growth in excess of forecasted values in a scenario where no drought had occurred after growth recovery had occurred (Ovenden et al., 2021b). Whilst this work was limited to a single species in response to a single drought event, the prevalence of compensatory mechanisms in general has received relatively little attention in studies of stress impacts on ecological systems (Connell & Ghedini, 2015; Gessler et al., 2020). As a result, how widespread compensatory growth mechanisms are in tree species following different types of drought and under different site conditions is unknown, limiting our ability to understand where acclimatation may be occurring (Gessler et al., 2020), or how forests might be re-organising post-disturbance (Seidl & Turner, 2022). Understanding in what species and under which drought or recovery conditions compensatory growth occurs will be of considerable value in guiding forest management decisions that aim to increase forest resistance and resilience to drought (Connell & Ghedini, 2015). For example, does stand density reduction (thinning) confer drought resilience, or can we identify individuals to retain during thinning to promote a compensatory recovery mechanism?

In this study, we used the Climatic Water Deficit (CWD) and the SPEI to identify and characterise the timing, duration, intensity, and severity of all drought events during the lifetime of a 26-site dendrochronological dataset of UK grown Sitka spruce (*Picea sitchensis*). We then used a dynamic regression approach to forecast individual tree growth for each drought and post-drought period in a scenario where no drought had occurred, and against which observed tree growth was compared and growth resilience calculated to address the following questions:

1. How resilient is *P. sitchensis* growth to drought, and how are differences in the growth resilience of this species associated with the intensity, duration and severity of drought and soil type?

2. How widespread is post-drought compensatory growth in *P. sitchensis*, how long is it detectable following drought, and is the presences of compensatory growth associated with differences in the intensity, duration, or severity of a drought event?

3. How is drought recovery time associated with differences in drought characteristics?

6.3. Materials and Methods

6.3.1. Site description, sampling design and dendrochronological data

In 2010 and 2011, 47 monospecific sites of Sitka spruce (*Picea sitchensis*) were selected for dendrochronological sampling (Adams, 2014). Site selection followed a factorial design to give a representative sample of stand productivity, elevation (Low <= 280m or High > 280m) and latitude, which resulted in eight classifications (Adams, 2014). Sites were then randomly selected from the Forestry Commission's sub-compartment database (**Figure 6.1**). A 0.2ha plot was established at random at each site and the DBH of each tree > 7cm in each plot was recorded, along with stand density and range of other site level variables (Adams, 2014). A single 12mm diameter increment core taken bark-to-bark through the centre of the tree was then collected from ten randomly selected trees from each plot using a Tanaka TED-250RS increment corer (Tanaka Kogyo Co., Ltd.). These dendrochronological samples were trimmed to 2mm thick radial strips and scanned using an ITRAX Density Scanner built by Cox Analytical System (Adams, 2014). Annual ringwidths were then measured from the greyscale images produced by the ITRAX densitometer using WinDENDRO image analysis software (Regents Instruments, Quebec).

As these samples were originally collected to examine radial density and the radial variation in longitudinal stiffness (Adams, 2014), the bark of many of these samples was not retained. To have confidence that each tree-ring was aligned to the correct calendar year during dendrochronological crossdating, only sites where at least 50% of the samples had evidence of bark in the ITRAX image were used in the present analysis. This approach was necessary to have enough trees from which a reliable site-level chronology could be developed and used to confidently crossdate other samples, resulting in 26 of the original 47 sites being retained for analysis (**Figure 6.1**). These 26 sites were subsequently crossdated both visually and statistically using the *dplR* package in R (Bunn et al., 2019) resulting in a final dataset of 227 confidently crossdated trees across 26 sites. For further details on site selection, data collection and processing of these samples, see Adams (2014).

Figure 6.1 *- Map showing the location of all 26 crossdated Sitka spruce (Picea sitchensis) monoculture sites (coloured dots represent the location of each site) used in the final analysis in this study, produced using the mapview package in R (Appelhans et al., 2022).*

6.3.2. Drought identification and characterisation

To identify and characterise drought events in the climate record at all 26 sites, we calculated the monthly Climatic Water Deficit ($\mathrm{CWD}_{\mathrm{mon}}$) at each site and every year between 1961 and 2011 following (Lutz et al., 2010) using R code developed by (Redmond, 2019) and summed these 12 monthly values to obtain an annual CWD value ($\mathrm{CWD}_{\mathrm{ann}}$) at each site. We then calculated the mean $\mathrm{CWD}_{\mathrm{ann}}$ ±2 SD across the 50-year study period for each site separately and considered a year to be an extreme drought event if $\mathrm{CWD}_{\mathrm{ann}}$ was > 2SD above the mean for that site. The $\mathrm{CWD}_{\mathrm{ann}}$ values for each extreme drought year ($\mathrm{CWD}_{\mathrm{dr}}$) were then used in subsequent analysis as an absolute measure of drought intensity for that year.

To obtain a relative measure of drought severity and to provide further evidence that the years identified using the approach detailed above were drought years, we calculated the Standardised Precipitation Evapotranspiration Index (SPEI) in R using the

SPEI package (Begueria & Vicente-Serrano, 2017). SPEI is a commonly used index of drought severity and requires two parameters to be defined by the user; the focal month and a timescale (i.e., the number of months prior to the focal month) over which the difference between precipitation and potential evapotranspiration (P – PET) should be integrated. Many approaches to defining the values for these two SPEI parameters exist (Andivia et al., 2018; Camarero et al., 2018), however by definition, the *a priori* selection of a single focal month and integration timescale means the SPEI cannot provide details on the timing and duration of different droughts at a given site, as these parameters are pre-defined by the user. To address this issue, for each drought event initially identified using the CWD approach above, we parameterised the focal month in the SPEI calculation as the last month with a positive CWD_{mon} value (i.e., the last month with a water deficit). The SPEI integration period was then defined as the number of months preceding the focal month with a positive CWD_{mon}. If a month with a positive CWD_{mon} value was separated by two or more months with no positive CWD_{mon} value, it was considered a separate drought event. In this way the SPEI for each drought event (and thus an estimate of each drought's severity) was calculated using only data from the period where there was evidence of drought conditions i.e., a climatic water deficit. This approach allowed us to characterise each drought event more comprehensively by obtaining estimates of the intensity (CWD_{dr}), duration (number of months with a water deficit), severity (using the SPEI) and the timing (the month(s) or season) of each event, as opposed to relying solely on the SPEI as an aggregate measure of inherently multidimensional events. To retain a sufficient number of pre-drought growth years to use in the dynamic regression modelling (see Section 6.3.3 – Growth forecasting and resilience) we only considered droughts from the 1995 event onwards, resulting in 29 droughts from 26 sites. Similarly, every identified drought across all sites in this study occurred during the summer months and so drought timing was not considered further in this analysis.

6.3.3. Growth forecasting and resilience

In order to estimate the growth resilience of each tree, at each site, to each drought event, we first used dynamic regression to forecast basal area increments (BAI_{for}) in a scenario where no drought had occurred, against which observed BAI (BAI_{obs}) could be compared, following the approach developed by Ovenden et al. (2021b). This approach captures each tree's unique relationship between selected predictor variables and growth every year up to and including the year before a drought event, as in a normal least-squares regression model. However, in a dynamic regression model, the errors from the regression are modelled as an autoregressive integrated moving average (ARIMA) p, d, q process (where p, d and q represent the auto-regressive order, the degree of differencing and the moving average order, respectively).

In this study, we used total annual precipitation ($Precip_{sum}$), total annual growing degree days above 5°C (gdd), and total annual solar radiation ($Solar_{rad}$), as predictors in the dynamic regression models. All interpolated climate data used in this study was at 1km resolution and was obtained from the Climate Hydrology and Ecology Research Support System (CHESS) meteorology dataset for Great Britain (Robinson et al., 2017). $Precip_{sum}$ and $Solar_{rad}$ were calculated by summing daily values across the whole year, while gdd was calculated following **Eq. 6.1**.

Eq. 6.1

$$gdd = \sum_{i=1}^{365} (T_i - 5),\ \ if\ T_i > 5$$

In **Eq. 6.1**, annual gdd is the sum of the positive differences between daily mean air temperature (T_i) with a threshold value of +5°C, where *i* runs from 1 to 365 days of the year.

To obtain point forecasts for annual tree growth (BAI_{for}) in a 'no-drought' scenario and the 95% CI of these point forecasts, the values for $Precip_{sum}$, $Solar_{rad}$ and gdd in each drought year were first replaced with mean values, calculated across the entire pre-drought lifetime of each tree. These average values were then used in conjunction with observed annual post-drought values of these same variables to obtain annual forecasts from the dynamic regression models for each tree in the drought year and five post-drought years in a ‘no-drought’ scenario. This approach kept $Precip_{sum}$, $Solar_{rad}$ and gdd in the post-drought years as similar as possible to actual recovery conditions. We then applied **Eq. 6.2** following Ovenden et al. (2021b) to estimate growth resilience (Gr) in the drought year (equivalent to resistance) and each of the five post-drought years for each tree, where BAI_{obs} is the observed basal area increment in a given year and BAI_{for} is the forecasted basal area increment for that same year. The difference between BAI_{for} and BAI_{obs} was then calculated for each tree annually following **Eq. 6.3** to give a measure of annual growth deficit (AGD). This annual growth deficit was then summed over time following **Eq. 6.4** to give a measure of cumulative annual growth deficit for each tree (CAGD). **Eq. 6.4** was calculated annually for each post-drought year where t_1 was the drought year and t_n was the post-drought year being considered. Compensatory growth (CG) was considered to have occurred if BAI_{obs} ever exceeded the upper 95CI associated with the point forecast (BAI_{for}) for each tree in any year. Tree growth and size recovery was considered to have occurred if AGD or CAGD was ever < 0, respectively which indicates tree growth rate or size was at least as fast/big as would have been expected if no drought had occurred.

