Drought tolerance of western Canadian forests tree species inferred from dendrochronology

by

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Abstract

Western Canadian forests have been subject to periods of drought stress over the last three decades, resulting in growth reductions, dieback, and increased wildfires in the context of climate change. To contribute to adaptive forest management, this study compares drought vulnerabilities of eight common western Canadian tree species based on 392 tree-ring chronologies. Chronologies were grouped into clusters with similar climatologies and assessed for drought resistance, resilience and recovery. The results show that the most severe drought impacts occurred in dry boreal mixedwood ecosystems, east of the Rocky Mountains. The dominant species in these ecosystems (white spruce and jack pine) were most vulnerable in the north, rather than at the southern fringe of the boreal forest, suggesting lack of adaptive traits to cope with drought conditions in northern populations. The same pattern emerges for sub-boreal ecosystems further west. For example, interior Douglas-fir was most vulnerable to drought at the northern edge of its distribution. In moister montane ecosystems, Douglas-fir and limber pine showed the least drought resistance, but all species recovered well from drought events. The results have implications for forest management in western Canada: interior Douglas-fir should not be planted beyond its northern range limitations despite significant regional warming trends. Across large sections of western boreal forests, not just the southern boreal fringe, the most common species such as white spruce and jack pine appear vulnerable in the long term, while submontane forest ecosystems of British Columbia and Alberta may serve as regional climate change refugia.

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Preface

This thesis is being prepared for submission as a journal article. The contributors are Benjamin Panes, Andreas Hamann, and Charles Nock. The study was conceived and designed by myself, with input from AH and CN. I curated and analyzed the data, created all figures and tables, and I wrote the first draft of the thesis. AH provided feedback on the analysis, suggested additional analytical approaches, and contributed to editing and interpretation of the results. CN provided research funding and contributed to editing and interpretation as well.

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Table of Contents

List of Tables

List of Figures

1. Introduction

Forests are facing moisture limitations due to climate warming when water demand from higher evapotranspiration exceeds water availability for trees (Allen et al. 2010, Babst et al. 2019). Among the most vulnerable forest ecosystems in this regard are the western boreal forests of Canada, because growing conditions are generally dry, yet these ecosystems are able to support tree growth because of the cold temperatures that result in low evapotranspirative demand. Above average observed warming trends over the last several decades across northern forest regions threaten this evapotranspirative balance. For western Canada, Zhang et al. (2019, pp. 126, 157) report a mean annual temperature increase between 1.5 in the south and 3.5°C in the north since the 1950s, compared to a global average increase of 0.8°C. For the same period, precipitation was observed to increase by up to 10% in the north, while remaining unchanged at the southern fringe of the boreal forest.

Although the overall changes to the evapotranspirative balance in northern ecosystems has been moderate (Levesque and Hamann 2022), climate induced changes are expected to accelerate non-linearly in the future, and are expected to causes significant ecosystem disruptions through direct climate impacts, insect and pest outbreaks, and fire disturbance (Soja et al. 2007). Some of these expected ecosystem disruptions have already occurred in recent years, such as exceptional fire seasons (Hanes et al. 2019, Yu et al. 2019), large-scale insect outbreaks (Kurz et al. 2008), and direct climate impacts during drought periods, leading to pervasive forest dieback (Peng et al. 2011), as well as large scale regional tree mortality events (Michaelian et al. 2011).

Western boreal forest regions of Canada have been compared to a ‘canary in the coalmine’, with respect to global climate change, for its above average warming rates and impacts on ecosystems (Gauthier et al. 2015). The region will likely be one of the first where large scale management interventions will be needed to mitigate the effects of climate change on forest ecosystems. One option is to change reforestation practices through planting different species or different genotypes of the same species with higher drought tolerances (e.g., Depardieu et al. 2020), but such prescriptions usually require long-term field testing that is only available for few species of commercial interest (e.g., Eilmann et al. 2013, Park and Rodgers 2023, Sang et al. 2023). An alternative approach to evaluate the tolerance of species and their populations to climatic stress factors is through dendrochronology, taking advantage of historical records of both tree growth contained in tree rings, as well as archival climate data. The approach can be used to monitor forest growth and health in response to climate trends (e.g., Girardin et al. 2016, Hogg et al. 2017), quantify drought sensitivity (e.g., D'Orangeville et al. 2018), and even identify population-level genetic adaptation in drought tolerance traits (Isaac-Renton et al. 2018, Sebastian-Azcona et al. 2020, Depardieu et al. 2021).

Drought response of forest trees can be broken down into three components that can be calculated from ring width patterns: resistance, recovery, and resilience (Lloret et al. 2011). Resistance refers to a tree’s ability to resist drought induced decreases in growth by comparing growth during a specified period before the event to growth levels during the drought. Recovery refers to the rate at which growth returns to pre-drought levels following disturbance within that same period. Resilience is the ability to return to pre-drought growth and uses the time frames specified for resistance and recovery, so that when recovery is equal to resistance, resilience is one. In addition, relative resilience, weighted by the drought impact measured as resistance, can be calculated. All metrics provide useful aspects of drought response (e.g., Vitasse et al. 2019, Pardos et al. 2021, Serra-Maluquer et al. 2022), but the most straight-forward inferences are the interpretation of resistance as an indicator of short-term impact on growth during the drought event, and resilience as an indicator of longer-term damage to the tree’s water transport system, such as xylem cavitation, leaf wilting, or root damage (Bartlett et al. 2016).

This study uses a previously compiled dendrochronology dataset for western Canada (Hynes and Hamann 2020), including data from the Climate Impacts on the Productivity and Health of Spruce project (Hogg et al 2017), as well as chronologies from the International Tree-Ring Data Bank (ITRDB) (GrissinoMayer and Fritts 1997). I compare drought tolerance traits of eight common western Canadian tree species within multivariate clusters of similar climate and drought response histories. Our specific objectives are (1) to assess geographic regions, species, and tree populations within western Canada with respect to their vulnerability to drought conditions; (2) to identify relatively drought tolerant species and genotypes that maintain productivity or quickly recover after drought events; and (3) on this basis develop recommendations for assisted migration of species and their populations for reforestation programs.

2. Literature Review

2.1 Climate trends and projections for Canada

Canada contains climate zones that range in condition from arctic tundra, to desert, to temperate rainforests. Climate-related concerns in each of these regions can differ based on their average historical climate and the capacity of their ecosystems to adapt to observed and predicted rates of change. For example, boreal forest north of the western Canadian prairies is sensitive to fluctuations in moisture (Hogg, 1994), while trees further north at the treeline are typically limited by cold temperatures (Rossi et al. 2008). This thesis focuses on moisture limitations, which are a key concern in the north-western boreal forest, where they are predicted to intensify under climate change (Levesque and Hamann 2022). Generally, far northern ecosystems are expected to benefit from increased productivity due to higher temperatures (Brooks et al. 1998). However, these growth improvements may be compromised by future moisture limitations as populations shift from cold- to moisture-limited due to changing climate (Chagnon et al. 2023).

While growth limitations and climate related concerns vary throughout Canada, climate change trends have also occurred at different rates for each region. Average annual temperature in Canada has increased by 1.7°C from 1948 to 2016, yet these rates range from 0.5 in the south to 3.5°C in the north of Canada (Zhang et al. 2019, pp. 125-126, 156-157). However, on average Canada has experienced warming at a faster rate compared to the global average increase of 0.8°C for the same period. Changes in precipitation have also been spatially heterogeneous, with a range of 0-50%, although most areas of Canada fall into the range of a 0-10% increase and the areas with greater changes are in unforested, arctic areas with lower data density. There have also been changes in timing of and variability of moisture throughout the past century, such as a lower extent and duration of snow cover during the winter months limiting moisture in the drier season immediately following winter (Mote et al. 2018), and less days with precipitation, and an increase in heavy rainfall (Peterson et al. 2008),

Several climate models have made predictions about how these trends will continue to progress, summarized by the Intergovernmental Panel on Climate Change's (IPCC) sixth assessment report (2022). Under five Shared Socioeconomic Pathways (SSPs) greenhouse gas emission scenarios, Canada is projected to experience significant warming throughout the 21st century. These pathways range from most (SSP 5-8.5) to least severe (SSP 1-1.9), where SSP 5-8.5 represents an increase in fossil-fuel based development causing CO_2 emissions to triple by 2075 and global climate warming exceed 4°C, while SSP 1-1.9 reflects a shift towards more sustainable methods that cut CO_2 emissions to net zero by 2050 and limit warming at 1.5°C. Under SSP 5-8.5, Canada's average annual temperature is projected to increase by approximately 2.8 to 5.4°C by mid-century (2041-2060) and by 4.7 to 8.7°C by late century (2081-2100) compared to the baseline period of 1986-2005. Under the most optimistic SSP 1, the average annual temperature in Canada is still projected to increase by 1.3 to 2.3°C by mid-century then 1.8°C to 4.4°C by late century, where the range in projected temperatures represents uncertainty due to the assumptions and parameters that go into general circulation models for climate change modeling.

