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Drought causes reduced growth of trembling aspen in western Canada

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Abstract

Adequate and advance knowledge of the response of forest ecosystems to temperature-induced drought is critical for a comprehensive understanding of the impacts of global climate change on forest ecosystem structure and function. Recent massive decline in aspen-dominated forests and an increased aspen mortality in boreal forests have been associated with global warming, but it is still uncertain whether the decline and mortality are driven by drought. We used a series of ring-width chronologies from 40 trembling aspen (*Populus tremuloides* Michx.) sites along a latitudinal gradient (from 52° to 58°N) in western Canada, in an attempt to clarify the impacts of drought on aspen growth by using Standardized Precipitation Index (SPI) and Standardized Precipitation Evapotranspiration Index (SPEI). Results indicated that prolonged and large-scale droughts had a strong negative impact on trembling aspen growth. Furthermore, the spatiotemporal variability of drought indices is useful for explaining the spatial heterogeneity in the radial growth of trembling aspen. Due to ongoing global warming and rising temperatures, it is likely that severer droughts with a higher frequency will occur in western Canada. As trembling aspen is sensitive to drought, we suggest that drought indices could be applied to monitor the potential effects of increased drought stress on aspen trees growth, achieve classification of eco-regions and develop effective mitigation strategies to maintain western Canadian boreal forests.

Keywords: boreal forest, drought, radial growth, spatial variation, trembling aspen

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Introduction

Drought is defined as a prolonged period of relatively extreme climate during which precipitation is lower than what is considered normal for that region (Maliva & Missimer, 2012). While intensity, magnitude and duration of drought are important, the timescales during which water deficits accumulate are critical for explaining variability in different available water resources (McKee *et al.*, 1993). According to the length of timescales, drought can be classified into three categories: meteorological drought, agricultural drought and hydrological drought (Wilhite & Glantz, 1985; Dai, 2011). Meteorological drought refers to a certain period over which precipitation is lesser than the average amount. Agricultural drought is related to conditions of soil moisture, which contributes to reduced productivity (Wilhite & Glantz, 1985). Hydrological drought indicates the water availability in groundwater, streams and reservoirs (Dai, 2011). Therefore, it is critical to investigate the drought stress on multiple timescales to understand the impacts of different drought types.

A number of drought indices have been developed to investigate the impacts of different drought types on terrestrial ecosystems (Mishra & Singh, 2010; Dai, 2011). For example, the Palmer Drought Severity Index (PDSI) has been widely applied for drought analyses at a global scale. However, although PDSI incorporates both precipitation and evapotranspiration, it cannot address drought impacts on multiple timescales. The Standardized Precipitation Index (SPI) can deal with drought on different timescales and uses a simple calculation method (McKee *et al.*, 1993). Hence, the SPI has been recommended as a standard drought indicator by the World Meteorological Organization (WMO) (Hayes *et al.*, 2011). The limitation of the SPI is that only

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precipitation is incorporated, while impacts of evapotranspiration on water deficits are excluded. This issue was solved by Vicente-Serrano *et al.* (2010), who developed Standardized Precipitation–Evapotranspiration Index (SPEI), which considers the impacts of both potential evapotranspiration and precipitation.

In recent decades, severe drought events associated with global warming have contributed to forest decline and mortality in many forest ecosystems (Allen *et al.*, 2010; Peng *et al.*, 2011; Huang *et al.*, 2015; Luo & Chen, 2015; Assal *et al.*, 2016). The boreal forest encompasses about 11% of the earth's land surface and contains approximately 49% of the carbon stored in global forest ecosystems (Dixon *et al.*, 1994; Lindahl *et al.*, 2007). As the boreal forest is sensitive to increased temperature (Lutz *et al.*, 2013) and that is considered as a potential driver of drought (Williams *et al.*, 2013), temperature-induced drought is projected to exert strong large-scale negative impacts on productivity of these ecosystems (Bonan *et al.*, 1992; Kellomäki *et al.*, 2008; Luo & Chen, 2013). Trembling aspen (*Populus tremuloides* Michx.) is widely distributed in North America and is one of the dominant species in Canadian boreal forests (Peterson & Peterson, 1992). Decline in productivity and increased tree mortality have been observed in both western USA and Canadian boreal forests (Rehfeldt *et al.*, 2009; Michaelian *et al.*, 2011). A variety of factors (e.g., wildfires and insects), especially drought, contributed to this decline in forest productivity (Hogg & Bernier, 2005; Hogg *et al.*, 2008, 2013; Worrall *et al.*, 2008). The responses of forest ecosystems to the temperature-induced drought are critical to understand the impacts of global climate change on forest structure and function (Luo & Chen, 2013, 2015). Therefore, it is essential to understand how aspen forests will respond to drought in order to monitor and mitigate the potential effects of increasing drought stress on aspen forests growth.

Tree rings provide a high-resolution climate proxy and are often used to reconstruct past climate change (Mann *et al.*, 1998; Esper *et al.*, 2002; Cook *et al.*, 2004; D'Arrigo *et al.*, 2006, 2008) and also to analyze the impacts of drought on tree growth (Gray *et al.*, 2003; Lebourgeois *et al.*, 2013; Williams *et al.*, 2013; Macalady, 2015; Rammig *et al.*, 2015). Traditional climatic indices, such as precipitation and temperature, provide limited information about drought events (Mishra & Singh, 2010). These indices alone do not provide complete information about the intensity, magnitude and duration of drought and also the impacts on tree growth at multiple timescales (Mishra & Singh, 2010; Dai, 2011). Therefore, it is extremely important to investigate the responses of radial growth of aspen to amplified climate change and drought stress on different timescales by means of drought indices. The use of drought indices, other than temperature and precipitation, to investigate the effects of climate change on growth of forest tree species, in particular trembling aspen, is becoming essential to better understand the long-term impacts of drought on forest productivity at multiple timescales.

Spatial heterogeneity of climate change might be the result of combination of factors including elevation, latitude and site-specific effects (Gewehr *et al.*, 2014). In boreal forests, it has been demonstrated that the response of radial growth to climate variables varies with latitude (Mäkinen *et al.*, 2002; Huang *et al.*, 2010; Lloyd *et al.*, 2011). Due to the complexity of these predicted climatic changes, it is necessary to identify spatial regions with similar climate–growth relationships to develop effective management strategies. The use of large-scale tree-ring networks appears as one of the most accurate and effective ways to accomplish this task (Savva *et al.*, 2006; Sidor *et al.*, 2015). However, little research has demonstrated the impacts of drought on aspen growth, and simultaneously addressed the spatial variability of drought responses using a large-scale tree-ring network by combing traditional climatic indices (e.g., temperature and precipitation) with drought indices.

We conducted a large-scale dendroclimatic investigation using a network of ring-width chronologies from 40 trembling aspen sites in western Canadian boreal forest from 52° to 58° N to comprehensively understand the impacts of drought on trembling aspen growth by combining traditional climatic indices and drought indices (SPI and SPEI). The main objectives of this study were to (i) quantify the relationship between the radial growth of trembling aspen and traditional climate variables (e.g., precipitation and temperature), (ii) determine the impacts of drought on the radial growth of trembling aspen using SPI and SPEI indices and (iii) determine the spatiotemporal variability of trembling aspen growth with respect to climate variables (precipitation and temperature) and drought indices (SPI and SPEI). We hypothesized that the radial growth response of trembling aspen to climate variables and drought indices would spatially vary as a complex function of climate and topography.