Eq. 6.2

$$\text{Growth resistance/resilience } (Gr) = \frac{BAI_{obs}}{BAI_{for}}$$

Eq. 6.3

$$AGD = BAI_{for} - BAI_{obs}$$

Eq. 6.4

$$CAGD = \sum_{i=t1}^{tn} AGD$$

6.3.4. Modelling tree growth responses to drought

We fitted a linear mixed-effects model using the *nlme* package (Pinheiro et al., 2020) to establish the relative importance of the different components of drought (intensity, duration and severity), site conditions (soil moisture and nutrient regime) and stand density on growth resilience to drought following **Eq. 6.5.**

Eq. 6.5

$$Gr_{ijk} = X_{ijk}\beta + b0_{ijk} + \varepsilon_{ijk}$$

In **Eq. 6.5**, Gr_i refers to growth resilience in the *i*th year, for the *j*th tree in the *k*th site. X is an *n* x *p* matrix of *p* fixed effect variables, including the *Intensity, Duration* and *Severity* of the drought event*, Stand Density*, *Soil Moisture Regime (SMR)*, *Soil Nutrient Regime (SNR),* and *Post-drought Year* while *n* is the number of droughts (*n* = 29). Both SMR and SNR were factorial predictors with six levels (Slightly Dry, Fresh, Moist, Very moist, Wet and Very Wet) and three levels (Medium, Poor and Very Poor) respectively, the data for which was obtained for all sites from Forest Research's Ecological Site Classification system (Pyatt et al., 2001). For *Post-drought Year*, 0 indicated the drought year and one to five represented each of the five post-drought years across all measured trees, β is a *p* x *1* column vector of regression estimates, $b0_{ijk}$ represents the random effect of *Calendar Year,* and the nested random effects of *TreeID* in *SiteID*, where b_{ijk} ~ N(0, σ^2_{b0}) and ε_{ijk} represents error term, where ε_{ijk} ~ N(0, σ^2_{ε}). σ^2_{b0} and σ^2_{ε} are estimates of variance of random effects and residual error, respectively. Initially, all possible two-way interactions were included between drought *Intensity, Duration* and *Severity*. Model selection was then conducted by minimising AIC values, with the final best fitting model containing no interactions and a correlation structure for Gr modelled using a corARMA correlation structure set to p = 1 and q = 2. Multicollinearity between predictor variables was checked using the generalised variance inflation factor ($GVIF^{(\frac{1}{2\times Df})}$< 2 in all cases) (Fox & Monette, 1992). We then used estimated marginal means from the *emmeans* package (Lenth, 2020) to run pairwise comparisons of growth resilience values between the drought year and five post-drought years as well as between the different SMRs. No pairwise comparisons were conducted for the different levels of SNR due to the main effect of the predictor variable being non-significant.

For each tree, growth recovery time was the number of years it took for AGD to become < 0 (if at all). Then, to investigate whether different drought characteristics were associated with growth recovery time we fit a linear mixed-effects model following **Eq. 6.6** using the data for those trees whose growth rate had recovered within the first five years (*n* = 213).

Eq. 6.6

$$GRecovery\ Time_i = X_i\beta + b0_i + \varepsilon_i$$

In **Eq. 6.6**, $GRecovery\ Time_i$ refers to the year (zero to five, where zero is the drought year and one to five are the first five post-drought recovery years) in which growth recovery occurred for the *i*th *SiteID*. X is an *n* x *p* matrix of *p* fixed effect variables, including the *Intensity, Duration* and *Severity* of the drought event, β is a *p* x *1* column vector of regression estimates, $b0_i$ represents the nested random effects of *TreeID in SiteID*, where b_i ~ N (0, σ^2_{b0}) and ε_i represents error term, where ε_i ~ N(0, σ^2_ε). We tested for non-linear relationships between the predictor and response variables using second and third order polynomials, however model selection found the linear mixed-effects model with no polynomials to have the lowest AIC value, and so this was selected as the final model.

Finally, we fitted 12 separate binomial mixed-effects models. The first six models (one model for the drought year and each of the five post-drought years) allowed us to investigate whether the probability of observed growth (BAI_{obs}) being at least as fast as the point forecast (BAI_{for}) for each tree in a 'no-drought' scenario was associated with drought intensity, duration, or severity, and whether this association changed over time. The second set of six models (one model for the drought year and each of the five post-drought years) allowed us to understand whether these same predictor variables (drought intensity, duration, and severity) were associated with the probability of observing compensatory growth (i.e., where observed tree growth in a given year was > 95CI of the point forecast). The *ggeffects* package was then used to extract and plot model predictions.

6.4. Results

A significant, positive relationship was found between growth resilience and the SPEI (*$p < 0.019$*), meaning that less severe droughts were associated with greater growth resilience (**Table 6.1**). Similarly, a significant negative relationship between CWD_{dr} (i.e., drought intensity) and growth resilience was found (*$p = 0.005$*), so that higher intensity droughts were associated with lower drought resilience. No relationship between drought duration and growth resilience was found (*$p = 0.313$*) (**Table 6.1**).

Table 6.1 *- Type 2 ANOVA table for the mixed effects model of growth resilience. Df = degrees of freedom and significant results (p < 0.05) are highlighted in bold. Post-drought Year represents the number of years since drought (where zero was the drought year and one to five were post-drought years), SNR = Soil Nutrient Regime, SMR = Soil Moisture Regime and Stand density indicates the number of tree/ha.*

Fixed effect	Chisq	*df*	*p-value*
Post-drought Year	**63.765**	**5**	**<0.001**
Drought Severity (SPEI)	**5.532**	**1**	**0.019**
Drought Duration (*n* months)	1.020	1	0.313
Drought Intensity (CWD_{dr})	**7.872**	**1**	**0.005**
Stand density	0.622	1	0.430
SNR	5.196	2	0.074
SMR	**32.981**	**5**	**< 0.001**

Table 6.2 *- Type 2 ANOVA table for the mixed effects model of growth recovery time. Df = degrees of freedom, significant results (p < 0.05) are highlighted in bold and Severity, Duration and Intensity represent the three drought characteristics considered.*

Fixed effect	Chisq	*df*	*p-value*
Severity (SPEI)	0.352	1	0.553
Duration (*n* months)	0.005	1	0.945
Intensity (CWD_{dr})	**6.845**	**1**	**0.009**

While no relationship between soil nutrient regime (SNR) and growth resilience was detected, a significant relationship was found between soil moisture regime (SMR) and growth resilience ($p < 0.001$) (**Table 6.1**). Post-hoc pairwise comparisons between the different SMRs showed that “Slightly dry” soils (the driest of those considered in the present study) had the highest growth resilience while sites classified as “Very moist” showed the lowest growth resilience (**Figure 6.2b**). Pairwise comparisons of growth resilience between the drought year and all five post-drought years showed growth resilience was significantly lower in the drought year compared to all of the post-drought years, and significantly lower than the second and third post-drought years in the first post-drought year ($p < 0.02$ in all cases) (**Figure 6.2a**).

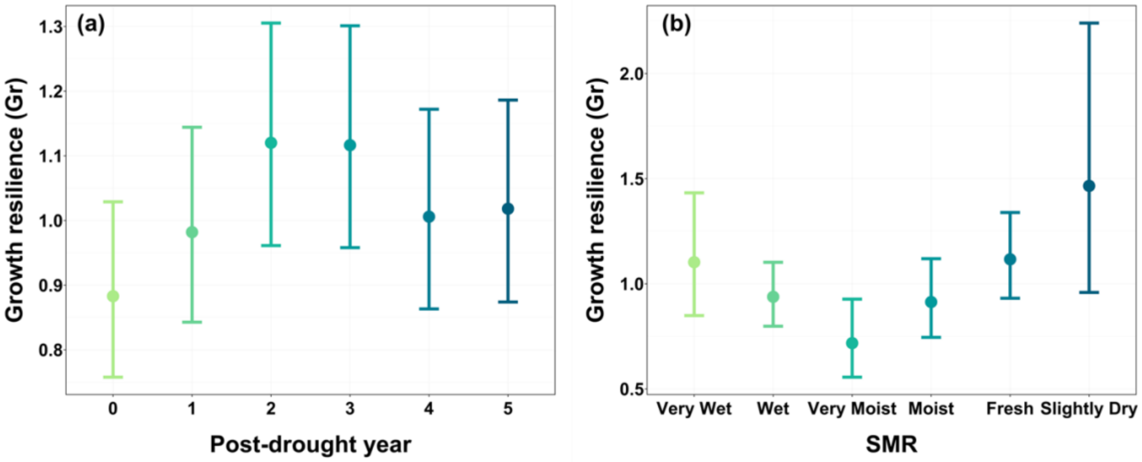

Figure 6.2 *- Estimated marginal means and 95% unadjusted confidence intervals for the growth resilience of Sitka spruce (Picea sitchensis) in (a) the drought year (zero) and five post drought years (1-5) and (b) for the different Soil Moisture Regimes (SMR) across all 29 droughts and 26 study sites.*

Drought intensity (CWD_{dr}) was the only drought aspect of those tested (intensity, duration, and severity) that was associated with growth recovery time (i.e., the number of years taken for observed growth to return to, or exceed forecasted growth), with higher intensity droughts linked to longer recovery times ($p = 0.009$, **Table 6.2**).

When considering all sites and drought events collectively, observed growth was greater than the point forecast for 31% of trees in the drought year (**Figure S6.1a**) suggesting that nearly 1/3 of trees did not experience a negative impact on radial growth in the drought year at all. Observed growth was also greater than the point forecast for between 46 – 59% of trees depending on the post-drought year considered, indicating a large proportion of trees throughout the post-drought period were growing at least as fast as would have been expected if no drought had occurred (**Figures S6.1b – 6.1f**). Similarly, up to 12% of trees were growing at rates more than the upper 95CI associated with their point forecasts in the post-drought period (**Figure 6.4**), indicating the presence of compensatory growth in some trees. Mixed-effects model results showed no relationship between either the SPEI or drought duration with the time taken for growth to recover, however a significant positive relationship (p = 0.009) was found between drought intensity (CWD_{dr}) and growth recovery time, indicating tree growth took longer to recover from more intense droughts. Based on point forecasts, 80% of trees recovered to growth rates and 62% of trees recovered to a size that was not less than would have been expected if no drought had occurred by the fifth post-drought year (**Figure 6.3b**).