Additionally, the warming climate will influence precipitation patterns, resulting in altered moisture regimes. Under more optimistic scenarios, Canada wide annual precipitation could increase by just 0.4 – 11.9% by the end of the century, or in the event of increased carbon emissions, precipitation could increase by 13.7-36.2%. However, these increases in precipitation are spatially heterogeneous, and will likely not compensate for increased evapotranspiration due to climate warming. For example, median summer temperatures in the Canadian prairie provinces will increase by approximately 6.5°C by 2081-2100 under SSP5-8.5, but precipitation will only increase by 15.3%. These changes in temperature and precipitation patterns will cause heightened water stress during drought events, potentially leading to reduced tree growth and increased mortality rates.

2.2 Climate impacts on forest ecosystems

Changes in climate have impacted tree growth, caused large-scale tree mortality, exacerbated wildfire events, and increased levels of insect and disease outbreaks (Soja et al. 2007). Examples from recent years include the severe 2001-2002 drought in the western Canadian prairies where 35% of observed tree biomass was lost to mortality south of the boreal transition zone (Michaelian et al. 2011), and the 2004 mountain pine beetle outbreak in British Columbia that was larger and more severe than any previously recorded outbreak in the province (Kurz et al., 2008).

Climate change-induced alterations in temperature and precipitation patterns can significantly impact water availability in forest ecosystems as rising temperatures increase evapotranspiration rates and lead to greater water demand. Forest mortality events in most of the world’s ecosystems have been attributed to climate change as a result of these processes (Allen et al. 2010). Further, water stress and drought can affect tree drought tolerance and overall forest health; during drought periods, trees experience reduced water uptake, resulting in decreased photosynthetic rates, limited growth, and increased susceptibility to pests and diseases (Anderegg et al. 2013). As a result, prolonged drought can lead to tree mortality and potentially alter species compositions within forests.

Climate change impacts can also range beyond direct changes in temperature and precipitation. One vulnerability is an increased frequency and severity of wildfires (Bentz et al. 2010). As temperatures rise, the frequency of extreme heat events further reduces moisture in forest fuels, leading to larger and more intense fires. This can create a positive feedback loop, where large fire years burn deeper organic layers and increase the chance of overwintering fires that further increase risk in the subsequent season (Sholten et al. 2021).

Additionally, the warming climate can exacerbate the prevalence of forest pests, such as mountain pine beetles, which have already expanded past their historical range and through the Rocky Mountains (Cullingham et al. 2011). These insect outbreaks lead to extensive tree mortality and disrupt forest dynamics, affecting both tree drought tolerance and overall ecosystem resilience.

Climate change-induced alterations in temperature and precipitation patterns can also disrupt species interactions and alter forest biodiversity (Garcia et al. 2014). Some tree species may become more susceptible to pests and diseases, leading to declines in their populations. At the same time, other species may thrive under changing conditions and experience population growth, potentially leading to imbalances in forest ecosystems. Shifts in tree species composition due to climate change can have cascading effects on other plant and animal species that depend on specific tree species for habitat and food. Moreover, changes in the timing of seasonal events, such as flowering and migration, can disrupt critical ecological interactions, affecting species' survival and reproduction. These changes can compound with larger anthropogenic factors, like land-cover and land-use changes, and cause further loss to biodiversity (Mantyka-Pringle et al. 2015)

Further, climate change can limit tree growth and exacerbate forest dieback. Despite expected increases in growth in specific regions due to current cold-limitations, Girardin et al. (2016), found that areas like the northern Yukon will shift to being moisture limited due to increased rates of evapotranspiration. Similarly, moisture will also limit the advance of the northern tree line even with increased temperature (Rees et al. 2020). These moisture limitations will also have the greatest effect on large, old-growth trees where a higher proportion of carbon is stored (McDowell & Allen 2015).

Forests can help to mitigate climate change by sequestering carbon dioxide through photosynthesis and storing it as biomass. However, climate change impacts, such as drought-induced tree mortality and increased wildfire activity, can reduce forest carbon sequestration capacity. As forests experience water stress and drought, photosynthesis rates decline, limiting the amount of carbon dioxide that trees can sequester (Brzostek et al. 2014). More importantly, wildfire events release large amounts of stored carbon back into the atmosphere, exacerbating the greenhouse effect and further contributing to climate change. Further, this has non linear effects, such as more frequent fire potentially increasing the likelihood of burning in legacy carbon deeper in the soil (Walker et al. 2019). Nevertheless, it should be noted that CO_2 increases from climate effects pale in comparison to other sources, for example, in the western United States, wildfire emissions were 6% when compared with fossil fuel emissions over the last decade (Bartowitz et al. 2022).

2.3 Climate change adaptation in forestry

Adapting forestry to climate change requires a shift towards sustainable forest management practices that consider these new conditions. One approach is the adoption of different silviculture techniques that are tailored to enhance the resilience of forest ecosystems, like ecosystem-based forest management (Price et al. 2009). This method considers the interplay between ecological components, where emphasizing mixed-species forests and maintaining structural diversity can improve resilience to climate-related stresses. Variable retention harvesting is another silvicultural technique that can improve resilience that involves leaving patches of mature forest within harvested areas. These residual patches act as seed sources and create microclimates that facilitate natural regeneration and support biodiversity (Soler et al. 2016). By maintaining a diverse age structure and species composition, forests become more adaptable to changing conditions, including increased drought and pest pressures. Selective thinning is another silvicultural technique that can improve forest health by reducing competition among trees, enhancing their resistance to drought stress (Sohn et al. 2016). Another alternative is the use of nitrogen fertilization, which can especially improve growth when soil water is limited due to increased water use efficiency (Ibáñez et al. 2018). These silvicultural practices contribute to the creation of more diverse and resilient forests that can better withstand climate change-related pressures.

Alternatively, assisted migration is an approach that involves the intentional movement of tree species or provenances to areas with projected suitable climates where they are not currently found. Assisted migration aims to establish climate-resilient tree populations that can thrive under changing conditions (Pedlar et al. 2012). By strategically selecting and planting tree species that are better adapted to projected future climates, assisted migration can improve forest health and productivity (Aitken et al. 2008). However, consideration must be given to potential negative ecological and social impacts, such as displacing native species and disrupting local ecosystems. Some species that have been introduced to new ecosystems have become invasive and outcompeted local vegetation. Typically, these species exhibit either vegetative reproduction or long-distance seed dispersal (Nunez-Mir et al. 2019)

Developing tree varieties with improved drought tolerance through genetic selection is another adaptation strategy. Tree breeding programs can identify and propagate individuals that demonstrate better resilience to water stress, improving the overall drought tolerance of future forest stands.
Advances in genetic research and biotechnology offer new opportunities to accelerate the development of drought-resistant tree varieties by defining genomic attributes that affect phenotypic performance for focus in tree improvement programs (Nelson & Johnsen 2008). Genetic approaches can also address other climate change impacts, such as resistance to pests and diseases associated with shifting temperature patterns.

As the frequency and severity of wildfires increase with climate change, effective fire management and mitigation strategies will have more opportunities to effect change. Implementing proactive fire management strategies can reduce the risk of wildfires and promote forest resilience (Stevens-Rumann et al. 2018). Prescribed burning, for instance, can be employed to reduce fuel loads and mitigate the risk of severe wildfires (Duane et al. 2019). Forest restoration efforts also play a crucial role in adapting to climate change impacts. Restoring degraded or fire-prone areas with native and climate-resilient tree species can aid ecosystem recovery and enhance the overall resilience of the landscape.

Continuous climate monitoring can also be implemented in adaptive forest management (Molina et al. 2021). Regular monitoring of temperature, precipitation, and other climate variables helps track changes and informs decision-making processes. Adaptive management involves flexible and iterative approaches, where forest management practices are continually adjusted based on the latest information and feedback from ongoing monitoring. This adaptive approach allows for quick responses to unforeseen climate impacts and ensures that management strategies remain effective over time.

3. Materials and Methods

3.1 Tree-ring data

Tree ring data for western Canada was obtained through the Canadian Forest Service, Northern Forestry Center’s sample plot network (Hogg et al. 2017) and additional chronology samples from the International Tree-Ring Data Bank (ITRDB) (GrissinoMayer and Fritts 1997), previously compiled for western Canada (Hynes and Hamann 2020). Raw tree-ring data was detrended with the Friedman method (Friedman 2001), a non-parametric regression based on a kernel smoothing algorithm that primarily preserves short-frequency variability. The method was chosen because I am specifically interested in tree response to short-frequency drought events (not longer term climate trends) in this analysis, and the method was implemented with the dplR package (Bunn 2010) for the R programming environment (R Core Team 2022).