Materials and methods

Study area

The study area is located within the mixedwood boreal forests of Alberta, Canada, which covers 75% of the forested area in the province and is commonly known as boreal mixedwoods. The co-dominant species in the boreal mixedwoods are trembling aspen (*Populus tremuloides* Michx.), white spruce [*Picea glauca* (Moench.) Voss], balsam poplar (*Populus balsamifera* L.), paper birch (*Betula papyrifera* Marshall) and balsam fir [*Abies* *balsamea* (L.) Mill.] (Cumming *et al.*, 2000; Stadt *et al.*, 2007). Lodgepole pine (*Pinus contorta* Douglas ex Loudon) also exists within these mixed forests. Forty trembling aspen sites distributed throughout this region were sampled (Fig. 1). These sites are mainly affected by typically dry continental climate conditions with cold winters and warm summers. In the study area, the annual mean temperature and total precipitation during the period between 1930 and 2010 were around 1 °C and 460 mm, respectively (Appendices S1 and S2). Both annual total precipitation and mean annual temperature from 1930 to 2010 declined with the increasing latitudinal gradients (Appendices S1 and S3). The main soil types were brunisols and orthic gray luvisols (Beckingham *et al.*, 1996).

Climatic data

The interpolated climate data for all the 40 sites for the period from 1930 to 2010 were generated using ANUSPLIN (version 4.3) by the Great Lakes Forestry Centre of the Canadian Forest Service, which employs thin plate-smoothing splines to develop continuous climate surfaces across space based on the limited observed data (Hutchinson, 2004). In this study, monthly total precipitation (P) and monthly mean temperature (T_{mean}) were used to explore the climate–growth relationship. In addition to these traditional climatic indices, the SPI and SPEI were also calculated to quantify the impacts of drought on trembling aspen growth. The SPI was calculated by fitting precipitation data to a Gamma probability density function, which was then transformed using a standard normal distribution (McKee *et al.*, 1993). In contrast, the SPEI was calculated based on the difference of precipitation and evapotranspiration, which was estimated with a simplified Penman–Monteith equation (Hogg, 1994, 1997), and the Log-logistic distribution was used for standardization (Vicente-Serrano *et al.*, 2010). We computed SPI and SPEI at 3-, 6- and 12-month scales, to explore impacts of drought on multiple timescales on trembling aspen growth. Positive values of SPI and SPEI indicate wet conditions, while negative ones represent dry conditions.

Tree-ring data

We randomly sampled 40 accessible trembling aspen-dominated mixedwood stands, ranging from 25 to 100 years, according to the Phase 3 inventory database (AFS, 1985). Stands with even-aged trembling aspen and indications of fires were not included in our sampling. The field tree-ring sampling was conducted in all 40 trembling aspen stands. In each stand, a belt transect (ca. 420 m^2 on average) was employed. The transect area was primarily depended on spruce density. An average of 16 live trees were cored in each transect. Two 5.1 mm increment cores in diameter were collected at 1.3 m height from each tree. In the laboratory, all

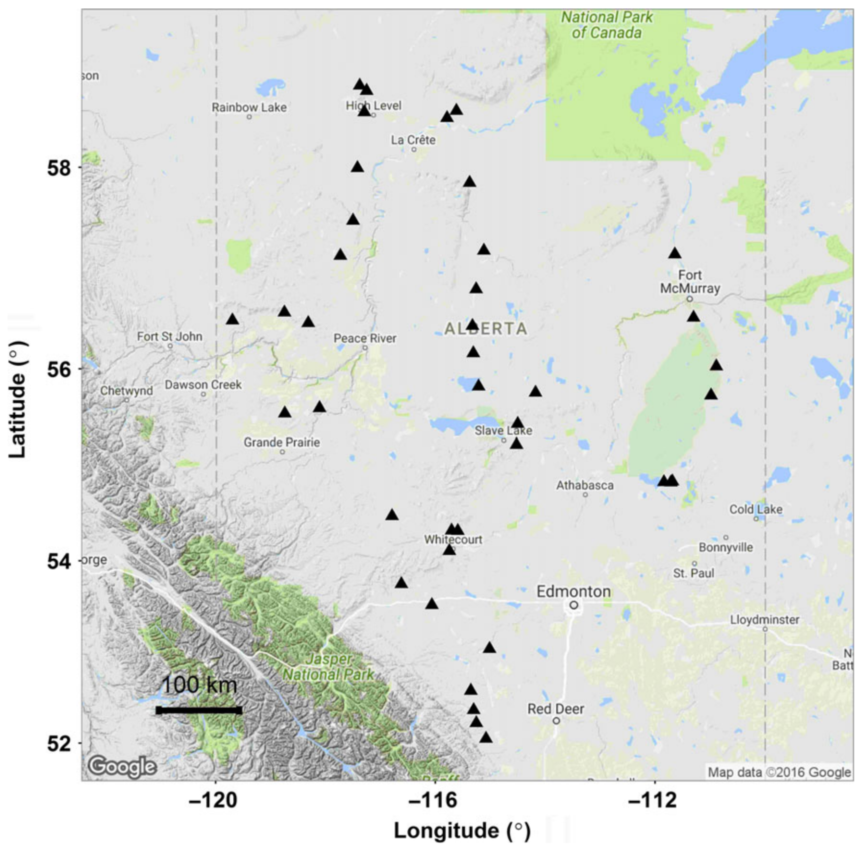

Fig. 1 Locations of the sample sites.

tree-ring cores were dried and polished with successively finer grits of sandpaper. All samples were visually cross-dated, and measured using a Velmex measuring system with the 'Time Series Analysis Program' (TSAP; Frank Rinntech, Heidelberg, Germany) to 0.001 mm resolution. Visual cross-dating was verified using COFECHA (Holmes, 1983). Age- and size-related growth trends were removed by detrending raw tree-ring series using a spline with a 50% frequency response (Cook & Kairiukstis, 1990). Radial growth in 1 year is often associated with the growth in next year due to biological process, which is defined as biological persistence (Cook & Kairiukstis, 1990). As a result, standardized tree-ring series often contain low-frequency variation. Therefore, we used an autoregressive (AR) model to remove the low-frequency persistence and enhance the residual common signal. Residual chronologies were developed using a biweight robust mean to reduce the effect of outliers. The chronology was constructed using the DPLR package (Bunn, 2008) of R (R Core Team 2015). In total, 40 trembling aspen residual ring-width chronologies were constructed for the final analysis. In addition, a master residual chronology was also developed by aggregating all the raw tree-ring series of the 40 aspen sites.

Climate–growth relationship

A linear mixed model (LMM) was used to investigate the effects of climate variables on trembling aspen growth. The linear mixed model is written as

$$Y_{ij} = \beta_0 + \beta_1 x_{ij} + \tau_{i1} + \varepsilon_{ij}, \qquad (1)$$

where Y_{ij} and x_{ij} represent the ring width of residual chronologies and the climate variables for site i and year j; β_0 and β_1 are the fixed effects; τ_{i1} is the random intercept across sites; $\varepsilon_{ij} \sim N(0, \sigma^2)$ are the errors in within-site measurement, τ_{i1} and ε_{ij} are assumed to be independent.

Monthly total precipitation and mean temperatures as well as the drought indices at the end of each month were analyzed as fixed effects, with random intercepts for each site. Linear mixed model analysis was performed using the LME4 package (Bates *et al.*, 2014) of R (R Core Team, 2015).

Spatial variability of drought indices

Principal component analysis (PCA) is broadly applied to identify similarities and differences in climate data (Santos *et al.*, 2010; Gocic & Trajkovic, 2014). We used PCA to determine the spatial variability of drought indices on multiple timescales. The principal components (PCs) were rotated with the varimax method to obtain more stable spatial patterns (Richman, 1986; Bonaccorso *et al.*, 2003; McCabe *et al.*, 2004). A thorough description of the methodology can be found in the study by Vicente-Serrano *et al.* (2010). At last, the spatial interpolation with the kriging method (Oliver & Webster, 1990; Stein, 2012) was used to map the loadings of PCs, which represent the weights of original variables in PCs, and demonstrate the spatial variability of drought indices. As precipitation and temperature have an important role for drought, the spatial variability of the annual total precipitation during the growing season and growing degree-days (GDD > 5 °C) were analyzed using kriging method as well.