Binomial regression showed that neither drought duration nor drought severity (SPEI) were associated with the probability of observed growth rates being at least as large as forecasted values in a ‘no-drought’ scenario, in either the drought year or any of the post drought years. However, CWD_{dr} was negatively associated with the probability that observed growth rates were at least as large as forecasted values in a ‘no-drought’ scenario, but only in the drought year (**Figure 6.5a**, $p < 0.001$) and 1st post drought year (**Figure 6.5b** $p < 0.05$). As such, lower intensity droughts were associated with a greater probability of annual growth being indistinguishable from a no-drought scenario, but as drought intensity increased, this probability declined as observed growth was lower than in a ‘no-drought’ scenario (**Figure 6.5**). No association between drought duration, intensity or severity and the probability of observing compensatory growth was detected in the drought year or any of the post-drought years (**Figure S6.2**).

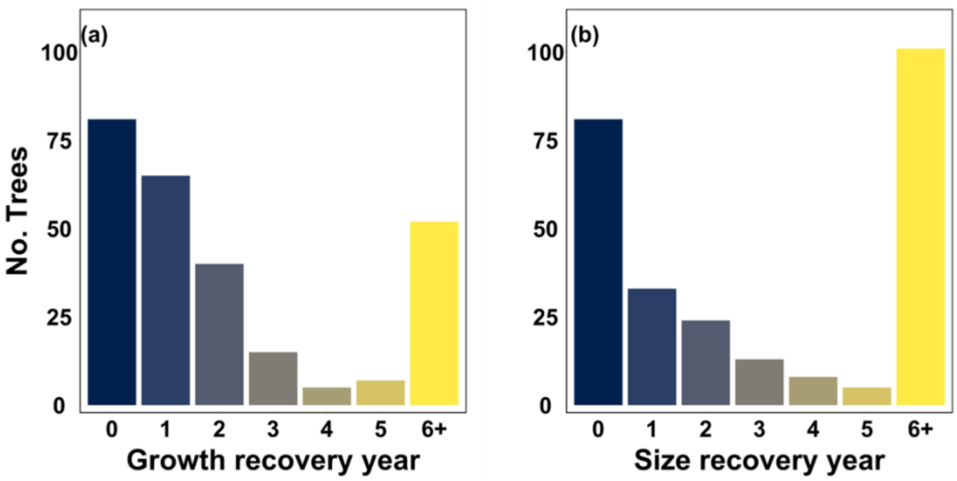

Figure 6.3 *- The frequency of trees across all experimental sites and droughts where (a) observed tree growth recovered to forecasted levels in a 'no-drought scenario' or (b) observed tree size recovered to forecasted levels in a 'no-drought scenario' in the drought year (year zero), each of the post drought year considered (years one to five) or at no point during the five post-drought years (six plus).*

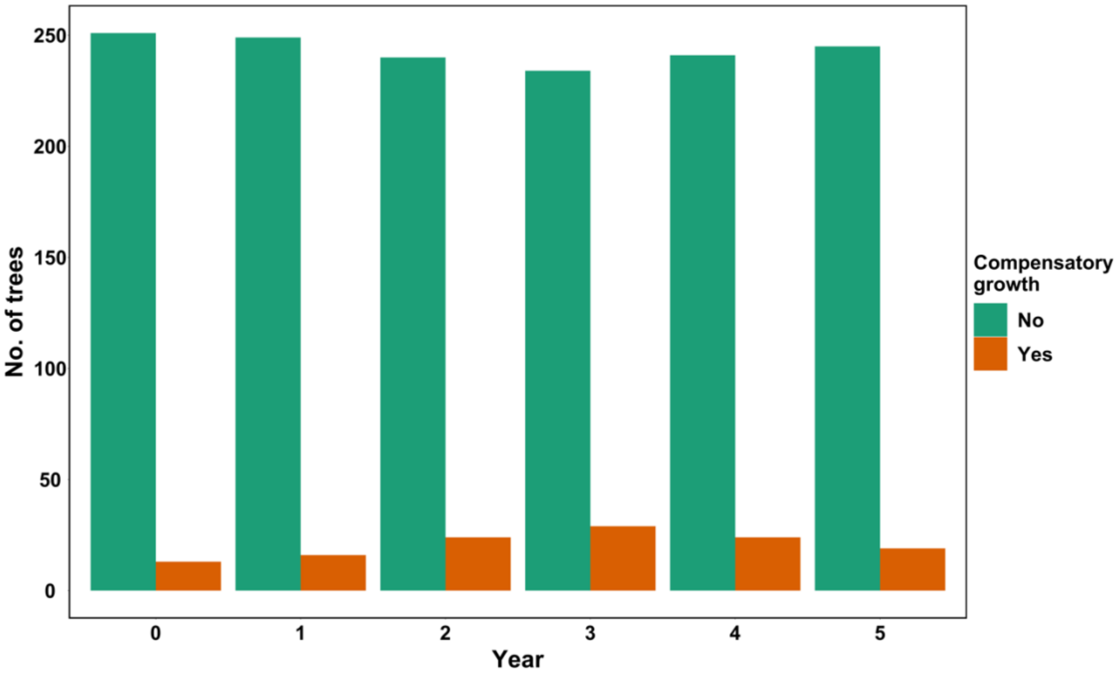

Figure 6.4 *- The annual frequency of trees across all experimental sites (n = 26) and droughts (n = 29) where observed growth was in excess of the upper 95CI associated with the point forecasted for annual growth in a 'no-drought scenario' (i.e., trees exhibiting "Compensatory Growth") in the drought year (Year 0) and five post-drought years (years 1-5).*

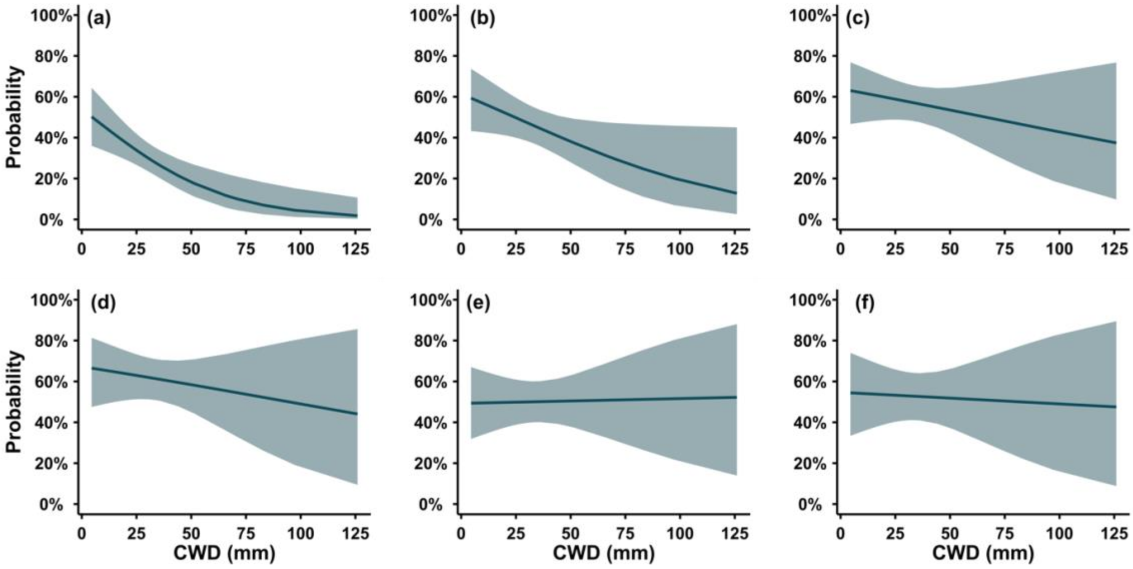

Figure 6.5 *- Predicted probability (solid line) of observed growth being in excess of the point forecast for individual tree growth in a 'no drought' scenario in the drought year*

(a) or five post drought years (b – f) as a function of drought intensity, measured in terms of Climatic Water Deficit (CWDdr). Shaded areas indicate the 95% CI of predictions.

6.5. Discussion

Despite concerns of the impacts that recent widespread extreme drought events have had on tree growth and forest health across much of Europe (Buras et al., 2020; Turner et al., 2021), our understanding of the historic impact of drought on coniferous tree species in the UK is limited to a handful of studies (Green et al., 2008; Ovenden et al., 2021a, 2021b, 2022). Understanding how the different characteristics of drought might influence a species response is critical if we are to effectively increase the resistance and resilience of our forests to these events in the future. In this study, we investigated whether soil type, or the intensity, duration or severity of drought was associated with differences in the growth resilience and recovery time of Sitka spruce monocultures across 26 UK sites. We also looked for any evidence of compensatory growth in this species over five post-drought years and whether the probability of compensatory growth occurring was linked to any of these drought characteristics.

Of the three drought characteristics we considered, drought intensity (CWD_{dr}) was the strongest predictor of growth resilience and the only significant predictor of the time taken for tree growth to recover, with higher drought intensity being associated with lower growth resilience and longer growth recovery times. While greater drought severity (SPEI) was also linked to lower growth resilience, drought duration was not a significant predictor of growth resilience, the probability of compensatory growth occurring, or the time taken for growth to recover, suggesting that drought intensity (measured in absolute terms using the climatic water deficit) is the most important characteristic of drought for regulating the growth response of this species. We also found evidence of compensatory growth in up to 12% of trees, where observed growth exceeded the upper 95CI associated with forecasted growth in a 'no-drought scenario' at some point during the five post-drought years we considered. While, neither drought duration, intensity or severity was associated with the probability of observing compensatory growth, 62% of all trees did return to a size similar to what would have been expected if no drought had occurred when observed growth was compared to point forecasts.