For quality control, I calculated mean inter-series correlations (R-bar) and the expressed population signal (EPS) statistics, considering R-bar values above 0.2 and EPS values above 0.85 in individual site chronologies acceptable. Furthermore, dendrochronologies were required to be 90% complete within the 1978 to 2010 time period to capture major drought events in western Canada for a relatively recent period. Note that because of incremental sampling to build dendrochronology databases, only very limited samples reach the present time. Lastly, I required at least 15 site chronologies that met the above criteria for a species to be included in the analysis. In total, these criteria yielded 392 site chronologies, including seven species: three spruce species, three pine species and Douglas-fir (Table 1). The overall R-bar and EPS statistics across all included chronologies were 0.4 and 0.95, indicating excellent data quality, with Douglas-fir and limber pine showing the strongest inter-series correlations and expressed population signals. The average sample depth per site chronology was approximately 25 cores, typically with two cores per tree (Table 1).

Table 1. Species and chronology statistics included in the study. Number of site chronologies for each species, as well as mean inter-series correlations (R-bar), expressed population signal (EPS) and mean sample depth (S-Depth) are listed as averages across site chronologies.

Common Name	Scientific Name	Sites	R-bar	EPS	S-Depth
White spruce	*Picea glauca* (Moench) Voss	206	0.40	0.91	23.3
Engelmann spruce	*Picea engelmanii* Parry ex Engelm.	60	0.37	0.95	22.9
Black spruce	*Picea mariana* (Mill.) Britton	24	0.33	0.93	38.2
Jack pine	*Pinus banksiana* Lamb.	24	0.38	0.94	22.7
Whitebark pine	*Pinus albicaulis* Engelm.	15	0.33	0.96	29.9
Limber pine	*Pinus flexilis* E. James	15	0.44	0.97	22.3
Douglas-fir	*Pseudotsuga menziesii* (Mirbel) Franco	48	0.54	0.97	25.2

3.2 Climate and soil moisture data

Monthly climate data for chronology sites for the period 1978-2010 were obtained with the software ClimateNA v6.40 (Wang et al. 2016). The ClimateNA software extracts monthly historical time series of interpolated climate data for particular locations and variables of interest. The interpolated climate grids are based on the Parameter Regression of Independent Slopes Model (PRISM) interpolation method for weather station data (Daly et al. 2008). In the above version of the ClimateNA software package, historical anomaly data for average monthly temperature and monthly precipitation were obtained from CRU-TS 4.04 (Harris et al. 2020), and overlaid as deviation from the 1961-1990 PRISM baseline data. The software version used to query historical data and future projections is available for download at http://tinyurl.com/ClimateNA. The latest version of the software is maintained at http://ClimateNA.ca.

As drought index, I use a climate moisture index that was specifically developed for western Canada (Hogg 1997). This climate moisture index (CMI) is comparable to the Palmer drought severity index (PDSI) or the standardized precipitation evapotranspiration index (SPEI), deriving a water balance from precipitation and temperature data. The PDSI index was primarily developed for semi-arid climates and agricultural applications and can take soil type, soil recharge, and runoff into account -- but such additional data are not available for boreal forest regions. In contrast, SPEI is a multiscale index that can be calculated for any region of the world. While similar to SPEI, the CMI metric uses an empirically optimized method to estimate potential evapotranspiration for boreal forests of western Canada (a modified Penman-Monteith equation), and is calibrated so that the zero-CMI value for long-term climate normal data corresponds to the boreal forest grassland transition zone. As such, positive CMI values can be interpreted as excess water and negative values as water deficit conditions for boreal forest trees (in units of mm precipitation).

For the application of the CMI metric in this study, I summed monthly CMI estimates provided by the ClimateNA software package over a 15-month period from the previous June to the current August of each year, potentially accounting for lagged effects of water available to trees through storage in the soil. The approximation of available soil water for the current growing season from 15-month CMI water balance (as well as other potential indices) were evaluated against remotely sensed data from the European Space Agency's Climate Change Initiative's (ESA CCI) soil moisture database (Gruber et al. 2019). The ESA CCI data is available at a spatial resolution of approximately 0.25 degrees and a temporal resolution of 1 to 3 days. I calculated monthly soil moisture values for each grid cell containing a chronology site and averaged those values for the current growing season (May to August). The subsequent dendroclimatology analysis was carried out for both remotely sensed and CMI-inferred water availability. While I include the remotely sensed data in some figures, the CMI-inferred water availability generally had slightly better correlations with tree ring chronologies. I therefore report statistics and main findings for CMI as the water availability metric.

3.3 Drought response analysis

For assessment of drought tolerance metrics, the 392 site chronologies of all species were first clustered according to their similarity in historical climate conditions and their similarity in growth response. Clustering was implemented with the k-means method, a way of grouping observations to a specified number of clusters by minimizing the variance of variables within each cluster. This method can handle relatively high dimensional datasets -- in this case 64 variables: detrended ring width index (RWI) values for 32 years, and a transformed 32-variable CMI or remotely sensed soil moisture data set. Clustering based on these variables grouped chronologies with similar standardized values during the same years together, so observations in the same cluster would have similar trends in growth and moisture. Three transformations were carried out on the drought metric. First, a log transformation fine-tuned with a constant was used to achieve an exact normal distribution across the entire dataset of the water availability metric. While not strictly necessary, this makes subsequent multivariate ordinations easier. Second, rows (each corresponding to an individual chronology site) were scaled so that the drought metric was expressed in standard deviations from a mean of zero (i.e., it becomes an index of relative drought conditions for a chronology site), and third, columns were scaled in the same way, so that each of the 64 variables had equal weight in subsequent clustering and ordinations. Clustering was implemented with the *kmeans* function of the *stats* package, which is part of the base-R programming environment (R Core Team 2022), using a Euclidean distance matrix. An optimal cluster number of 10 was determined with the help of silhouette width, gap, and within-cluster sum of square statistics, obtained with the *fviz_nbclust* function of the *factoextra* library (Kassambara and Mundt 2020) for the R programming environment.

The 10 clusters of similar climate histories and ring width patterns were visualized with principal component analysis, implemented with the *princomp* function of the base-R programming environment, and principal component loading with the original variables displayed as vectors in the ordination using the *vf* function of the *ecodist* library (Goslee and Urban 2007). The vectors representing each variable (i.e., each year of the 32-year timeframe for RWI or CMI) were flipped by multiplying with negative one, so that they point toward (not away from) the chronologies with the lowest values for each vector. This meant each vector would point to the clusters that have a small ring width and high water deficit in a specific year, allowing a concise summary of which geographic regions experienced drought conditions in which years, and when a drought response (small ring width) was observed – typically in the same and/or the subsequent year.

Lastly, resistance (Rt), recovery (Rc), and resilience (Rs) metrics were calculated for each drought event observed in each cluster across all species according to Lloret et al. (2011), and least squares means and their confidence intervals by cluster and species were estimated with a linear fixed effects model, implemented with the *lm* function of the R base package and the *emmeans* package (Lenth 2016) for the R programming environment (R Core Team 2022). The ratio of the drought to pre-drought ring width index values represents resistance, recovery is the ratio of post-drought to drought growth, and resilience is the ratio of post-drought to pre-drought growth. Pre-drought and post-drought growth were defined as the average ring width index value 2 years before and after a drought event, respectively. If the drought extended over multiple years, or if two subsequent drought periods were too close to allow for a 2 year intermediate reference period, then ring width index values for drought years were averaged and the two years before the onset of the first drought year, and the two years after the last drought year, were used as reference periods. A relatively short 2-year, post-drought period was chosen to measure the tree's capacity to recover quickly. As well, a relatively short 2-year pre-and post drought period allowed most drought events to be evaluated separately, so that a large number of estimates for drought tolerance metrics were available for inter-species comparisons of average drought tolerance traits.

To minimize bias for species comparisons, drought tolerance traits were calculated identically for all species within a cluster. Because of strong spatial autocorrelations in climate data, k-means clusters also delineate geographic regions, and therefore this design was best suited to compare species within geographic regions. However, I also discuss regional differences observed within a species' range, but it should be kept in mind that the drought tolerance statistics are then based on different drought periods that occurred at different times in different regions.