Spatial heterogeneity of climate–growth relationship

The climate–growth relationship of each site was assessed using bootstrapped Pearson's correlation analysis between the radial growth and climate variables, including monthly total precipitation and monthly mean temperature of both previous and current year (from January to December), and the drought indices on multiple timescales (3-, 6- and 12-month SPI and SPEI). Then, generalized additive models (GAMs), incorporated into the MGCV package (Wood, 2001) of R (R Core Team 2015), were used to explore the variation in the correlation coefficients along different elevations, latitudes and growing degree-days (GDD > 5 °C).

Results

Statistical parameters of the chronologies

Length of residual chronologies ranged from 29 to 81 years (Appendix S3). The average ring width and standard deviation for the 40 chronologies were 1.45 mm and 0.23 mm, respectively. Residual chronologies exhibited both positive and negative values of skew and first-order autocorrelation, suggesting large variability among sites (Appendix S3).

Response of tree-ring growth to climate variables

Precipitation and temperature. The linear mixed model estimates, for the effect of P and T_{mean} on radial growth, are provided in Table 1. Results showed that radial growth was positively correlated with the precipitations in June and August of previous year ($P < 0.05$). Also, the precipitations in June and October of current year had a significant positive impact on the radial growth ($P < 0.05$). In contrast, the response of radial growth to the temperatures of previous year was often negative, with significant responses from June to October ($P < 0.05$). In comparison, the radial growth was positively correlated with the temperatures of current May, August and September ($P < 0.05$).

SPI and SPEI. Estimates of the linear mixed models for the effect of SPI and SPEI on radial growth are presented in Table 2. In general, the radial growth of trembling aspen often shows a positive correlation with the drought indices. For example, the radial growth was positively correlated with both the 3-month SPI and SPEI at the end of July and August ($P < 0.05$). Meanwhile, the 6-month SPI and SPEI at the end of January and November had significant positive impacts on the

Table 1 Estimates of the linear mixed models (equation 1) for the effects of monthly total precipitation (P) and monthly mean temperature (T_{mean}) of previous and current year on radial growth

		Previous					Current				
Indices	Month	Estimate	SE	t-value	RMSE	AIC	Estimate	SE	t-value	RMSE	AIC
P	1	−1.32E−04	2.92E-04	−0.45	0.2283	−258.37	−2.32E-04	2.94E-04	−0.79	0.2282	−259.64
	2	6.14E-05	3.66E-04	0.17	0.2283	−258.65	−2.62E-04	3.65E-04	−0.72	0.2283	−259.96
	3	5.08E-04	3.53E-04	1.44	0.2282	−260.62	6.02E-06	3.57E-04	0.02	0.2283	−259.40
	4	−5.52E-05	2.71E-04	−0.20	0.2283	−258.07	−4.91E-04	2.73E-04	−1.8	0.2281	−262.09
	5	2.66E-04	1.61E-04	1.65	0.2282	−259.70	6.76E-05	1.60E-04	0.42	0.2283	−257.97
	6	2.34E-04	1.09E-04	2.15*	0.2281	−260.82	3.93E-04	1.09E-04	3.61**	0.2277	−270.06
	7	−2.09E-05	1.10E-04	−0.19	0.2283	−256.26	7.21E-05	1.10E-04	0.65	0.2283	−257.48
	8	5.12E-04	1.30E-04	3.93**	0.2276	−271.93	−1.13E-04	1.31E-04	−0.86	0.2282	−258.14
	9	4.80E-05	1.57E-04	0.31	0.2283	−257.03	−1.70E-04	1.56E-04	−1.08	0.2282	−258.93
	10	−4.22E-04	2.87E-04	−1.47	0.2282	−260.30	8.29E-04	2.86E-04	2.9**	0.2279	-267.38
	11	2.54E-05	3.17E-04	0.08	0.2283	−258.34	6.22E-04	3.17E-04	1.96	0.2281	−263.01
	12	1.75E-04	3.46E-04	0.51	0.2283	−258.77	−3.93E-04	3.48E-04	−1.13	0.2282	−260.63
T_{mean}	1	−1.88E-03	7.39E-04	−2.55*	0.2280	−266.51	−2.49E-04	7.42E-04	−0.34	0.2283	−260.98
	2	5.04E-04	8.53E-04	0.59	0.2283	−260.67	5.17E-04	8.55E-04	0.6	0.2283	−261.51
	3	−1.84E-03	1.13E-03	−1.63	0.2282	−263.53	−5.02E-04	1.12E-03	−0.45	0.2283	−261.89
	4	−1.91E-03	1.70E-03	−1.12	0.2283	−262.96	2.52E-03	1.72E-03	1.47	0.2282	−264.70
	5	−1.59E-03	2.75E-03	−0.58	0.2283	−262.99	1.65E-02	2.73E-03	6.05**	0.2266	−299.80
	6	−7.53E-03	3.12E-03	−2.41*	0.2280	−268.74	4.37E-04	3.14E-03	0.14	0.2283	−263.77
	7	−6.40E-03	3.25E-03	−1.97*	0.2281	−266.87	−2.87E-03	3.25E-03	−0.88	0.2282	−264.60
	8	−1.17E-02	2.79E-03	−4.2**	0.2275	−280.28	8.51E-03	2.81E-03	3.03**	0.2279	−272.69
	9	−7.27E-03	2.40E-03	−3.03**	0.2279	−271.54	6.17E-03	2.41E-03	2.56*	0.2280	−269.78
	10	−4.32E-03	2.15E-03	−2.01*	0.2281	−266.19	−4.07E-03	2.15E-03	−1.89	0.2281	−266.58
	11	−1.79E-03	1.01E-03	−1.77	0.2282	−263.80	−8.79E-04	1.02E-03	−0.87	0.2282	−262.24
	12	6.74E-04	8.38E-04	0.80	0.2283	−260.93	7.94E-05	8.46E-04	0.09	0.2283	−261.14

*$P < 0.05$, ** $P < 0.01$.

radial growth. Conversely, the radial growth was negatively correlated with the 3- and 6-month SPEI at the end of May. With the increase in timescales of drought indices, the significant positive drought responses extended to more month periods. Although the responses of radial growth to SPI and SPEI appear similar, differences still existed. For instance, the 6-month SPI at the end of June and July showed significant positive correlations with the radial growth, while no significant responses were found for SPEI at the same period.

Temporal variability of drought indices

According to the calculated SPI and SPEI, short-term series showed higher frequencies of drought than long-term series, and both the SPI and SPEI indicate frequent droughts from 1930 to 2010 (Figs 2 and 3). In particular, prolonged and severe drought events appeared over the periods of 1935–1950 and 2000–2010 (Figs 2 and 3), which is also corroborated by the low precipitation and elevated temperatures during these periods (Appendix S2). Similarly, reduced growth events from the residual chronology of tree-ring width were also found over the period of 2000–2010 (Fig. 4). This suggests that temporal variability of drought might be a determining factor for the reduction in trembling aspen growth.

Spatial variability of drought indices

We selected the first two principal components (PCs) from our analysis to represent the SPI and SPEI time series (3-, 6- and 12-month length), because these two PCs explain 62% and 69% of the total variation of the SPI and SPEI series (Appendix S4), respectively. The distribution of PC's loadings shows two opposite patterns (Figs 5 and 6). In general, the GDD in northern area was also higher than southern parts, which is opposed to the precipitation as well (Appendix S5). This suggests that the first two PCs could represent precipitation and the GDD, respectively. The spatial variance of SPI and SPEI was similar, both of which showed that two subregions: A relatively wet one and a relatively dry one can be identified with the boundary at approximately 56°N.