6.5.1. How resilient is Sitka spruce to drought?

We documented a clear, negative relationship between drought intensity (but not drought duration) and growth resistance and resilience in Sitka spruce, but a more complex relationship between growth resilience and soil moisture regime. While few studies have attempted to distinguish between the different dimensions of drought considered here, the relationship between drought intensity and resistance is in keeping with the general pattern observed in 60% of conifer species considered by Song et al. (2022). However, in contrast to our study, Song et al. (2022) did not document a significant relationship between drought intensity and resistance in Sitka spruce. The relatively stronger relationship in our study between growth resistance and resilience with drought intensity (CWD_{dr}) compared with drought severity (SPEI) likely reflects the way in which these two indices are calculated and the tree's ecophysiological response. As SPEI is a measure of how severe a drought was relative to average climate conditions at a site, a very negative SPEI value (suggesting high drought severity) can result from a relatively small CWD_{dr} value if a site is normally very wet (Zang et al., 2019). This also partly explains why the CWD_{dr} and SPEI showed no signs of collinearity in our study. Similarly, numerous studies have documented physiological thresholds associated with drought tolerance, such as the water potential at which 50% loss of hydraulic conductivity occurs (Adams et al., 2017), which are likely to be more closely associated with absolute water deficit, rather than a relative measures of drought severity.

In this study, the highest growth resistance (in the drought year) and resilience (in the post-drought years) was observed in trees growing on 'Slightly dry' soils (the driest of those we considered), which are typically sandy podzols and sandy brown earth soils. In contrast, the lowest growth resilience in our study was on "Very moist" gleyed mineral soils which represents an intermediate soil moisture content, while trees growing on wetter peaty mineral gley soils (SMR “Wet” and “Very wet”) had significantly higher growth resilience than “Very moist” soils (**Figure 6.2b**). These results indicate that Sitka spruce appears to be most vulnerable to drought linked impacts on radial growth on soils with an intermediate level of available water. This non-linear relationship between soil moisture regime and growth resilience might suggest that Sitka spruce trees growing on drier soils are partially acclimated to deal with lower moisture availability and low intensity droughts, while the additional soil moisture on relatively wet sites may help to buffer against some of the negative impacts of drought. Recent work on *Fagus sylvatica* has demonstrated how the highest drought sensitivity and lowest drought resistance is sometimes found in the core of a species range rather than at the dry range-edge of populations (Cavin & Jump, 2017), again suggesting a degree of acclimation to drought at drier sites relative to sites which are normally more climatically favourable for tree growth.

While acclimation to site conditions may help species tolerate some drought conditions, increases in the intensity and frequency of future extreme events (Dai, 2013) may still cross species ecophysiological thresholds as forests are exposed to drought conditions outside of the normal range of variability. Several examples of the crossing of such thresholds have already been documented in UK forests. For example, the extreme UK drought of 1976 was associated with a shift in the competitive dominance of *Fagus sylvatica* and *Quercus petraea* (Cavin et al., 2013), the 1984 drought exceeded a drought threshold in *Pinus sylvestris* with negative impacts on tree growth for several years (Ovenden et al., 2021a) and the 2003 drought was linked to extensive damage and 22% mortality in pole-stage *Picea sitchensis* on sandy, well drained soils in the north-east of Scotland (Green et al., 2008).

6.5.2. Post-drought compensatory growth in Sitka spruce

In addition to quantifying growth resilience, calculating the annual and cumulative growth deficit for each tree in the drought year and five post-drought years allowed us to estimate how detrimental drought was for radial tree growth and look for evidence of compensatory mechanisms. Remarkably, we found no evidence of a drought impact on tree size in 62% of trees after five years when comparing observed tree size with point forecasts in a ‘no-drought’ scenario, suggesting that for many trees, tree size was eventually indistinguishable from a scenario where no drought had occurred. For some trees, this pattern seems to be the result of some trees growing faster expected under a ‘no drought’ scenario (observed growth was > 95CI associated with point forecasts in 12% of trees) during the post-drought period, providing some evidence of compensatory growth in *Picea sitchensis*. While compensatory growth following drought has been documented in both *Pinus sylvestris* seedlings (Seidel et al., 2019) and mature trees (Ovenden et al., 2021b), to our knowledge this study is the first to document evidence of this mechanism in mature *Picea sitchensis* trees.

A common assumption of resilience studies based on dendroecological methods is that the growth response to drought detected in tree-rings is representative of whole tree response, however carbon allocation patterns under drought conditions are still far from being well understood (Hartmann et al., 2020). The ‘optimal partitioning theory’ (Bloom et al., 1985) predicts that resources can be preferentially allocated to belowground organs under stressful conditions to alleviate the constraints imposed by the limiting resource (Hartmann et al., 2020). This theory leaves open the possibility that the patterns of radial growth decrease that are often interpret as ‘low resilience’ may instead be reflective of a far more plastic response to stress, whereby trees prioritise the allocation of carbon away from radial growth to other organs (e.g., roots) or mycorrhizal symbionts. Patterns of compensatory growth in the tree-ring record such as those documented here during the recovery phase may then reflect the re-prioritisation of resources to counterbalance losses in radial growth once drought conditions no longer exist and resources are no longer limited. The existence of compensatory mechanisms is predicted to occur at the level of an individual and be intimately tied to system resistance as a process to prevent system change in the face of disturbance (Connell & Ghedini, 2015). Here we find evidence that such compensatory mechanisms are detectable at the level of individual trees, but our results suggest that compensatory mechanisms are a lagged responses that are equally important for recovery and resilience.

While some trees did exhibit higher than forecasted growth during the drought year, it is unlikely that this is attributable to compensatory effects. As all of the droughts we considered were during the summer months, the majority of the growing season would have concluded by the time drought conditions abated, leaving little time for trees to 'catch up' any lost radial growth in the same year. The negative association between drought intensity and both growth resilience and the probability that observed growth was indistinguishable from forecasted growth in the drought year suggests that lower intensity droughts may have had a positive effect on the radial growth of some trees. It is possible that these beneficial effects detected under lower intensity droughts may also be linked to tree size, as drought has been shown to favour small trees while larger trees suffer more (Bennett et al., 2015; Pretzsch et al., 2018). However, as drought intensity increased, any beneficial effects of warmer conditions soon became detrimental for radial tree growth, which manifested as a near-zero probability of observing growth rates larger than forecasted under a no drought scenario in the drought year under the highest intensity droughts in our study (**Figure 5a**). While not directly tested, both the beneficial effects of low-level drought stress and acclimation following relatively frequent exposure to low level stress (as might be expected on drier soils) would be suggestive of a non-linear, biphasic dose-response relationship. This relationship is consistent with the theory of hormesis in plants, which predicts modest beneficial effects under a low stress dose (i.e., stimulation) but a detrimental effect under high dose (i.e., inhibition) (Agathokleous et al., 2019, 2020). Understanding carbon allocation patterns under drought and the role compensatory and hermetic processes play in regulating forest drought resilience and recovery dynamics are an exciting but largely unexplored aspect at the frontier of stress-ecological studies (Agathokleous et al., 2020; Gessler et al., 2020) with the potential to progress our understanding of how to adapt these systems to deal with the challenges of a changing climate.

6.6. Conclusion

In this study we documented patterns of compensatory growth in a limited number Sitka spruce (*Picea sitchensis*) following drought and showed how absolute drought intensity rather than drought duration or relative severity was the strongest predictor of growth resilience and drought recovery time, being negatively associated with both. Up to 62% of trees returned to sizes which were similar to what might have been expected if no drought had occurred by five years after the event, demonstrating a considerable capacity for this species to recover following drought. However, these results highlight the importance of considering both the different dimensions of extreme events and post-drought compensatory mechanisms when trying to understand forest resilience and suggests that increasing drought intensity in the future may negatively impact the growth of Sitka spruce and the ability of this species to recover.

6.7. References

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6.8. Supplementary Material

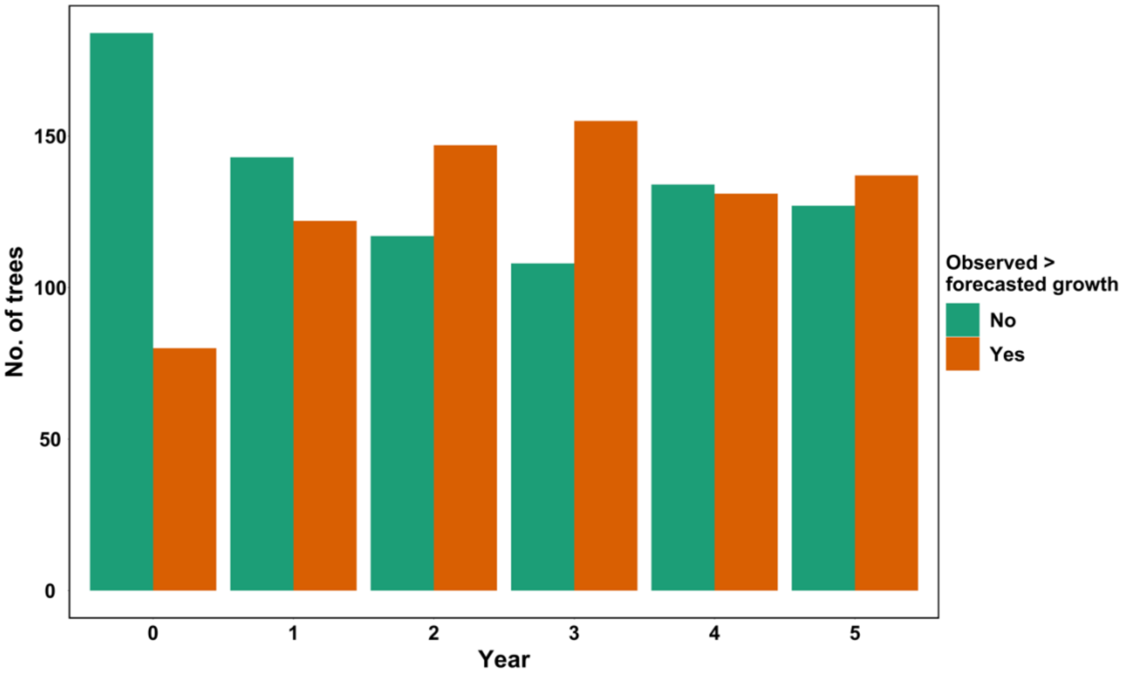

Figure S6.1 *- The annual frequency of trees across all experimental sites and droughts where observed growth was in excess of the point forecasted for annual tree growth in a 'no-drought scenario' in the drought year (Year 0) and five post-drought years (years 1-5).*