4. Results

4.1 Geography of droughts and growth impacts

Cluster analyses revealed ten fairly geographically distinct groups of chronologies, where each cluster represents chronologies with similar trends in growth and moisture from 1978 to 2010 (Figs. 1 and 2). The geographic clustering is expected because climate variables (15-month CMI sums for the years 1978 to 2010) constituted half of the clustering criteria, and climate patterns are spatially autocorrelated. I therefore labeled the clusters by approximate geographic location for reference. These clusters are overlayed with the vectors that represent the variables used to cluster chronologies (Fig. 1). The black vectors point towards chronologies with the lowest relative CMI values for that period (each labeled year corresponding to the 15-month period that contributed to that growing season). Similarly, the direction a grey vector points indicates the chronologies with the lowest relative RWI values for that year. The northwestern clusters appear most distinct, partially driven by their geographic separation and consequently different climatic histories. For example, the cluster of chronologies primarily located within the Northwest Territories (NWT, yellow) experienced a drought in 1995 that was most pronounced in this specific region (Fig 3, panel NWT). This leads to the 1995 CMI vector pointing towards this cluster (Fig. 1, black vector). This is mirrored by the 1995 growth response vector pointing in the same direction (Fig. 1, gray vector, negated to point towards chronologies with small ring widths in that year).

Of course, this is a somewhat imperfect representation of a very complex data set in two dimensions. For example, the 1995 growth response vector is somewhat shorter because other regions showed drought responses in that that year, with most clusters falling within Alberta and Saskatchewan. Nevertheless, the principal component analysis provides a high-level summary of the regionally most severe droughts and growth responses for western Canada, with regional droughts occurring between 1980 and 2009. The most notable regional drought was a two-year event in 2001-2002, affecting the central and southern portion of Alberta and Saskatchewan (Fig 1, vectors pointing towards the right), which lead to agricultural crop failures and massive tree mortality at the southern fringe of the boreal forest (Michaelian et al. 2011). The ordination also reveals delayed growth responses to drought periods. For example, the severe two-year drought in 2001-2002 had pronounced growth responses in 2002 and 2003 (c.f. black and gray vectors for these years in Fig 1). Similarly, the 1980-1982 drought had its most severe response in 1982, while the 1984-1985 drought showed responses in 1985 and 1986.

Note that only the most important drought events and corresponding growth response vectors could be included in Fig 1. All drought events considered for subsequent analysis of drought tolerance traits are listed in Table 2. Measured in standard deviations of 15-month CMI values, the highest relative drought severity occurred during the 2001-2002 drought period (1.42 and 2.08 standard deviations below average). Other prolonged drought periods affecting Alberta and Saskatchewan occurred in the early- and mid-1980s, with relative water deficits as low as -1.28 standard deviations below normal conditions. The drought with the highest observed absolute water deficit was a single-year event in 2004 with an average 15-month CMI value of -23.3 mm (Table 2), which affected the Northwest Territories cluster. Note that in some cases absolute CMI values can be positive, indicating a positive water balance despite a negative relative drought score. This occurs in relatively moist regions such as the southern Alberta foothill regions (Table 3, sAB), which receives relatively high precipitation, but nevertheless contains species that strongly respond to these moderate water limitations.

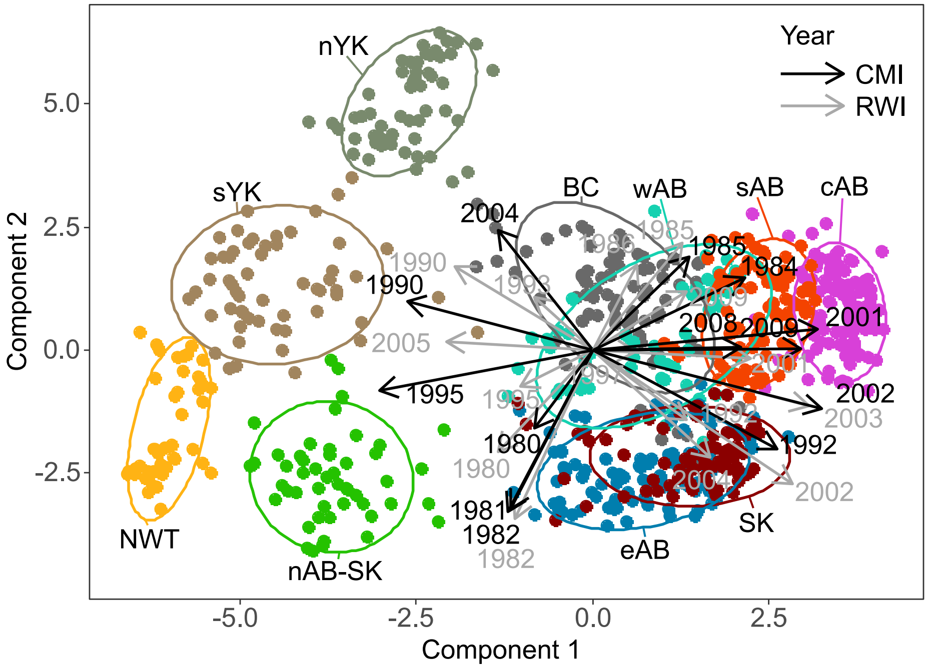

Figure 1. Principal component ordination of k-means clusters for chronologies, based on similarities in timing of drought events and growth responses. Variables included a scaled and negated climate moisture index (CMI, black vectors) and a detrended and negated ring width index (RWI grey vectors). Vectors point towards groups of chronologies that most severely experienced drought events and growth reductions in these years.

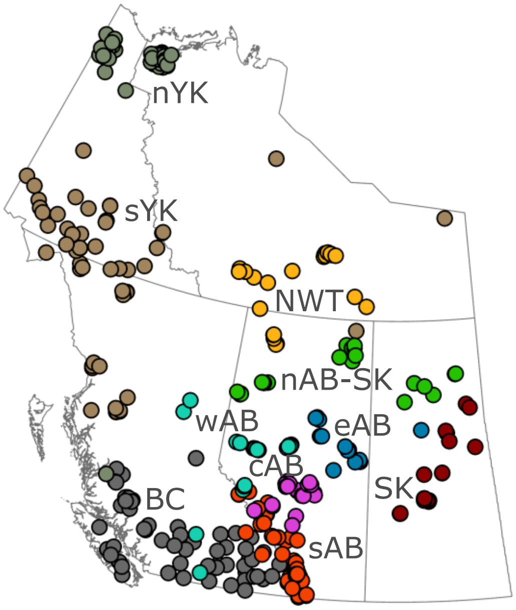

Figure 2. K-means clusters of chronology sites labeled according to their approximate geographic locations: northern Yukon (nYK), southern Yukon (sYK), British Columbia (BC), western Alberta (wAB), Northwest Territories (NWT), northern Alberta and Saskatchewan (nAB-SK), central Alberta (cAB), southern Alberta (sAB), eastern Alberta (eAB), Saskatchewan (SK).

4.2 Comparative analysis of species drought tolerance

To be included in comparative analysis of drought-tolerance traits in tree species, I restricted the analysis to clusters where growth response was in fact limited primarily by water availability. This excluded the western regions of British Columbia and the Yukon Territories (BC, nYK, sYK) where the ring width index was not strongly correlated to either water availability inferred from the average 15-month CMI (Fig 3, black line), or to remotely sensed soil moisture during the growing season (Fig 3, dark gray line). These regions either had high precipitation and a positive evapotranspirative balance (Table 3, high MAP and CMI values for BC and sYK), but it also applied to the most northern cluster