Table 2 Estimates of the linear mixed models for the effects of 3-month (3M), 6-month (6M) and 12-month (12M) Standardized Precipitation Index (SPI) and Standardized Precipitation–Evapotranspiration Index (SPEI) on radial growth

		SPI					SPEI				
Periods	Month	Estimate	SE	*t*-value	RMSE	AIC	Estimate	SE	*t*-value	RMSE	AIC
3M	1	−1.97E-04	4.61E-03	−0.04	0.2283	−263.69	−2.65E-04	4.68E-03	−0.06	0.2283	−263.72
	2	−1.04E-03	4.64E-03	−0.22	0.2283	−263.75	−8.97E-04	4.70E-03	−0.19	0.2283	−263.76
	3	−2.10E-03	4.55E-03	−0.46	0.2283	−263.88	−9.42E-04	4.55E-03	−0.21	0.2283	−263.71
	4	−5.59E-03	4.68E-03	−1.19	0.2282	−265.15	−6.08E-03	4.63E-03	−1.31	0.2282	−265.42
	5	−4.28E-03	4.64E-03	−0.92	0.2283	−264.55	−1.22E-02	4.61E-03	−2.64**	0.2280	−270.65
	6	1.36E-02	4.56E-03	2.98**	0.2279	−272.54	6.58E-03	4.63E-03	1.42	0.2282	−265.72
	7	1.50E-02	4.57E-03	3.27**	0.2278	−274.37	1.14E-02	4.65E-03	2.44*	0.2280	−269.68
	8	1.14E-02	4.63E-03	2.45*	0.2280	−269.71	9.62E-03	4.71E-03	2.04*	0.2281	−267.91
	9	−1.89E-03	4.70E-03	−0.40	0.2283	−263.89	−4.66E-03	4.74E-03	−0.98	0.2283	−264.71
	10	−1.30E-03	4.60E-03	−0.28	0.2283	−263.77	−4.59E-03	4.67E-03	−0.98	0.2283	−264.68
	11	6.69E-03	4.61E-03	1.45	0.2282	−265.79	3.39E-03	4.73E-03	0.72	0.2283	−264.26
	12	1.11E-02	4.59E-03	2.43*	0.2280	−269.57	1.28E-02	4.66E-03	2.75**	0.2280	−271.25
6M	1	1.25E-02	4.60E-03	2.72**	0.2280	−271.09	1.88E-02	4.67E-03	4.03**	0.2276	−279.88
	2	−1.73E-03	4.62E-03	−0.37	0.2283	−263.84	2.83E-03	4.69E-03	0.60	0.2283	−264.09
	3	−3.36E-03	4.60E-03	−0.73	0.2283	−264.22	−1.45E-03	4.61E-03	−0.31	0.2283	−263.79
	4	−3.93E-03	4.60E-03	−0.85	0.2283	−264.42	−4.84E-03	4.63E-03	−1.04	0.2283	−264.79
	5	−3.40E-03	4.71E-03	−0.72	0.2283	−264.25	−1.12E-02	4.68E-03	−2.39*	0.2280	−269.42
	6	1.11E-02	4.61E-03	2.42*	0.2280	−269.52	5.44E-03	4.63E-03	1.17	0.2282	−265.08
	7	1.21E-02	4.62E-03	2.62**	0.2280	−270.56	8.65E-03	4.69E-03	1.85	0.2282	−267.13
	8	8.83E-03	4.67E-03	1.89	0.2281	−267.29	3.76E-03	4.75E-03	0.79	0.2283	−264.38
	9	6.27E-03	4.68E-03	1.34	0.2282	−265.52	9.06E-05	4.77E-03	0.02	0.2283	−263.76
	10	1.10E-02	4.69E-03	2.34*	0.2281	−269.19	4.94E-03	4.75E-03	1.04	0.2283	−264.83
	11	1.26E-02	4.68E-03	2.69**	0.2280	−270.97	9.76E-03	4.74E-03	2.06*	0.2281	−267.98
	12	3.26E-03	4.79E-03	0.68	0.2283	−264.23	8.44E-04	4.80E-03	0.18	0.2283	−263.80
12M	1	1.53E-02	4.74E-03	3.23**	0.2278	−274.16	2.20E-02	4.77E-03	4.61**	0.2273	−284.92
	2	1.45E-02	4.71E-03	3.09**	0.2279	−273.24	2.11E-02	4.75E-03	4.45**	0.2274	-283.48
	3	1.35E-02	4.70E-03	2.87**	0.2279	-271.95	2.05E-02	4.74E-03	4.32**	0.2275	-282.38
	4	1.23E-02	4.73E-03	2.61*	0.2280	−270.53	1.73E-02	4.76E-03	3.63**	0.2277	−276.87
	5	1.06E-02	4.75E-03	2.23*	0.2281	−268.71	1.33E-02	4.78E-03	2.79*	0.2280	−271.52
	6	1.40E-02	4.72E-03	2.96**	0.2279	−272.49	1.50E-02	4.75E-03	3.15**	0.2279	−273.67
	7	1.63E-02	4.64E-03	3.51**	0.2277	−276.02	1.73E-02	4.71E-03	3.68**	0.2277	−277.26
	8	7.15E-03	4.70E-03	1.52	0.2282	−266.04	5.11E-03	4.77E-03	1.07	0.2283	−264.91
	9	4.48E-03	4.70E-03	0.95	0.2283	−264.64	−1.87E-04	4.75E-03	−0.04	0.2283	−263.75
	10	8.03E-03	4.72E-03	1.70	0.2282	−266.63	3.11E-03	4.77E-03	0.65	0.2283	−264.18
	11	9.61E-03	4.72E-03	2.04*	0.2281	−267.88	4.49E-03	4.79E-03	0.94	0.2283	−264.65
	12	8.62E-03	4.74E-03	1.82	0.2282	−267.06	3.54E-03	4.80E-03	0.74	0.2283	−264.32

*$P < 0.05$, ** $P < 0.01$.

Variance of the growth–climate relationship along different latitudes, elevations and growing degree-days (GDD > 5 °C)

The correlation coefficients of radial growth and monthly total precipitation of previous April and current August showed nonlinear variations along latitudes ($P < 0.05$), which reached its extreme at approximately 56° N (Fig. 7). Correlations of radial growth with monthly mean temperature of previous March, and monthly total precipitation of current May decreased with increase in latitudes ($P < 0.05$) (Fig. 7). The correlations of radial growth and 3-month SPI and SPEI showed similar nonlinear variations along latitudes ($P < 0.05$) (Fig. 8). Correlations of radial growth and 6-month SPEI at the end of December also varied along latitudes ($P < 0.05$) (Fig. 8). Overall, the responses of radial growth to 3- and 6-month drought indices were first positive, then negative and finally became positive again along the latitudes, which is consistent with the U-shaped trend with minimum values at approximately 56°N (Fig. 8).