***Table S6.1** - Drought characteristics and site-specific variables. Site ID is the unique name for each of the 26 sites, Year is the drought year, CWD_{dr} is the summed Climatic Water Deficit for the drought year in mm, SPEI is the Standardised Precipitation Evapotranspiration Index for the drought year (see main text for how the CWD_{dr} and SPEI are calculated) Duration is the drought length in months. Density is the number of trees/ha at each site and SMR and SNR are the Soil Moisture and Soil Nutrient Regime at each site, respectively.*

Site ID	Year	CWD_{dr}	SPEI	Duration	Density	SMR	SNR
UKSS_2013	1995	10.87	-2.10	3	1599	Fresh	Poor
UKSS_280	1995	19.91	-1.90	3	1393	Wet	Very Poor
UKSS_2042	1995	7.78	-2.02	3	1121	Fresh	Poor
UKSS_2191	1995	30.80	-2.10	3	1429	Moist	Very Poor
UKSS_4301	1995	125.97	-1.94	6	1045	Moist	Very Poor
UKSS_6619	1995	4.50	-1.26	3	2687	Very Moist	Very Poor
UKSS_7643	1995	82.95	-1.94	5	1149	Very Moist	Very Poor
UKSS_9004	1995	24.91	-2.00	3	1742	Very Wet	Very Poor
UKSS_9008	1995	9.82	-2.01	3	2563	Very Wet	Very Poor
UKSS_EXM7	1995	16.75	-1.94	3	669	Fresh	Poor
UKSS_FERN	1995	23.91	-1.95	3	679	Moist	Very Poor
UKSS_QUA6	1995	44.11	-2.22	3	1026	Slightly Dry	Very Poor
UKSS_279	1995	32.78	-1.80	3	2140	Wet	Very Poor
UKSS_303	1995	30.25	-1.88	3	2365	Wet	Medium
UKSS_1390	1995	21.09	-2.18	3	2116	Fresh	Very Poor
UKSS_1600	1995	27.09	-1.91	3	1796	Wet	Poor
UKSS_2142	1995	11.84	-2.08	3	2866	Wet	Poor
UKSS_2185	1995	68.17	-2.08	3	2193	Moist	Very Poor
UKSS_2304	1995	36.19	-2.02	3	1932	Moist	Very Poor
UKSS_2436	1995	51.38	-2.27	3	2645	Wet	Poor
UKSS_2559	1995	71.35	-2.19	3	544	Fresh	Poor
UKSS_2723	1995	14.65	-2.12	3	3317	Moist	Poor
UKSS_2789	1995	65.59	-2.33	3	498	Fresh	Poor
UKSS_5234	1995	97.28	-2.17	3	1058	Fresh	Medium
UKSS_5945	1995	10.89	-1.92	3	995	Very Moist	Very Poor
UKSS_461	1997	20.64	-1.83	3	1543	Very Moist	Very Poor
UKSS_2142	2003	6.44	-1.92	1	2866	Wet	Poor
UKSS_9004	2006	23.10	-2.13	2	1742	Very Wet	Very Poor
UKSS_9008	2006	11.49	-2.14	2	2563	Very Wet	Very Poor

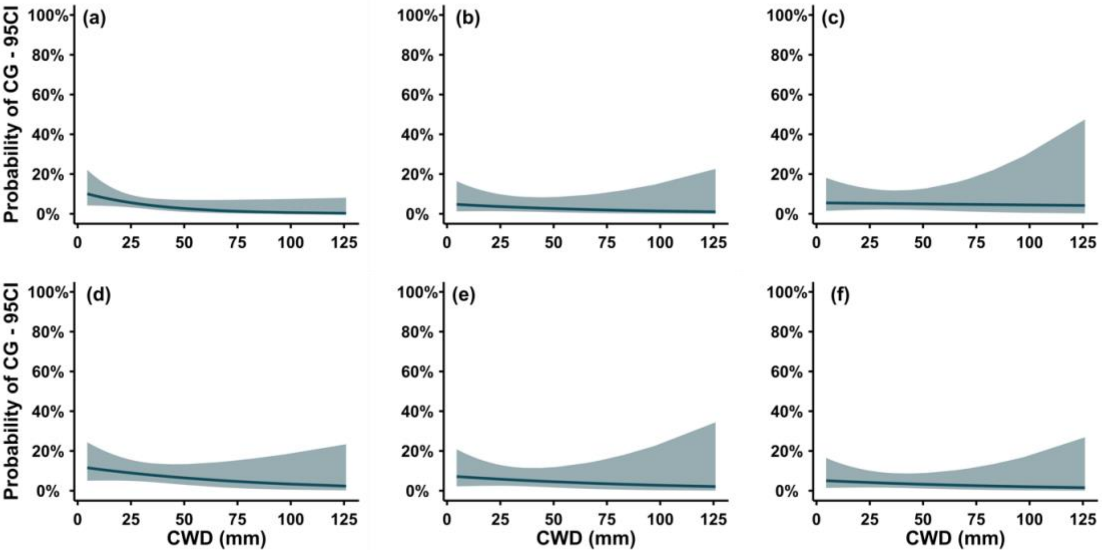

Figure S6.2 *- Predicted probability (solid line) of observed growth being in excess of the 95CI associated with the point forecast for individual tree growth under a 'no drought' scenario (i.e., compensatory growth) in the drought year (a) or five post drought years (b – f) as a function of drought intensity, measured in terms of Climatic Water Deficit (CWDdr). Shaded areas indicate the 95% CI of predictions.*

CHAPTER 7 - Conclusion

This concluding chapter is a modified version of an article published in the Royal Forestry Society's Quarterly Journal of Forestry. The unmodified version of this manuscript is presented in Appendix 1.

Ovenden, T., Perks, M., & Jump, A. (2022). How resilient are planted UK forests to drought? A summary of recent research on Sitka spruce and Scots pine. Quarterly Journal of Forestry, 116(4), 256–263.

7.1. Summary

As our climate warms, record breaking temperatures, changes in precipitation patterns and increases in the frequency and intensity of extreme climate events means that identifying ways to improve the resilience of our forests to the impacts of climate change is an urgent priority. Here I summarise the evidence presented in this thesis on how resilient Scots pine (*Pinus sylvestris*) and Sitka spruce (*Picea sitchensis*) really are to drought in the UK, how differences in short vs long terms responses might influence our understanding of how forests recover, and how both forest composition and the nature of the drought itself modify forest resistance and resilience to extreme drought events.

7.2. The current state of knowledge

As our climate warms, the pressures on global forest ecosystems from extreme climate events are expected to increase across much of the world (Anderegg et al., 2020; Brodribb et al., 2020). Of particular concern is the increasing threat to tree health and productivity posed by drought. Despite a predominantly cool maritime climate, forest ecosystems in the UK are vulnerable to drought, as the effects of both the historic droughts of 1976 and 2003 (Cavin et al., 2013; Cavin & Jump, 2017) and the more recent drought of 2018/19 demonstrate, the latter extending across much of mainland Europe (Zang, 2020; Turner et al., 2021).

Despite the pressing need to increase the overall resilience of natural and managed forests, remarkably little work has attempted to quantify the impact of historic drought events on forest growth in the UK. As a result, very little is known about the drought resilience of some of our most abundant and economically important tree species. A recent series of Quarterly Journal of Forestry (QJF) articles reviewed progress made by the UK forest sector so far, and the current state of resilience knowledge (Tew et al., 2021a, 2021b), including evidence of the historic impact, and future threat of extreme events on UK conifers (Spencer, 2018). In terms of the risks posed by drought, these articles largely drew on evidence from other countries and translated it to a UK setting. These knowledge gaps are particularly relevant for key conifer species such as Scots pine (*Pinus sylvestris*) and Sitka spruce (*Picea sitchensis*) which collectively make up >68% of all coniferous forest area in the UK (Forest Research, 2020). This lack of UK specific knowledge on how key UK tree species are likely to respond to drought hampers our ability to act to improve the resilience of UK forestry to our changing climate (Tew et al., 2021a).

In this context, the work contained within this thesis has sought to better understand drought impacts and resilience in planted UK forests using dendrochronological methods and broadly address the following key questions:

- How resistant and resilient are Scots pine and Sitka spruce to drought under UK conditions?

- Is there any evidence of a threshold response to drought severity, such that tree growth is relatively resistant to drought up to a point, but once a threshold is crossed, small increases in drought severity result in dramatic changes in tree growth?

- Do differences in stand density, tree size or species mixtures help to mitigate the negative impacts of drought on tree growth?

- Do differences in the characteristics of a particular drought event, such as the duration or intensity of an event change how trees respond?

7.3. Measuring resilience

A common definition of resilience is the capacity of a system to return to its pre-disturbance state, remaining relatively unchanged. While this definition is useful, the ability to ‘get back to normal’ might not be the only thing we are interested in, particularly because seeking to get back to a pre-disturbance state may be undesirable where conditions continue to change - such as under ongoing climate change. By adding a little more complexity, we can break the concept of resilience down into components that capture different aspects of how a tree or forest responds to a stressful event, such as drought. These ‘components of tree resilience’ were formalised in the dendrochronological community by Lloret et al. (2011) as resistance, recovery, and resilience itself.

This framework allows us to explore interesting differences in how drought impacts tree growth and stand dynamics (i.e., how forests change over time). For example, a tree species might be very resistant to drought but, if a drought is intense enough to overwhelm this resistance, the same species may take a long time to recover. Conversely, a different species may have low drought resistance but recover very quickly. This framework allows us to explore how planting designs (such as intimate mixtures of different species) or stand management (such as thinning) might alter these patterns of drought response and where trade-offs might exist, by comparing their relative responses.