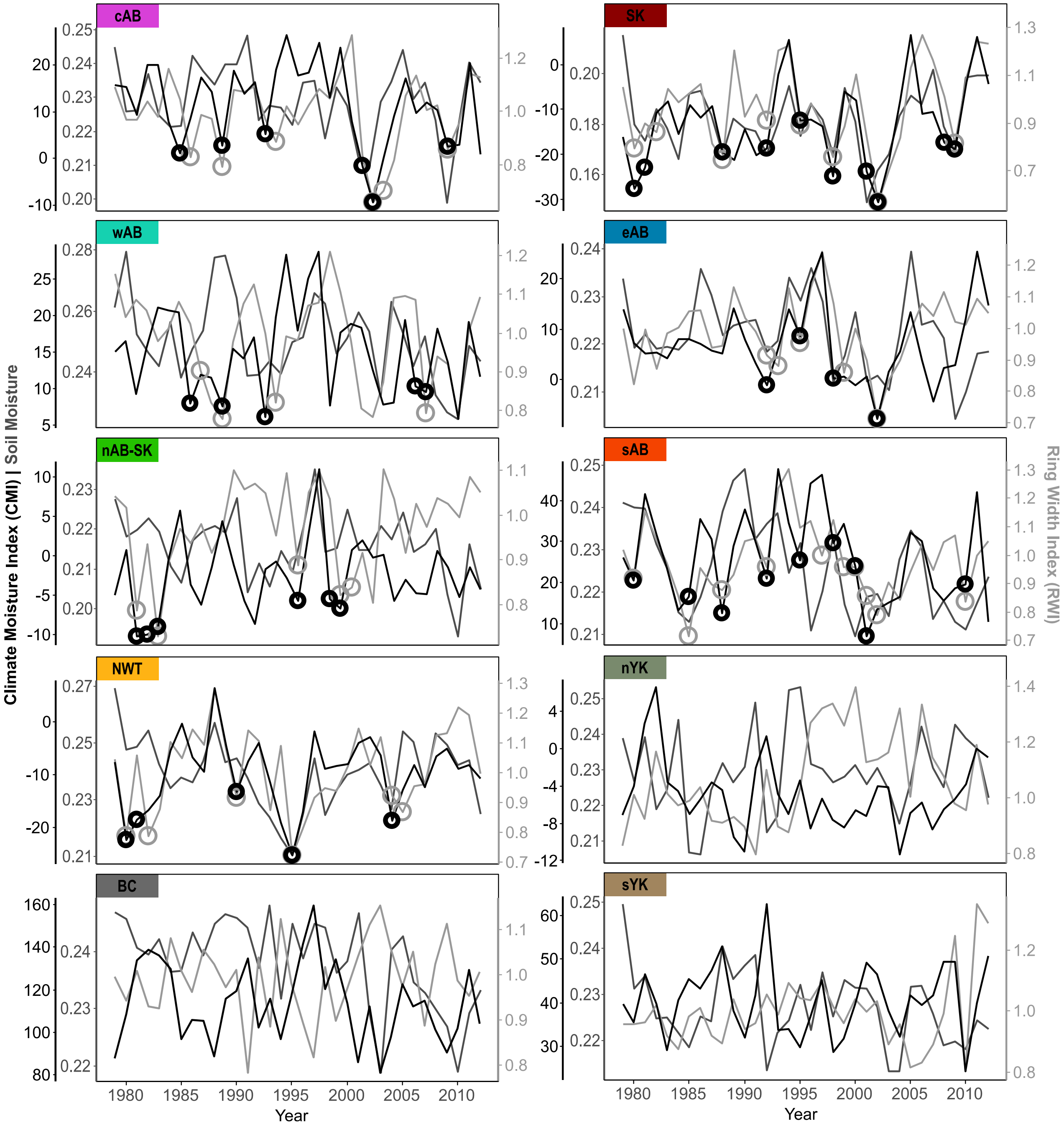

Figure 3. Time series of climate moisture index (mm, black lines), remotely sensed soil moisture ($cm^3 cm^{-3}$, dark gray), and detrended ring width index (light gray), for each cluster (colors and cluster abbreviations as in Fig. 2). Drought events that caused a significant growth reduction (defined as a ring width index <0.8 in at least 50% of chronologies of at least one species in a cluster), with growth responses in the same or subsequent year are highlighted with circles.

Table 2. Drought events ordered chronologically, and clusters (as in Fig. 2) affected by each drought period. Response years refer to years with a low detrended ring width index value. Drought severity was measured as absolute water deficits of a 15-month CMI value (mm), and the relative drought severity is the same CMI value expressed in standard deviations from chronology means of zero for the study period, averaged across all chronologies within the affected clusters.

Drought years	Response years	Relative drought severity (stdev)	Absolute drought severity (mm)	Regional clusters affected by the drought						
1980-82	1980-82	-1.28, -1.18, -1.15	-12.5, -21.4, -11.3	sAB	SK				nAB-SK	NWT
1984-85	1985-86	-1.19, -0.90	1.5, 15.2	sAB		cAB	wAB			
1988	1988	-0.99	1.0	sAB	SK	cAB	wAB			
1990	1990	-0.46	-16.6							NWT
1992	1992-93	-0.8	3.1	sAB	SK	cAB	wAB	eAB		
1995	1995-97	-0.44	-2.3	sAB	SK			eAB	nAB-SK	NWT
1998-99	1998-99	-0.58, -0.72	-0.2, -8.5	sAB	SK			eAB	nAB-SK	
2001-02	2001-03	-1.42, -2.08	-7.7, -19.9	sAB	SK	cAB		eAB		
2004	2004-05	-1.23	-23.3							NWT
2006-07	2007	-0.58, -0.78	12.8, 11.9				wAB			
2008-09	2009	-0.43, -0.81	-21.8, -10.1		SK	cAB				
2010	2010	-0.66	24.5	sAB						

Table 3. Long-term climate normal conditions for regional clusters as shown in Fig 2. Regional clusters are ordered from left to right based on their water balance according to Hogg's (1999) climate moisture index, where a value near zero is calibrated for the boreal forest to grassland transition zone in western Canada (last row).

Climate normals (1978-2010)	SK	NWT	nAB-SK	nYK	eAB	cAB	wAB	sAB	sYK	BC
Mean annual temperature (°C)	1.7	-2.4	0.0	-7.8	1.4	2.7	2.7	1.4	-1.6	2.1
Mean coldest month temp. (°C)	-17.8	-23.9	-19.5	-27.8	-17.0	-13.4	-12.5	-12.5	-17.1	-8.8
Mean warmest month temp. (°C)	17.7	16.3	15.6	14.1	15.9	15.6	14.9	13.3	11.8	12.7
Mean annual precipitation (mm)	424	358	435	260	490	555	585	671	693	1456
Climate moisture index (mm/yr)	-6.1	0.0	3.4	3.8	6.4	8.6	15.3	27.8	42.0	112.0

where the primary growth limitation was not drought, but cold (Table 3, low MAT value for nYK). In all other regional clusters drought periods were consistently associated with growth reduction, and I evaluate a drought period in subsequent analysis if it was associated with a ring width index less than 0.8 in at least 50% of the chronologies of at least one species in a cluster in the same or subsequent year (Fig 3, indicated by circles).

Drought responses varied considerably among species and clusters. Growth reductions during drought periods (indicated by the resistance metric) were largest for Douglas-fir and jack pine (Fig 4, *Pseudotsuga menziesii, Pinus banksiana*). Recovery largely mirrored resistance but with some exceptions that lead to resilience values that significantly deviated from complete recovery (Fig 4, 95% confidence intervals that do not overlap with the 1.0 reference line). Complete recovery to pre-drought growth levels, as indicated by resilience values near 1.0, were prevalent in the Southern Alberta and Saskatchewan clusters that geographically border the prairie grassland ecosystems (c.f. clusters sAb and SK in Fig 2 and 4). Despite these clusters having rather different climatologies (Table 3) with the Prairies being bordered by moister foothill forests in the west (sAB) and the dry southern fringe of the boreal forest (SK), all species in these groups appear well adapted to fully recover from drought periods.

Notable deviations from a complete recovery to pre-drought growth within two years were observed for Douglas-fir, jack pine and with spruce in dry, boreal and sub-boreal ecosystems. Lack of drought resilience for both jack pine and white spruce was most pronounced in the Northwest Territories (Fig 4, NWT, *Pinus banksiana, Picea glauca*), followed by the northern Alberta – northern Saskatchewan cluster (nAB-SK) and approaching full recovery to pre-drought levels in the central and eastern Alberta clusters (cAB and eAB). Resilience values therefore appear to represent a geographic cline (c.f., Fig 2) from fully resilient near the forest-grassland transition zones, to least resilient in the northern boreal forest for white spruce and jack pine in the clusters where the species is represented. Other notable within-cluster species differences include Douglas-fir, which showed the lowest resilience value across all species and all regional groups in the western Alberta cluster (Fig 4, wAB, *Pseudotsuga menziesii*), where 4 of the 6 sites correspond with the northern range limit of the interior Douglas-fir subspecies in Alberta, and the other 2 are in similarly dry areas of BC. It was also the most sensitive species to drought at its eastern range limit in the southern