Climate–growth relationship also varied along the elevations and GDD but with latitude (Appendices S6–S8). Thus, correlations of radial growth with monthly total precipitation of current May decreased with

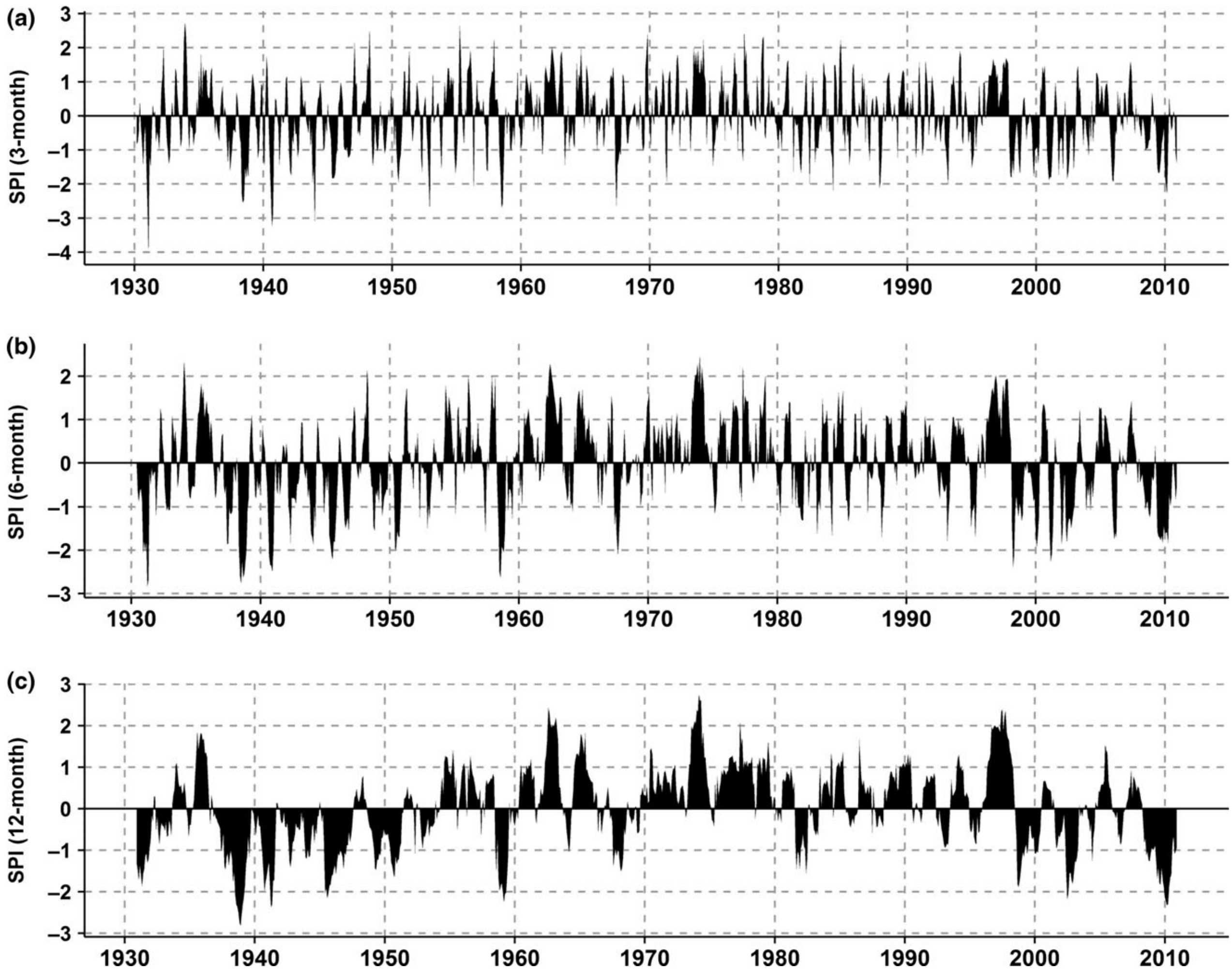

Fig. 2 Time series (1930–2010) of the 3-, 6- and 12-month Standardized Precipitation Index (SPI).

increase in GDD, while it showed an upward trend with increase in elevation (Appendix S6). Furthermore, correlations of radial growth and the 6-month drought indices generally showed a downward trend while increasing GDD (Appendix S7). Likewise, the response of radial growth to 12-month drought indices showed a decreasing trend when GDD increased (Appendix S8). In total, eight significant variations for the response of radial growth to 12-month SPI along GDD were found. However, significant correlation of radial growth and 12-month SPEI was only observed at the end of June (Appendix S8).

Discussion

Massive aspen forest mortality in Canadian boreal forests has been observed in recent years (Michaelian *et al.*, 2011); therefore, understanding of how the mixedwood boreal forest ecosystems will respond to severe drought is important to develop mitigation strategies and maintain forest productivity (Assal *et al.*, 2016). Results indicated that the spatiotemporal variability of drought indices was closely linked to aspen radial growth, suggesting that drought might be the triggering factor of reduced growth of trembling aspen in western Canadian boreal forests. In addition, the spatiotemporal variability of drought indices can explain the spatial heterogeneity in the radial growth of trembling aspen as well. As the trembling aspen growth is sensitive to drought (Krishnan *et al.*, 2006; Barr *et al.*, 2007), drought indices can be applied to monitor and mitigate potential effects of increased drought stress and develop or improve the current classification of eco-regions.

Response of radial growth to climate variables

Precipitation and temperature. Trembling aspen radial growth was positively influenced by precipitations of previous year, while temperatures of previous summer imposed negative impacts on the growth of

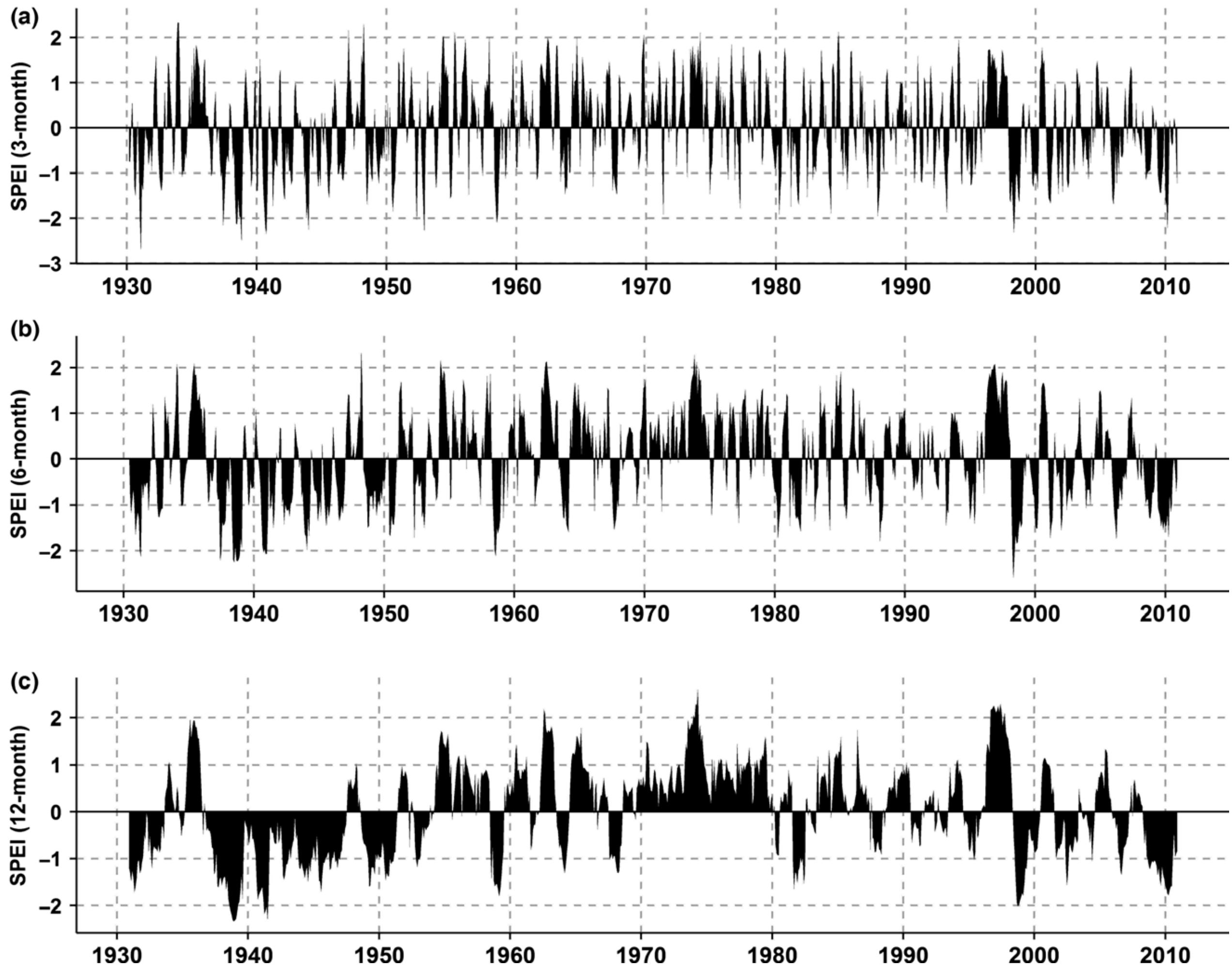

Fig. 3 Time series (1930–2010) of the 3-, 6- and 12-month Standardized Precipitation Evapotranspiration Index (SPEI).