Although widely adopted, the Lloret et al. (2011) framework often relies on a comparison of tree growth averaged over a number of years before and after the drought event. This averaging of tree growth means that the influence of both pre- and post-drought climate conditions, which are necessary to define the context within which both drought, and drought recovery occurs is generally not adequately captured (**Chapter 2**). As an analogy, if two people were exposed to an identical stressful event at the same time, but the first person was fit and healthy before the event and received expert care afterwards, whereas the second was already ill and received no care while they recovered, these two people might experience the impact of, and recovery from this event in different ways. Consequently, it is not only how ‘bad’ an event is that matters, but also the context within which this event occurs, as these two things likely interact to determine the outcome for the individual. Similarly, the frequency and timescales over which recovery is monitored will likely influence our understanding of the total impact of an event. With long-lived species such as most trees, having an approach that captures pre- and post-drought climate and allows us to monitor recovery over longer timescales at an annual resolution would allow a more comprehensive and nuanced understanding of how forests respond to, and recover from disturbance events such as drought, and so this became a key focus of my early work.

7.4. Assessing historic drought impact on Scots pine

Following the successful development of a statistical approach that builds on the Lloret et al. (2011) framework to capture pre- and post-drought climate, we used a tree-ring dataset collected from a Scots pine spacing experiment established in 1935 on the Black Isle (Scotland) to begin building a picture of how this species has responded to drought in the UK (**Chapters 2** and **3**). This site had been exposed to three major drought events (1976, 1984 and 1995) that varied in terms of their severity, with climatological data indicating that the 1984 event was the most severe (**Chapter 3**). At this site, we found that while the two lower severity droughts of 1976 and 1995 had only a very small impact on average tree growth, the slightly more severe drought of 1984 was associated with a large growth depression across most trees (**Chapter 3**). The negative effects of this 1984 drought on average stand growth was still detectable for up three years after drought, while some individual trees never fully recovered. Surprisingly, after recovery had occurred, we documented evidence of ‘compensatory growth’ in a post-recovery phase, where some trees grew faster after they had recovered than might have been expected if no drought had occurred, compensating for some of their lost radial growth (**Chapter 2**). The net effect of this compensatory growth meant that the cumulative impact of the 1984 drought across all trees was less nine years after drought than it was after four years.

These results paint a more dynamic picture of how Scots pine responds to drought than previously observed. Our results suggest that the growth response of this species to drought is non-linear, in that Scots pine can tolerate unfavourable conditions up to a certain threshold, after which it exhibits drastic declines in productivity. These results are consistent with studies of tree ecophysiology (i.e. how tree vascular tissues and water transport function) (Adams et al., 2017; Bartlett et al., 2016) and recent work which suggests the existence of drought thresholds in other species of pine (*Pinus edulis* and *Pinus ponderosa*) (Huang et al., 2015). As our climate warms and the intensity and frequency of drought events increases (Arias et al., 2021), it's likely that a larger proportion of droughts will cross the severity threshold of Scots pine, resulting in greater losses in forest productivity. However, the discovery of compensatory mechanisms in a post-recovery phase suggests that given sufficient time and the absence of further drought events, Scots pine might recover some of this lost productivity.

While encouraging, the pervasiveness of this compensatory phenomenon both within Scots pine and other species is currently unknown and should be a key focus of future work. If compensatory growth is more widespread, it could suggest forests are more resilient than previously thought, if considered over longer timescales. One key aspect of such compensatory mechanisms is that before any lost basal area can be recovered, trees must first return to (and then exceed) their 'normal' or expected growth rate under a given set of climate conditions. As a result, the combination of future increases in both the intensity and frequency of drought may overwhelm the ability of this mechanism to result in positive effects where, for example, a second extreme drought (or other disturbance event) occurs before recovery is complete and compensatory growth can occur.

7.5. Implications for stand management

In terms of practical implications for stand management, the results from our same study of UK-grown Scots pine suggested that smaller and faster-growing trees were more resilient to drought (**Chapter 2**), reflecting the findings of a large-scale study which found that larger trees suffer more under drought conditions (Bennett et al., 2015). A recent meta-analysis of the findings from 23 separate studies suggests that moderate and heavy thinning close to when a drought occurs is beneficial for stand resilience, but that this benefit declines over time (Sohn et al., 2016). Together, these results suggest that the targeted removal of large trees during thinning may improve the resilience of overall stand growth to drought. However, in contrast to this work, we found that higher density stands actually exhibited greater drought resilience than lower density stands. Several other studies (including Scots pine) have noted that the beneficial effect of thinning can actually become detrimental if the thinning occurred a long time prior to the drought event (D'Amato et al., 2013; Sohn et al., 2016), suggesting that the relationships between thinning intensity, stand density and the timing of any intervention relative to the drought event are not easy to predict.

It is also worth noting that in our study, during the two lower severity droughts, while average stand growth rate remained fairly constant, this was partly the result of variability in the growth of individual trees during drought, that is, some trees showed positive, while others showed negative impacts on growth. This finding raises the possibility that a variety of tree sizes may act as a form of response diversity (**Chapter 3**), promoting stand level resilience to lower severity droughts.

Collectively, this evidence highlights how complex it is for forest managers to reliably operationalise resilience concepts. As the occurrence of extreme drought is unpredictable, future research needs to determine whether there is an optimal time for thinning at a given stand age, target quantities of volume to remove and reliable ways of selecting which trees to harvest if increasing drought resilience is a key management objective. Understanding the interplay between these and other factors for a range of UK tree species will be a crucial next step in developing management strategies that increase the resilience of our forests to future drought events.

7.6. How drought resilient is Sitka spruce?

Extreme drought, like many other extreme events is a complex phenomenon that varies over both space and time (AghaKouchak et al., 2021). This complexity makes studying drought events and the impacts they have on forests particularly challenging. To characterise drought, we often rely on indices which allow us to understand how severe a year was relative to 'normal' conditions at a particular site, yet few studies attempt to distinguish between different 'types' of drought. For example, two droughts might be equally severe (that is, how bad a drought year was relative to 'normal' conditions at a given site) but may be the product of a very different set of circumstances. The first drought might have been very short but very intense (where intensity is measured in terms of the absolute water deficit at a site during drought), while the second may have been mild but lasted for a very long time. In turn, we might expect different species to be more or less vulnerable to these different types of drought, as their physiology is more or less adapted to deal with a particular range of conditions.

We assessed the drought response of Sitka spruce monocultures using tree-ring data collected from 26 sites from across the UK (Adams, 2014) which had been exposed to a range of drought conditions to understand what types of drought Sitka spruce might be most vulnerable to (**Chapter 6**). We also looked for any evidence of whether the same compensatory growth phenomenon we observed in Scots pine occurred in Sitka spruce, and to understand the drought conditions under which it might occur, implementing the approach developed in **Chapter 5**.

We found that drought intensity, rather than drought duration, is associated with lower levels of drought resilience in Sitka spruce, however the probability of observing compensatory growth was not associated with either drought intensity, duration, or severity in this species (**Chapter 6**). While we found some evidence of compensatory mechanisms in Sitka spruce, our results also suggest that if drought events in the future become more intense, the number of trees experiencing the negative impact of drought on radial growth will likely increase.

In our study, Sitka spruce was more resistant and resilient to drought than expected, with results suggesting that some trees grew at least as fast as predicted during a ‘no drought scenario’ as was observed under low intensity droughts (**Chapter 6**). This might indicate that warmer temperatures associated with lower intensity droughts may initially be beneficial for growth, but soon become negative as drought intensity increases, raising questions regarding the future suitability of this species on some UK sites.

7.7. Can species mixtures mitigate drought impact on tree growth?

There is great interest in the potential benefits species mixtures might provide for increasing forest resistance or resilience to drought, but supporting evidence is limited (Messier et al., 2021), often contradictory, and does not indicate a simple positive relationship between species diversity and drought resilience (Grossiord, 2019). While some evidence suggests mixtures may be beneficial under lower severity droughts, mixing effects may become maladaptive under more extreme events (Haberstroh & Werner, 2022). Such a ‘flip’ from a positive to a negative effect at a certain threshold of drought severity is broadly in keeping with our recent work discussed above, highlighting that forest dynamics under global change are complex and challenging to incorporate into adaptation management strategies.

Different combinations of species and their proportions lead to different drought responses for each species in a given mixture (Vitali et al., 2018), and so the commonly (but not uniformly) observed positive effects of species mixtures on stand productivity under non-drought conditions does not automatically mean these same species mixtures will also perform better during drought (Muñoz-Gálvez et al., 2020). For example intimate mixtures of Scots pine and Sitka spruce grown in the UK can result in overyielding (where mixtures of the two species grow faster than at least one of the admixed species in monoculture) (Mason et al., 2021), but is this reflected in the growth performance of these same mixtures under drought conditions? We collected tree-cores from the same intimate mixtures experiment of Scots pine and Sitka spruce that was assessed by Mason et al., (2021) to understand how much of an impact an extreme drought in the spring of 2012 had had on the growth of these two species in mixtures compared with monocultures (**Chapter 4**).

Scots pine was more resistant and resilient to drought than Sitka spruce, but trees growing in monocultures of both species were more resilient to drought than in any of the intimate mixtures (**Chapter 4**). While we should be cautious of extrapolating the results from a single experiment too widely, these findings do suggest that intimate mixtures of these two species may not be an effective way to mitigate the negative impacts of future extreme spring drought events when the stand is relatively young (this experiment was 24 years old at the time of drought). Species mixtures clearly provide a range of benefits, from economic to environmental and social (Liu et al., 2018), but we must be careful to ensure that any decisions to adapt our forests to climate change are supported by evidence. What is now needed is a more comprehensive understanding of how these and other species mixtures are likely to respond to a range of drought conditions across the diversity of UK soils.