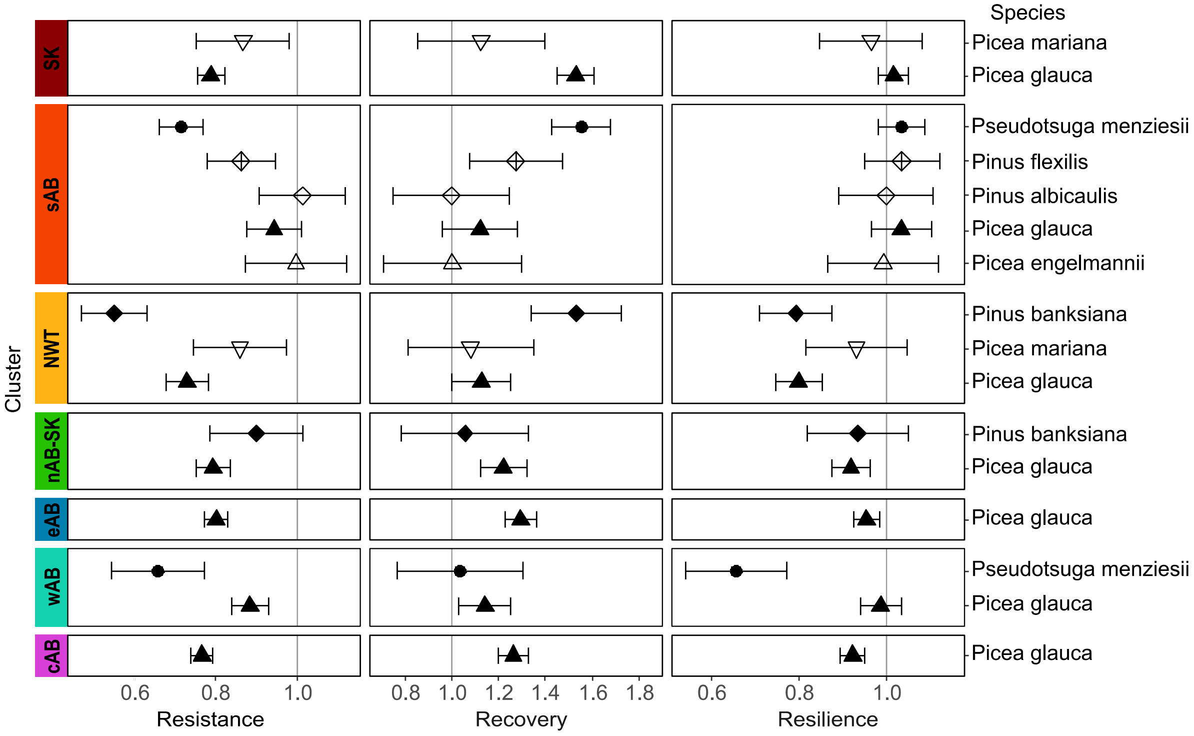

Figure 4. Drought resistance, recovery, and resilience metrics according to Loiret et al. (2011) for each species and cluster. Clusters where growth was not primarily limited by water availability were omitted (BC, nYK and sYK), as were species with an insufficient number of sample locations (<5 sites within a cluster). Error bars represent a 95% confidence interval, and therefore indicate statistically significant deviations from the reference values, indicating no impact on growth for a resistance value of 1, no post-drought improvement for a recovery value of 1, and recovery to pre-drought growth values for a resilience value of 1 (gray lines).

Alberta foothills (Fig 4, sAB, resilience values). Lastly, black spruce showed substantially different behaviour than white spruce and Jack pine in the Northwest Territory cluster, with better resistance values and resilience values not significantly different from full recovery (Fig 4, NWT, *Picea mariana*).

5. Discussion

Regional drought vulnerabilities observed in this study generally conform to geographic patterns expected when considering historical normal climate conditions and climate change trends observed over the last several decades (Zhang et al. 2019, Levesque and Hamann 2022). Warming trends over the last 50 years show a fairly uniform latitudinal gradient across western Canada with approximately +1.5°C of change in mean annual temperature in the south of British Columbia (~50°N latitude), approximately +2°C at the southern fringe of the boreal forest in Alberta and Saskatchewan (~55°N), +2.5°C for northern boreal tree populations in Saskatchewan and Alberta (~58°N), +3°C for populations of the Northwest Territories and southern Yukon (~58°N), and +3.5°C for the most northern populations in this study. This gradual warming trend combined with only small regional increases in precipitation would be expected to cause vulnerabilities in northern boreal regions, where normal levels of precipitation are already low. This gradient of environmental change potentially explains the trend towards lower resilience at higher latitudes that I observed in white spruce and jack pine.

In addition to gradients of environmental change, the genetic adaptation of populations to local environments may also play an important role in explaining regional differences in drought response within species. The cluster of populations from Saskatchewan was the group with the highest water deficit under normal conditions, yet chronologies from this region near the forest to grassland transition zone suggested trees in this area are able to rapidly recover from drought impacts. I think this indicates local adaptation of populations to drought conditions, and interestingly, that genotypes could prove valuable as a source for more drought resilient planting stock for reforestation programs in western Canadian boreal forests. Although I am not aware of studies that tested genetic traits of tree populations from the southern boreal fringe specifically, southern populations of lodgepole pine have shown the highest drought resilience inferred from tree ring and isotope-based analysis of genotypes from throughout its western range when grown in common garden experiments (Montwe et al. 2016, Isaac-Renton et al. 2018). In a similar common-garden experiment with white spruce populations from eastern Canada, the data suggest that populations that originated in dry environments showed local adaptation to drought (Depardieu et al. 2020).

Our results conform to the fairly obvious expectation that drought limitations are less problematic under generally wetter climatic conditions, even under climate trends toward warmer environments that increase evapotranspirative demand (Ibanez et al. 2019). The western chronology groups in British Columbia and the southern Yukon, with the highest and second highest positive water balance, did not show consistent correlations of tree growth with drought. The group with the third highest water balance, the southern Alberta foothill region, did show drought limitations to growth for some species, but all species were able to fully recover to pre-drought productivity in the two years following a drought event. Therefore, moister sub-boreal and sub-montane ecosystems may serve as climate change refugia for western Canadian tree species, at least with respect to areas not immediately threatened by water deficits under climate warming. Another important type of climate change refugia may be boreal peatlands (Stralberg et al. 2020). This expectation is also supported by our data. Boreal peatlands are typically dominated by black spruce, and for the clusters where sample size was sufficient for the species to be included in our analysis (Fig 4, SK, NWT, *Picea mariana*), resistance and resilience statistics were more favorable for black spruce than for white spruce and jack pine that dominate drier sites within the same regions. The example also highlights that species' drought tolerance traits are not necessarily intrinsic, but can well be a function of the species preferred site conditions within a regional cluster.

Another notable result is that this study suggests there will be cases where species growth limitations may change from current cold to drought limitations under continued warming. At present, factors other than 15-month CMI or remotely sensed soil moisture are more prevalent for the cluster of chronology sites in the northern Yukon. Presumably, these are cold limitations given that this cluster had by far the coldest mean annual temperature (–7.8°C). At the same time, the group had exceptionally low mean annual precipitation (260 mm), leading to an overall near-zero water balance that suggests the region will quickly become marginal for supporting forest ecosystems under continued climate warming. In some years there is already a drought response observable for this region (Fig 3, nYT, subsequent to 1990 and 2004 droughts). This conforms to research by Girardin et al. (2016), where chronologies from the northern Yukon showed a long-term decline with increasing temperature due to climate change.

A second species-specific example of cold limitations switching to drought limitations under observed and projected climate warming are Douglas-fir chronology sample sites that are located near the northern range limit (eAB cluster) and eastern range limit (sAB cluster) of the species' distribution in North America. It is well established that Douglas-fir growth and survival is limited by water availability at its southern range limit (Restaino et al. 2016), it is normally assumed that the northern and high elevation range limit is governed by the length of the growing season and cold tolerance traits. Douglas-fir is not considered to be a particularly cold-tolerant species and thought to be outcompeted by more cold tolerant competitors at its northern and high elevation range limits (Burns et al. 1990). There is, however, evidence that drought limits northern interior range of the species (Griesbauer and Green 2010). This finding is also supported by this study, showing that Douglas-fir is the least drought resistant species in the moist foothill forests of southern Alberta (Fig 4, sAB, *Pseudotsuga menziesii*), and the least resilient species in the eastern Alberta cluster (Fig 4, eAB), although it should be noted that 4 out of the 6 Douglas-fir sample sites in this cluster come from the northern limits of its Alberta range. Resilience is perhaps the most important indicator of drought tolerance, because low values of the metric indicate permanent damage from drought events to xylem through cavitation or carbon starvation (Bartlett et al. 2016), from which trees need time to recover by growing new functional tracheids for water transport or replenish energy stores.

6. Conclusions

In summary, the results of this study suggest that dry boreal ecosystems east of the Rocky Mountains are the most vulnerable to severe drought impacts, with trees showing low resistance and delayed recovery that indicates permanent damage to their xylem following severe drought events. The leading species in these ecosystems (white spruce and jack pine) were most vulnerable in the north, rather than at the southern fringe of the boreal forest, suggesting lack of adaptive traits to cope with drought conditions in northern populations. The same pattern emerges for sub-boreal ecosystems further west for interior Douglas-fir. The species was most vulnerable to drought at the northern edge of its distribution, with the lowest drought resilience estimate across any species in any region in this study. In moister montane ecosystems, Douglas-fir and limber pine showed the least drought resistance, but all species recovered well from drought events, suggesting that less water-limited sub-boreal ecosystems could serve as climate change refugia. Another type of climate change refugia, boreal peatlands, is indicated by favorable resistance and resilience metrics for black spruce, which dominates these wet sites.

The results have implications for forest management in western Canada: interior Douglas-fir should not be planted beyond its northern range limitations despite significant regional warming trends that would suggest a northward expansion of this generally desirable forestry species should be possible. Secondly, the geographic cline of increasing resilience of white spruce populations towards its southern range limits suggests local genetic adaptations to drought episodes. White spruce populations from the driest chronology sample sites in this study were able to fully recover to pre-drought growth in the two years subsequent to drought events, apparently avoiding permanent damage to water-conducting xylem. As such, these populations may be a suitable source of reforestation material for more drought resilient forests under continued climate warming in central and northern boreal forest regions as well.