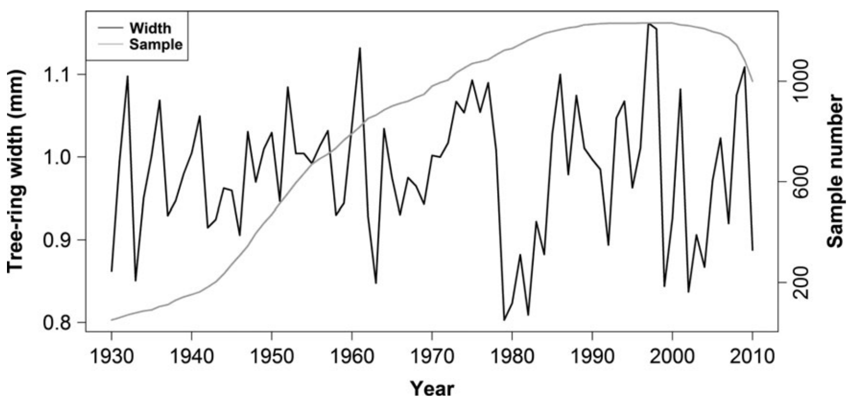

Fig. 4 Tree-ring width of the residual chronology by aggregating the tree-ring series of 40 sites.

trembling aspen (Table 1). The weak correlations between the radial growth and both precipitation and temperature of previous year could be explained by carryover effects, which denotes storage of photosynthates and nutrients from previous year could influence the radial growth of current year (Cook & Kairiukstis, 1990; Babst *et al.*, 2013; Rammig *et al.*, 2015). In summer, higher temperatures could contribute to moisture deficit and reduce the storage of carbohydrates (D'Arrigo *et al.*, 2004;

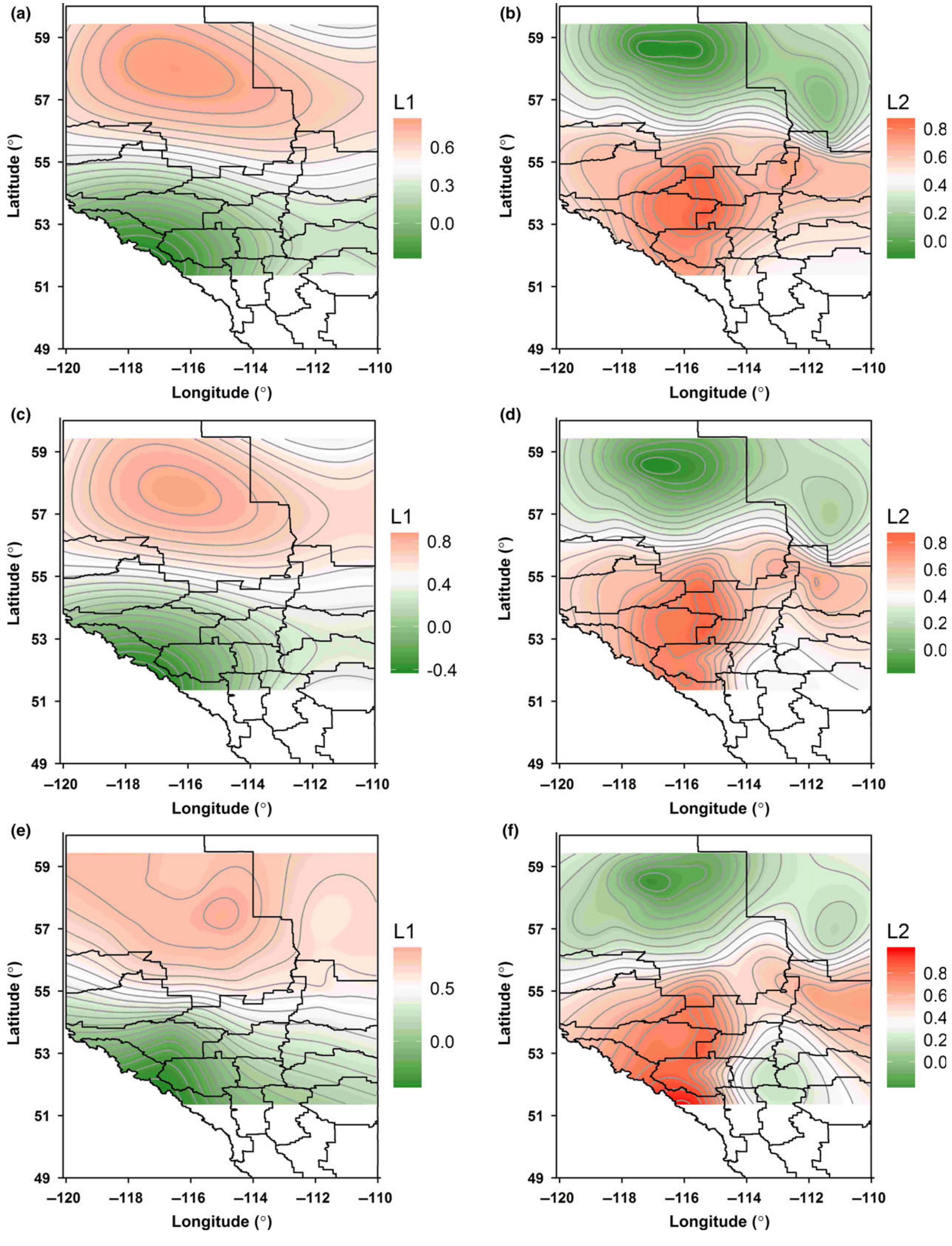

Fig. 5 Spatial distributions of the loadings of first two principal components of three-, six- and 12-month Standardized Precipitation Index (SPI): (a) the first loadings of 3-month SPI, (b) the second loadings of 3-month SPI, (c) the first loadings of 6-month SPI, (d) the second loadings of the 6-month SPI, (e) the first loadings of the 12-month SPI, (f) the second loadings of the 12-month SPI.