7.8. Conclusions

The question of “resilience of what, and to what?” (Hodgson et al., 2015) highlights the need to understand that choices to increase the resilience of one aspect of a system (such as tree growth) to one particular stressor (such as drought), are unlikely to be effective at increasing the resilience of all aspects of a system to all possible stressors. As our climate warms, the future will not be characterised by the emergence of a single threat to which we can tailor a limited number of very specific solutions. Instead, this future will be defined by a multitude of interacting biotic (e.g., pests and diseases) and abiotic (e.g., extreme droughts and storms) stressors which are likely to be outside the range of variability to which many existing ecological systems are adapted. Novel combinations of these stressors will require novel approaches to forest management and a solid evidence base on the performance and resilience of alternative tree species (and their combinations) to those commonly used in British forestry under a range of conditions. While diversification is an important aspect of adaptation, it is essential that we understand and consider the interactions between species and management practices, because simply adding more diversity in the form of more species does not automatically increase the overall resilience of a system. The research presented here contributes to a strong foundation of evidence which can now be used in conjunction with modelling work to assess the risks to UK forests posed by climate change and extreme climate events, and identify ways in which we can build resilience to them.

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Appendix 1

How Resilient are Planted UK Forests to Drought?

A summary of recent research on Sitka spruce and Scots pine

Thomas Ovenden, **Mike Perks** and **Alistair Jump** explore how resilient Scots pine and Sitka spruce are to drought, and how the nature of the drought itself modifies forest resistance and resilience to extreme drought events.

As our climate warms, the pressures on global forest ecosystems from extreme climate events are expected to increase across much of the world (Anderegg et al., 2020; Brodribb et al., 2020). Of particular concern is the increasing threat to tree health and productivity posed by drought. Despite a predominantly cool maritime climate, forest ecosystems in the UK are vulnerable to drought, as the effects of both the historic droughts of 1976 and 2003 (Cavin et al., 2013; Cavin and Jump, 2017) and the more recent drought of 2018/19 demonstrate, the latter extending across much of mainland Europe (Buras et al., 2020; Turner et al., 2021).

Despite the pressing need to increase the overall resilience of natural and managed forests, remarkably little work has attempted to quantify the impact of historic drought events on forest growth in the UK. As a result, very little is known about the drought resilience of some of our most abundant and economically important tree species. A recent series of *Quarterly Journal of Forestry* articles reviewed progress made by the UK forest sector so far, and the current state of resilience knowledge (Tew et al., 2021a, 2021b), including evidence of the historic impact, and future threat of extreme events on UK conifers (Spencer, 2018). In terms of the risks posed by drought, these articles largely drew on evidence from other countries and translated it to a UK setting. These knowledge gaps are particularly relevant for key conifer species such as Scots pine (*Pinus sylvestris*) and Sitka spruce (*Picea sitchensis*), which collectively make up over 68% of all coniferous forest area in the UK (Forest Research, 2020). This lack of UK-specific knowledge on how key UK tree species are likely to respond to drought hampers our ability to act to improve the resilience of UK forestry to our changing climate (Tew et al., 2021a).

In this context, a research collaboration between the University of Stirling and Forest Research has been seeking to better understand drought impacts and resilience in planted UK forests using dendrochronological methods. We have sought to address the following key questions:

- How resistant and resilient are Scots pine and Sitka spruce to drought under UK conditions?
- Is there any evidence of a threshold response to drought severity, such that tree growth is relatively resistant to drought up to a point, but once a threshold is crossed, small increases in drought severity result in dramatic changes in tree growth?
- Do differences in stand density, tree size or species mixtures help to mitigate the negative impacts of drought on tree growth?
- Do differences in the characteristics of a particular drought event, such as the duration or intensity of an event change how trees respond?

Measuring resilience

A common definition of resilience is the capacity of a system to return to its pre-disturbance state, remaining relatively unchanged. While this definition is useful, the ability to 'get back to normal' might not be the only thing we are interested in, particularly because seeking to get back to a pre-disturbance state may be undesirable where conditions continue to change – such as under ongoing climate change. By adding a little more complexity, we can break the concept of resilience down into components that capture different aspects of how a tree or forest responds to a stressful event, such as drought. These 'components of tree resilience' were formalised in the dendrochronological community by Lloret et al. (2011) as resistance, recovery, and resilience itself (Figure 1).

> "The frequency and timescales over which recovery is monitored will likely influence our understanding of the total impact of an event."

This framework allows us to explore interesting differences in how drought impacts tree growth and stand dynamics (i.e., how a forest changes over time). For example, a tree species might be very resistant to drought but, if a drought is intense enough to overwhelm this resistance, the same species may take a long time to recover. Conversely, a different species may have low drought resistance but recover very quickly. This framework allows us to explore how planting designs (such as intimate mixtures of different species) or stand management (such as thinning) might alter these patterns of drought response and where trade-offs might exist, by comparing their relative responses.

Although widely adopted, the Lloret et al. (2011) framework often relies on a comparison of tree growth averaged over a number of years before and after the drought event. This averaging of tree growth means that the influence of both pre- and post-drought climate conditions, which are necessary to define the context within which both drought and drought recovery occur, is generally not adequately captured (Ovenden et al., 2021b). As an analogy, if two people were exposed to an identical stressful event at the same time, but the first person was fit and healthy before the event and received expert care afterwards, whereas the second was already ill and received no care while they recovered, these two people might experience the impact of, and recovery from, this event in different ways. Consequently, it is not only how 'bad' an event is that matters, but also the context within which this event occurs, as these two things likely interact to determine the outcome for the individual. Similarly, the frequency and timescales over which recovery is monitored will likely influence our understanding of the total impact of an event. With long-lived species such as most trees, having an approach that captures pre- and post-drought climate and allows us to monitor recovery over longer timescales at an annual resolution would allow a more comprehensive and nuanced understanding of how forests respond to and recover from disturbance events such as drought, and so this became a key focus of our early work.

Assessing historic drought impact on Scots pine

Following the successful development of a statistical approach that builds on the Lloret et al. (2011) framework to capture pre- and post-drought climate, we used a tree-ring dataset collected from a Scots pine spacing experiment

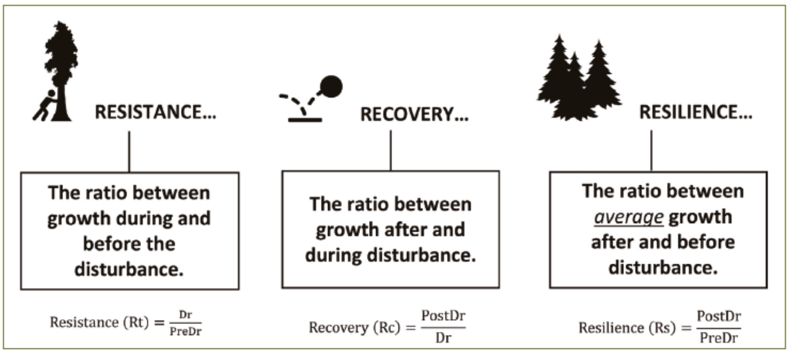

Figure 1. A graphical representation of how the resistance, recovery and resilience framework formalised by Lloret et al. (2011) is commonly implemented using tree growth. Dr indicates growth in the drought year, while PreDr and PostDr represent average growth in the pre- and post-drought periods, respectively.

established in 1935 on the Black Isle (Scotland) to begin building a picture of how this species has responded to drought in the UK. This site had been exposed to three major drought events (1976, 1984 and 1995) that varied in terms of their severity, with climatological data indicating that the 1984 event was the most severe (Ovenden et al., 2021a) (Figure 2). At this site, we found that while the two lower severity droughts of 1976 and 1995 had only a very small impact on average tree growth, the slightly more severe drought of 1984 was associated with a large growth depression across most trees (Ovenden et al., 2021a). The negative effects of this 1984 drought on average stand growth was still detectable for up three years after drought, while some individual trees never fully recovered (Ovenden et al., 2021b). Surprisingly, after recovery had occurred, we documented evidence of 'compensatory growth' in a post-recovery phase, where some trees grew faster after they had recovered than might have been expected if no drought had occurred, compensating for some of their lost radial growth (Figure 3). The net effect of this compensatory growth meant that the cumulative impact of the 1984 drought across all trees was less nine years after drought than it was after four years (Ovenden et al., 2021b) (Figure 3).

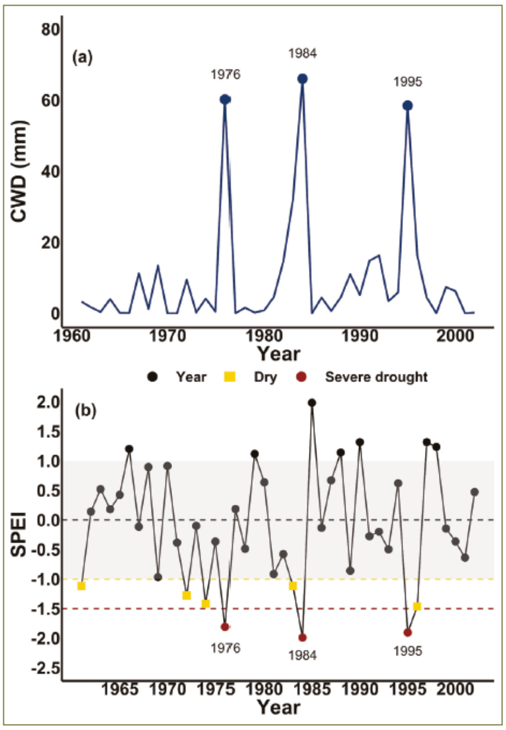

Figure 2. Two climate indices that are often used in conjunction with tree-ring analysis for the identification and classification of drought are the Climatic Water Deficit (CWD, measured in millimetres) and the Standardised Precipitation Evapotranspiration Index (SPEI, measured in standard deviations from the mean). The CWD provides an absolute measure of water deficit (i.e. drought intensity), while the SPEI provides a relative measure of drought severity compared with previous years' climate over a user defined period. The displayed CWD and SPEI values show how both indices agree that 1976, 1984 and 1995 were all drought years at our Scots pine experiment on the Black Isle (Scotland). Modified from Ovenden et al. (2021a).