7. References

Aitken, S.N., Yeaman, S., Holliday, J.A., Wang, T. and Curtis-McLane, S. 2008. Adaptation, migration or extirpation: climate change outcomes for tree populations. Evolutionary Applications, 1:95-111.

Allen, C. D., A. K. Macalady, H. Chenchouni, D. Bachelet, N. McDowell, M. Vennetier, T. Kitzberger, A. Rigling, D. D. Breshears, E. H. Hogg, P. Gonzalez, R. Fensham, Z. Zhang, J. Castro, N. Demidova, J. H. Lim, G. Allard, S. W. Running, A. Semerci, and N. Cobb. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. Forest Ecology and Management **259**:660-684.

Anderegg, W., Kane, J., and Anderegg, L. 2013. Consequences of widespread tree mortality triggered by drought and temperature stress. Nature Climate Change **3**:30-36.

Babst, F., O. Bouriaud, B. Poulter, V. Trouet, M. P. Girardin, and D. C. Frank. 2019. Twentieth century redistribution in climatic drivers of global tree growth. Science Advances **5**:eaat4313.

Bartlett, M. K., Klein, T., Jansen, S., Choat, B., Sack, L. 2016. The correlations and sequence of plant stomatal, hydraulic, and wilting responses to drought. Proceedings of the National Academy of Sciences. **113**:13098–13103.

Bartowitz, K.J., Walsh, E.S., Stenzel, J.E., Kolden C.A., Hudiburg T.W. 2022. Forest Carbon Emission Sources Are Not Equal: Putting Fire, Harvest, and Fossil Fuel Emissions in Context. Frontiers in Forests and Global Change **5**:867112.

Bunn, A. G. 2010. Statistical and visual crossdating in R using the dplR library. Dendrochronologia **28**:251-258.

Burns, R. M., B. H. Honkala, and United States. Forest Service. 1990. Silvics of North America. U.S. Dept. of Agriculture For sale by the Supt. of Docs., U.S. G.P.O., Washington.

Brooks, J. R., Flanagan, L.B., and Ehleringer, J.R. 2011. Responses of boreal conifers to climate fluctuations: indications from tree-ring widths and carbon isotope analyses. Canadian Journal of Forest Research. **28**:524-533.

Brzostek, E.R., Dragoni, D., Schmid, H.P., Rahman, A.F., Sims, D., Wayson, C.A., Johnson, D.J., and Phillips, R.P. 2014. Chronic water stress reduces tree growth and the carbon sink of deciduous hardwood forests. Global Change Biology **20**:2531-2539.

Chagnon, C., Guillaume, M., D’Orangeville, L., Caspersen, J., Labrecque-Foy, J., and Achim, A. 2023. Strong latitudinal gradient in temperature-growth coupling near the treeline of the Canadian subarctic forest. Frontiers in Forests and Global Change. **6**:1181653

Cullingham, C.I., Cooke, J.E.K., Dang, S., Davis, C.S., Cooke, B.J. And Coltman, D.W. 2011. Mountain pine beetle host-range expansion threatens the boreal forest. Molecular Ecology **20**:2157-2171.

D'Orangeville, L., J. Maxwell, D. Kneeshaw, N. Pederson, L. Duchesne, T. Logan, D. Houle, D. Arseneault, C. M. Beier, D. A. Bishop, D. Druckenbrod, S. Fraver, F. Girard, J. Halman, C. Hansen, J. L. Hart, H. Hartmann, M. Kaye, D. Leblanc, S. Manzoni, R. Ouimet, S. Rayback, C. R. Rollinson, and R. P. Phillips. 2018. Drought timing and local climate determine the sensitivity of eastern temperate forests to drought. Global Change Biology **24**:2339-2351.

Daly, C., M. Halbleib, J. I. Smith, W. P. Gibson, M. K. Doggett, G. H. Taylor, J. Curtis, and P. P. Pasteris. 2008. Physiographically sensitive mapping of climatological temperature and precipitation across the conterminous United States. International Journal of Climatology **28**:2031-2064.

Depardieu, C., S. Gerardi, S. Nadeau, G. J. Parent, J. Mackay, P. Lenz, M. Lamothe, M. P. Girardin, J. Bousquet, and N. Isabel. 2021. Connecting tree-ring phenotypes, genetic associations and transcriptomics to decipher the genomic architecture of drought adaptation in a widespread conifer. Molecular Ecology **30**:3898-3917.

Depardieu, C., M. P. Girardin, S. Nadeau, P. Lenz, J. Bousquet, and N. Isabel. 2020. Adaptive genetic variation to drought in a widely distributed conifer suggests a potential for increasing forest resilience in a drying climate. New Phytologist **227**:427-439.

Duane, A., Aquilué, N., Canelles, Q., Morán-Ordoñez, A., De Cáceres, M., and Brotons, L. 2019. Adapting prescribed burns to future climate change in Mediterranean landscapes. Science of The Total Environment. **677**:68-83.

Eilmann, B., S. M. G. de Vries, J. den Ouden, G. M. J. Mohren, P. Sauren, and U. Sass-Klaassen. 2013. Origin matters! Difference in drought tolerance and productivity of coastal Douglas-fir (Pseudotsuga menziesii (Mirb.)) provenances. Forest Ecology and Management **302**:133-143.

Friedman, J. H. 2001. Greedy function approximation: A gradient boosting machine. Annals of Statistics **29**:1189-1232.

Garcia, R.A. et al. 2014. Multiple Dimensions of Climate Change and Their Implications for Biodiversity. Science **344**:1247579.

Goslee, S. C., and D. L. Urban. 2007. The ecodist package for dissimilarity-based analysis of ecological data. Journal of Statistical Software **7**:1-19.

Griesbauer, H. P., and D. S. Green. 2010. Assessing the climatic sensitivity of Douglas-fir at its northern range margins in British Columbia, Canada. Trees-Structure and Function **24**:375-389.

GrissinoMayer, H. D., and H. C. Fritts. 1997. The International Tree-Ring Data Bank: An enhanced global database serving the global scientific community. Holocene **7**:235-238.

Gruber, A., T. Scanlon, R. van der Schalie, W. Wagner, and W. Dorigo. 2019. Evolution of the ESA CCI Soil Moisture climate data records and their underlying merging methodology. Earth System Science Data **11**:717-739.

Hanes, C. C., X. L. Wang, P. Jain, M. A. Parisien, J. M. Little, and M. D. Flannigan. 2019. Fire-regime changes in Canada over the last half century. Canadian Journal of Forest Research **49**:256-269.

Harris, I., T. J. Osborn, P. Jones, and D. Lister. 2020. Version 4 of the CRU TS monthly high-resolution gridded multivariate climate dataset. Scientific Data **7**:1-18.

Hogg, E. H. 1994. Climate and the southern limit of the western Canadian boreal forest. Canadian Journal of Forest Research **24**:1835-1845.

Hogg, E. H. 1997. Temporal scaling of moisture and the forest-grassland boundary in western Canada. Agricultural and Forest Meteorology **84**:115-122.

Hogg, E. H., M. Michaelian, T. I. Hook, and M. E. Undershultz. 2017. Recent climatic drying leads to age-independent growth reductions of white spruce stands in western Canada. Global Change Biology **23**:5297-5308.

Hynes, A., and A. Hamann. 2020. Moisture deficits limit growth of white spruce in the west-central boreal forest of North America. Forest Ecology and Management **461**.

Ibanez, I., Zak, D.R., Burton, A.J. and Pregitzer, K.S. 2018. Anthropogenic nitrogen deposition ameliorates the decline in tree growth caused by a drier climate. Ecology **99**:411-420.

Ibanez, I., K. Acharya, E. Juno, C. Karounos, B. R. Lee, C. McCollum, S. Schaffer-Morrison, and J. Tourville. 2019. Forest resilience under global environmental change: Do we have the information we need? A systematic review. PLoS One **14**.

IPCC. 2022. Climate Change 2022: Mitigation of Climate Change. Contribution of Working Group III to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press.

Isaac-Renton, M., D. Montwe, A. Hamann, H. Spiecker, P. Cherubini, and K. Treydte. 2018. Northern forest tree populations are physiologically maladapted to drought. Nature Communications **9**.

Kassambara, A., and F. Mundt. 2020. Factoextra: extract and visualize the results of multivariate data analyses. R package version 1.0.7, available at https://CRAN.R-project.org/package=factoextra.

Kurz, W. A., C. C. Dymond, G. Stinson, G. J. Rampley, E. T. Neilson, A. L. Carroll, T. Ebata, and L. Safranyik. 2008. Mountain pine beetle and forest carbon feedback to climate change. Nature **452**:987-990.