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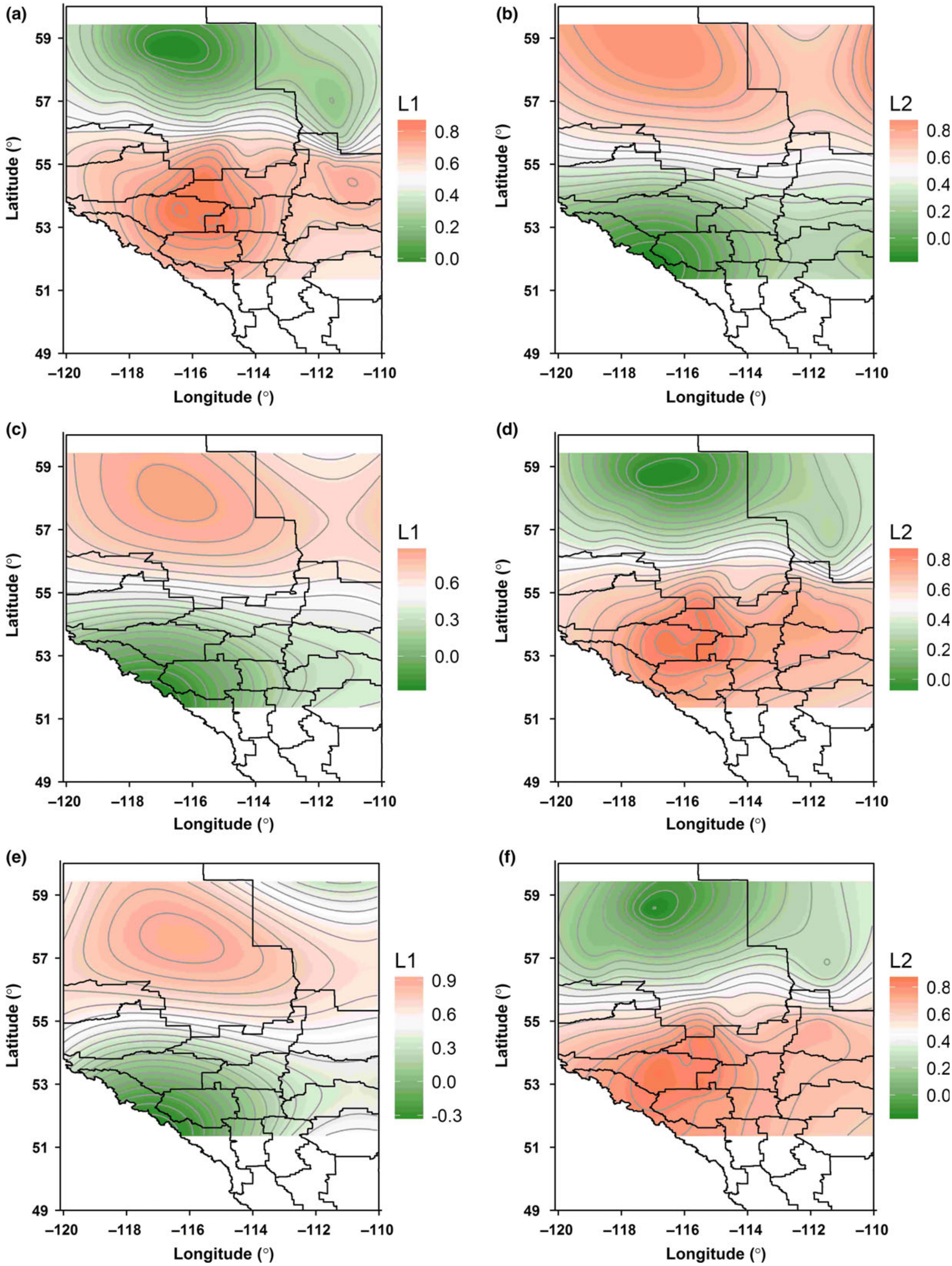

Fig. 6 Spatial distributions of the loadings of first two principal components of 3-, 6- and 12-month Standardized Precipitation–Evapotranspiration Index (SPEI): (a) the first loadings of 3-month SPEI, (b) the second loadings of 3-month SPEI, (c) the first loadings of 6-month SPEI, (d) the second loadings of the 6-month SPEI, (e) the first loadings of the 12-month SPEI, (f) the second loadings of the 12-month SPEI.

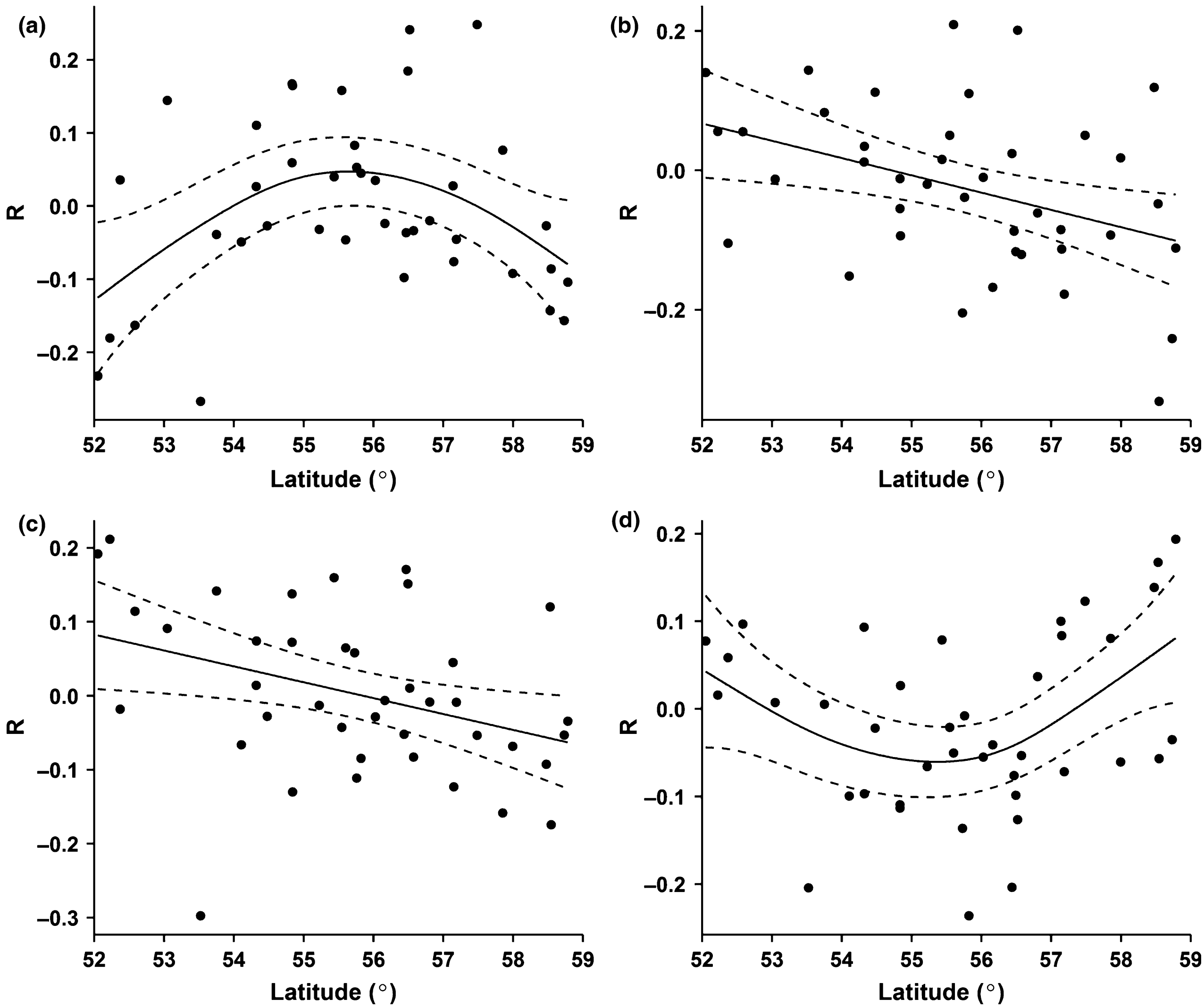

Fig. 7 Latitudinal variation of correlations between radial growth and (a) monthly total precipitation of previous April; (b) monthly mean temperature of previous March; (c) monthly total precipitation of current May; (d) monthly total precipitation of current August. The dashed lines indicate a 95% confidence interval. R represents the correlation coefficients of radial growth and climate variables.