These results paint a more dynamic picture of how Scots pine responds to drought than previously observed. Our results suggest that the growth response of this species to drought is non-linear, in that Scots pine can tolerate unfavourable conditions up to a certain threshold, after which it exhibits drastic declines in productivity. These results are consistent with studies of tree ecophysiology (i.e. how tree vascular tissues and water transport function) (Adams et al., 2017; Bartlett et al., 2016) and recent work that suggests the existence of drought thresholds in other species of pine (*Pinus edulis* and *Pinus ponderosa*) (Huang et al., 2015). As our climate warms and the intensity and frequency of drought events increases (Arias et al., 2021), it is likely that a larger proportion of droughts will cross the severity threshold of Scots pine, resulting in greater losses in forest productivity. However, the discovery of compensatory mechanisms in a post-recovery phase suggests that given sufficient time and the absence of further drought events, Scots pine might recover some of this lost productivity.

While encouraging, the pervasiveness of this compensatory phenomenon both within Scots pine and other species is currently unknown and should be a key focus of future work. If compensatory growth is more widespread, it could suggest forests are more resilient than previously thought, if considered over longer timescales. One key aspect of such compensatory mechanisms is that before any lost basal area can be recovered, trees must first return to (and then exceed) their 'normal' or expected growth rate under a given set of climate conditions. As a result, the combination of future increases in both the intensity and frequency of drought may overwhelm the ability of this mechanism to result in positive effects where, for example, a second extreme drought (or other disturbance event) occurs before recovery is complete and compensatory growth can occur.

Implications for stand management

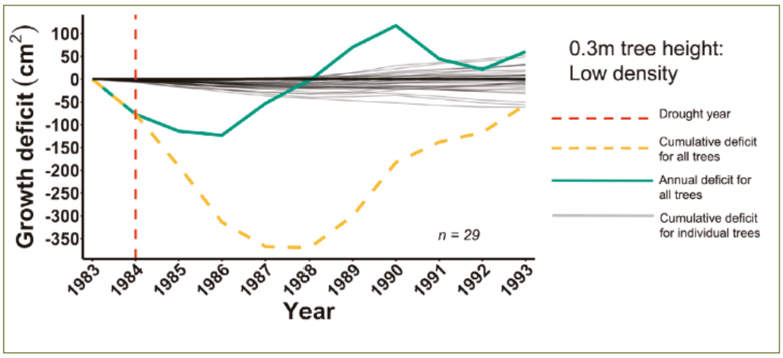

Figure 3. Compensatory growth following an extreme drought in Scots pine. Lines show the 1984 drought event (red dashed line), the annual (green) and cumulative (yellow dashed) growth deficit for all sample trees combined and the cumulative annual growth deficit for each tree (grey) over time (n = 29). Growth deficit for all trees was derived from the difference between observed growth (obtained from cross-sectional stem discs cut at 0.3m high) and forecasted growth (obtained from statistical modelling) in a scenario where no drought had occurred. Modified from Ovenden et al. (2021b).

In terms of practical implications for stand management, the results from our same study of UK-grown Scots pine suggested that smaller and faster-growing trees were more resilient to drought (Ovenden et al., 2021b), reflecting the findings of a large-scale study which found that larger trees suffer more under drought conditions (Bennett et al., 2015). A recent meta-analysis of the findings from 23 separate studies suggests that moderate and heavy thinning close to when a drought occurs is beneficial for stand resilience, but that this benefit declines over time (Sohn et al., 2016). Together, these results suggest that the targeted removal of large trees during thinning may improve the resilience of overall stand growth to drought. However, in contrast to this work, we found that higher density stands actually exhibited greater drought resilience than lower density stands. Several other studies (including Scots pine) have noted that the beneficial effect of thinning can actually become detrimental if the thinning occurred a long time prior to the drought event (D'Amato et al., 2013; Sohn, Hartig, et al., 2016), suggesting that the relationships between thinning intensity, stand density and the timing of any intervention relative to the drought event are not easy to predict.

It is also worth noting that in our study, during the two lower severity droughts, while average stand growth rate remained fairly constant, this was partly the result of variability in the growth of individual trees during drought, that is, some trees showed positive while others showed negative impacts on growth. This finding raises the possibility that a variety of tree sizes may act as a form of response diversity (Ovenden et al., 2021a), promoting stand level resilience to lower severity droughts.

Collectively, this evidence highlights how complex it is for forest managers to reliably operationalise resilience concepts. As the occurrence of extreme drought is unpredictable, future research needs to determine whether there is an optimal time for thinning at a given stand age, target quantities of volume to remove and reliable ways of selecting which trees to harvest if increasing drought resilience is a key management objective. Understanding the interplay between these and other factors for a range of UK tree species will be a crucial next step in developing management strategies that increase the resilience of our forests to future drought events.

> "Our results suggest Scots pine can tolerate unfavourable conditions up to a certain threshold, after which it exhibits drastic declines in productivity."

How drought resilient is Sitka spruce?

Extreme drought, like many other extreme events is a complex phenomenon that varies over both space and time (AghaKouchak et al., 2021). This complexity makes studying drought events and the impacts they have on forests particularly challenging. To characterise drought, we often rely on indices that allow us to understand how severe a year was relative to 'normal' conditions at a particular site (Figure 2), yet few studies attempt to distinguish between

Figure 4. Heading out to the Ardross 21 mixtures experiment before commencing fieldwork in November 2019, looking out across the forest facing the study site.

different 'types' of drought. For example, two droughts might be equally severe (that is, how bad a drought year was relative to 'normal' conditions at a given site) but may be the product of a very different set of circumstances. The first drought might have been very short but very intense (where intensity is measured in terms of the absolute water deficit at a site during drought), while the second may have been mild but lasted for a very long time. In turn, we might expect different species to be more or less vulnerable to these different types of drought, as their physiology is more or less adapted to deal with a particular range of conditions.

We assessed the drought response of Sitka spruce monocultures using tree-ring data collected from 26 sites from across the UK (Adams, 2014) that had been exposed to a range of drought conditions to understand what types of drought Sitka spruce might be most vulnerable to. We also looked for any evidence of whether the same compensatory growth phenomenon we observed in Scots pine occurred in Sitka spruce, and to understand the drought conditions under which it might occur.

Preliminary results seem to suggest drought intensity, rather than drought duration, is associated with lower levels of drought resilience in Sitka spruce. Similarly, as drought intensity increases, it appears the probability of observing compensatory growth declines. While these results provide some evidence of compensatory mechanisms in Sitka spruce, they also suggest that if drought events in the future become more intense, this mechanism may be less effective at mitigating the negative impacts on tree growth.

In our study Sitka spruce was more resistant and resilient to drought than expected, with initial results suggesting that some trees grew faster than predicted during drought. This might indicate that warmer temperatures associated with lower intensity droughts may initially be beneficial for growth, but soon become negative as drought intensity increases. Where negative impacts of drought on tree growth were clear, recovery for many trees was swift, with 80% of trees making a full recovery to growth rates that might have been expected if no drought had occurred within five years of the drought event.

Can species mixtures mitigate drought impact on tree growth?

There is great interest in the potential benefits species mixtures might provide for increasing forest resistance or resilience to drought, but supporting evidence is limited (Messier et al., 2021), often contradictory, and does not indicate a simple positive relationship between species diversity and drought resilience (Grossiord, 2019). While some evidence suggests mixtures may be beneficial under lower severity droughts, mixing effects may become maladaptive under more extreme events (Haberstroh and Werner, 2022). Such a 'flip' from a positive to a negative effect at a certain threshold of drought severity is broadly in keeping with our recent work discussed above, highlighting that forest dynamics under global change are complex and challenging to incorporate into adaptation management strategies.

Different combinations of species and their proportions lead to different drought responses for each species in a given mixture (Vitali et al., 2018), and so the commonly (but not uniformly) observed positive effects of species mixtures on stand productivity under non-drought conditions does not automatically mean these same species mixtures will also perform better during drought (Muñoz-Gálvez et al., 2020). For example, intimate mixtures of Scots pine and Sitka spruce grown in the UK can result in overyielding (where mixtures of the two species grow faster than at least one of the admixed species in monoculture) (Mason et al., 2021), but is this reflected in the growth performance of these same mixtures under drought conditions? We collected tree-cores from the same intimate mixtures experiment of Scots pine and Sitka spruce that was assessed by Mason et al. (2021) to understand how much of an impact an extreme drought in the spring of 2012 had had on the growth of these two species in mixtures compared with monocultures (Figure 4).

Scots pine was more resistant and resilient to drought than Sitka spruce, but trees growing in monocultures of both species were more resilient to drought than in any of the intimate mixtures (Ovenden et al., 2022). While we should be cautious of extrapolating the results from a single experiment too widely, these findings do suggest that intimate mixtures of these two species may not be an effective way to mitigate the negative impacts of future extreme spring drought events when the stand is relatively young (this experiment was 24 years old at the time of drought). Species mixtures clearly provide a range of benefits, from economic to environmental and social (Liu et al., 2018), but we must be careful to ensure that any decisions to adapt our forests to climate change are supported by evidence. What is now needed is a more comprehensive understanding of how these and other species mixtures are likely to respond to a range of drought conditions across the diversity of UK soils.

Conclusions

The question of "resilience of what, and to what?" (Hodgson et al., 2015) highlights the need to understand that choices to increase the resilience of one aspect of a system (such as tree growth) to one particular stressor (such as drought), are unlikely to be effective at increasing the resilience of all aspects of a system to all possible stressors. As our climate warms the future will not be characterised by the emergence of a single threat to which we can tailor a limited number of very specific solutions. Instead, this future will be defined by a multitude of interacting biotic (e.g., pests and diseases) and abiotic (e.g., extreme droughts and storms) stressors that are likely to be outside the range of variability to which many existing ecological systems are adapted. Novel combinations of these stressors will require novel approaches to forest management and a solid evidence base on the performance and resilience of alternative tree species (and their combinations) to those commonly used in British forestry under a range of conditions. While diversification is an important aspect of adaptation, it is essential that we understand and consider the interactions between species and management practices, because simply adding more diversity in the form of more species does not automatically increase the overall resilience of a system. The research presented here contributes to a strong foundation of evidence that can now be used in conjunction with modelling work to assess the risks to UK forests posed by climate change and extreme climate events, and identify ways in which we can build resilience to them.

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