Lenth, R. V. 2016. Least-Squares Means: The R Package lsmeans. Journal of Statistical Software **69**:1-33.

Levesque, K., and A. Hamann. 2022. Identifying Western North American Tree Populations Vulnerable to Drought under Observed and Projected Climate Change. Climate **10**.

Lloret, F., E. G. Keeling, and A. Sala. 2011. Components of tree resilience: effects of successive low-growth episodes in old ponderosa pine forests. Oikos **120**:1909-1920.

Mantyka-Pringle, C.S., Visconti, P., Marco, M., Martin, T.G., Rondinini, C., and Rhodes, J.R. 2015. Climate change modifies risk of global biodiversity loss due to land-cover change. Biological Conservation **187**:103-111.

McDowell, N., and Allen, C. 2015. Darcy's law predicts widespread forest mortality under climate warming. Nature Climate Change **5**:669-672.

Michaelian, M., E. H. Hogg, R. J. Hall, and E. Arsenault. 2011. Massive mortality of aspen following severe drought along the southern edge of the Canadian boreal forest. Global Change Biology **17**:2084-2094.

Molina, A.J., Navarro-Cerrillo, R.M., Perez-Romero, J. et al. 2021. SilvAdapt.Net: A Site-Based Network of Adaptive Forest Management Related to Climate Change in Spain. Forests **12**:12.

Montwe, D., M. Isaac-Renton, A. Hamann, and H. Spiecker. 2016. Drought tolerance and growth in populations of a wide-ranging tree species indicate climate change risks for the boreal north. Global Change Biology **22**:806-815.

Mote, P.W., Li, S., Lettenmaier, D.P. et al. 2018. Dramatic declines in snowpack in the western US. Climate and Atmospheric Science **1:**2.

Nelson, C.D., and Johnsen, K.H. 2008. Genomic and physiological approaches to advancing forest tree improvement. Tree Physiology, **28**: 7.

Nunez-Mir, G. C., Guo, Q., Rejmánek, M., Iannone, B. V., and Fei, S.. 2019. Predicting invasiveness of exotic woody species using a traits-based framework. Ecology **100**:e02797.

Pardos, M., M. del Rio, H. Pretzsch, H. Jactel, K. Bielak, F. Bravo, G. Brazaitis, E. Defossez, M. Engel, K. Godvod, K. Jacobs, L. Jansone, A. Jansons, X. Morin, A. Nothdurft, L. Oreti, Q. Ponette, M. Pach, J. Riofrio, R. Ruiz-Peinado, A. Tomao, E. Uhl, and R. Calama. 2021. The greater resilience of mixed forests to drought mainly depends on their composition: Analysis along a climate gradient across Europe. Forest Ecology and Management **481**.

Park, A., and J. L. Rodgers. 2023. Provenance trials in the service of forestry assisted migration: A review of North American field trials and experiments. Forest Ecology and Management **537**.

Pedlar, J.H., Mckenney, D.W., Audin, I, Beardmore, T., Bealieu, J., Iverson, L., O'Neill, G.A., Winder, R.S., and Ste-Marie, C. 2012. Placing Forestry in the Assisted Migration Debate. BioScience **62**:9.

Peng, C. H., Z. H. Ma, X. D. Lei, Q. Zhu, H. Chen, W. F. Wang, S. R. Liu, W. Z. Li, X. Q. Fang, and X. L. Zhou. 2011. A drought-induced pervasive increase in tree mortality across Canada's boreal forests. Nature Climate Change **1**:467-471.

Peterson, T. C., Zhang, X., Brunet-India, M., and Vázquez-Aguirre, J. L. 2008. Changes in North American extremes derived from daily weather data. Journal of Geophysical Research **113**.

Price, K., Roburn, A., and MacKinnon, A. 2009. Ecosystem-based management in the Great Bear Rainforest. Forest Ecology and Management **258**:4.

R Core Team. 2022. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Rees, W.G., Hofgaard, A., Boudreau, S., et al. 2020. Is subarctic forest advance able to keep pace with climate change? Global Change Biology. **26**:3965-3977.

Restaino, C. M., D. L. Peterson, and J. Littell. 2016. Increased water deficit decreases Douglas fir growth throughout western US forests. Proceedings of the National Academy of Sciences of the United States of America **113**:9557-9562.

Rossi, S., Deslauriers, A., Griçar, J., Seo, J.-W., Rathgeber, C.B., Anfodillo, T., Morin, H., Levanic, T., Oven, P. and Jalkanen, R. 2008. Critical temperatures for xylogenesis in conifers of cold climates. Global Ecology and Biogeography, **17**:696-707.

Sang, Z. H. H., A. Hamann, and D. Rweyongeza. 2023. Adapting reforestation programs to observed and projected climate change. Mitigation and Adaptation Strategies for Global Change **28**.

Sebastian-Azcona, J., U. Hacke, and A. Hamann. 2020. Xylem Anomalies as Indicators of Maladaptation to Climate in Forest Trees: Implications for Assisted Migration. Frontiers in Plant Science **11**.

Serra-Maluquer, X., A. Gazol, W. R. L. Anderegg, J. Martinez-Vilalta, M. Mencuccini, and J. J. Camarero. 2022. Wood density and hydraulic traits influence species' growth response to drought across biomes. Global Change Biology **28**:3871-3882.

Scholten, R.C., Jandt, R., Miller, E.A. et al. 2021. Overwintering fires in boreal forests. Nature **593**:399-404.

Sohn, J.A., Hartig, F., Kohler, M., Huss, J. and Bauhus, J. 2016. Heavy and frequent thinning promotes drought adaptation in *Pinus sylvestris* forests. Ecological Applications **26**:2190-2205.

Soja, A. J., N. M. Tchebakova, N. H. F. French, M. D. Flannigan, H. H. Shugart, B. J. Stocks, A. I. Sukhinin, E. I. Parfenova, F. S. Chapin, and P. W. Stackhouse. 2007. Climate-induced boreal forest change: Predictions versus current observations. Global and Planetary Change **56**:274-296.

Soler, R.M., Schindler, S., Lencinas, M.V., Peri, P.L., and Pastur, G.M. 2016. Why biodiversity increases after variable retention harvesting: A meta-analysis for southern Patagonian forests. Forest Ecology and Management **369**:161-169.

Stevens-Rumann, C.S., Kemp, K.B., Higuera, P.E., Harvey, B.J., Rother, M.T., Donato, D.C., Morgan, P. and Veblen, T.T. 2018. Evidence for declining forest resilience to wildfires under climate change. Ecological Letters, 21:243-252.

Stralberg, D., D. Arseneault, J. L. Baltzer, Q. E. Barber, E. M. Bayne, Y. Boulanger, C. D. Brown, H. A. Cooke, K. Devito, J. Edwards, C. A. Estevo, N. Flynn, L. E. Frelich, E. H. Hogg, M. Johnston, T. Logan, S. M. Matsuoka, P. Moore, T. L. Morelli, J. L. Morissette, E. A. Nelson, H. Nenzen, S. E. Nielsen, M. A. Parisien, J. H. Pedlar, D. T. Price, F. K. Schmiegelow, S. M. Slattery, O. Sonnentag, D. K. Thompson, and E. Whitman. 2020. Climate-change refugia in boreal North America: what, where, and for how long? Frontiers in Ecology and the Environment **18**:261-270.

Vitasse, Y., A. Bottero, M. Cailleret, C. Bigler, P. Fonti, A. Gessler, M. Levesque, B. Rohner, P. Weber, A. Rigling, and T. Wohlgemuth. 2019. Contrasting resistance and resilience to extreme drought and late spring frost in five major European tree species. Global Change Biology **25**:3781-3792.

Walker, X.J., Baltzer, J.L., Cumming, S.G. et al. 2019. Increasing wildfires threaten historic carbon sink of boreal forest soils. Nature **572**:520–523.

Wang, T. L., A. Hamann, D. Spittlehouse, and C. Carroll. 2016. Locally downscaled and spatially customizable climate data for historical and future periods for North America. PLoS One **11**:e0156720.

Yu, P. F., O. B. Toon, C. G. Bardeen, Y. Q. Zhu, K. H. Rosenlof, R. W. Portmann, T. D. Thornberry, R. S. Gao, S. M. Davis, E. T. Wolf, J. de Gouw, D. A. Peterson, M. D. Fromm, and A. Robock. 2019. Black carbon lofts wildfire smoke high into the stratosphere to form a persistent plume. Science **365**:587-590.

Zhang, X., G. Flato, M. Kirchmeier-Young, L. Vincent, H. Wan, X. Wang, R. Rong, J. Fyfe, G. Li, and V. V. Kharin. 2019. Changes in Temperature and Precipitation Across Canada. Pages 112-193 *in* E. Bush and D. S. Lemmen, editors. Canada’s Changing Climate Report. Government of Canada, Ottawa, Ontario.