Huang *et al.*, 2010), whereas a greater precipitation can maintain a proper soil moisture, favoring the assimilation of carbohydrates and promoting the radial growth of following year (Dang *et al.*, 1998). This is consistent with our results that the radial growth was positively and negatively affected by the precipitation and temperature of previous year, respectively.

In spring, a warm temperature is not only able to promote the emergence of leaves and buds (Huang *et al.*, 2010), but also to trigger the initiation of photosynthesis (Tanja *et al.*, 2003) through accelerating soil thawing (Goodine *et al.*, 2008). In our study, the temperature of current May was positively correlated with the radial growth of trembling aspen (Table 1). According to the Liebig's law of the minimum (Mitscherlich, 1909; De Baar, 1994), higher temperatures or more precipitation can enhance growth rate until a resource becomes limiting. Furthermore, Deslauriers *et al.* (2016) demonstrated that water availability is the most important factor for the production of xylem cell. Accordingly, in a water-deficit environment, the increment of precipitation in August might promptly alleviate the drought stress (Zeppel *et al.*, 2008; Jian *et al.*, 2016). This is consistent with results in our study, in which, in addition to the precipitation, the temperature of current August was found to be positively correlated with the radial growth as well (Table 1).

SPI and SPEI. The SPI on multiple timescales showed significant positive impacts on the radial growth of trembling aspen (Table 2). Likewise, the responses of

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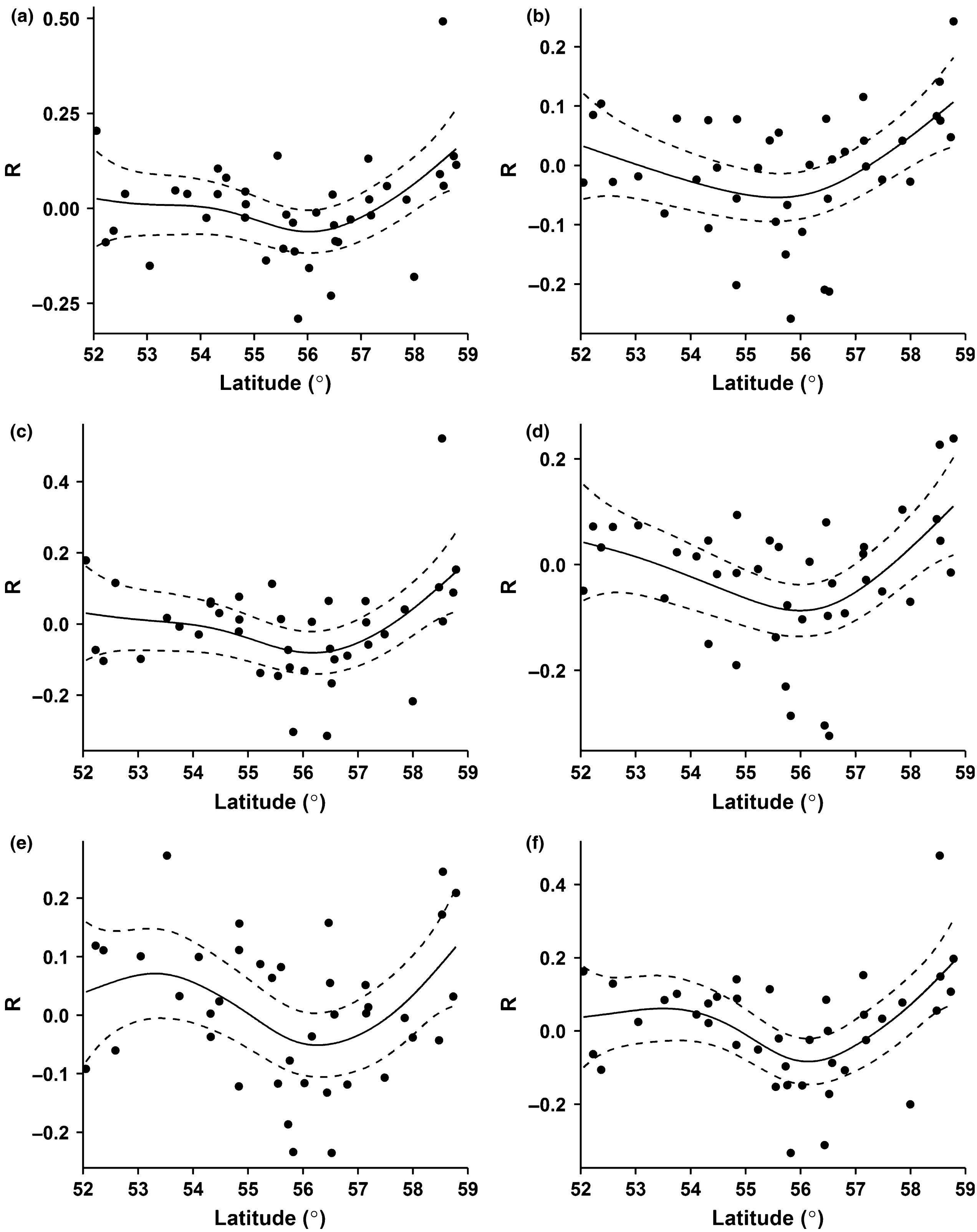

Fig. 8 Latitudinal variation of the correlations between radial growth and (a) 3-month Standardized Precipitation Index (SPI) at end of September; (b) 3-month SPI at the end of October; (c) 3-month Standardized Precipitation–Evapotranspiration Index (SPEI) at the end of September; (d) 3-month SPEI at the end of October; (e) 3-month SPEI at the end of November; (f) 6-month SPEI at the end of December. The dashed lines indicate a 95% confidence interval. R represents the correlation coefficients of radial growth and climate variables.

radial growth to the SPEI on 3-, 6- and 12-month scales were also often positive (Table 2). These results suggest that trembling aspen growth is limited by drought, which is confirmed by the positive impacts of current precipitation. Furthermore, differences still existed for the influence of SPI and SPEI on the radial growth, although both of them showed consistency in their effects on tree growth (Table 2). This suggests that temperature-induced evapotranspiration might be a potential factor responsible for the drought severity in western Canadian boreal forest. On the other hand, the effects of drought on multiple timescales on aspen growth were different (Table 2). Compared with 3-/6-month drought indices, significant responses of radial growth to 12-month drought indices extended to more month periods (Table 2). For example, a total of eight significant cases were found for the 12-month SPI. In contrast, for 3-month SPI, only three significant cases were only found at the end of June, July and August. This suggests that hydrological drought associated with the effects of streamflow, lake levels and groundwater (Wilhite & Glantz, 1985) exerted persistent stress on the radial growth of trembling aspen.

Relationship between growth and temporal variability of drought indices

According to the calculated drought indices (Figs 2 and 3), prolonged and severe drought events occurred over the periods of 1935–1950 and 2000–2010, and concurred with a reduction in trembling aspen growth, which suggests that drought is likely the initial driver of the declined growth of aspen (Michaelian *et al*., 2011; Anderegg *et al*., 2012, 2013; Worrall *et al*., 2013). Additional potential factor resulting in aspen growth reduction such as severe insect outbreak [e.g., forest tent caterpillar (*Malacosoma disstria* Hubner) and the large aspen tortrix (*Choristoneura conflictana* Walker)] in these two sustained periods was mostly excluded because white or pale rings that were unique and valid indicator for severe insect outbreaks (Hogg & Schwarz, 1999; Sutton & Tardif, 2005; Huang *et al*., 2008) were neither observed from our samples, nor reported previously, except some sporadical years such as 2000 or 2001 (Hogg & Schwarz, 1999; Cooke & Lorenzetti, 2006; Cooke & Roland, 2007; Huang *et al*., 2008). However, the maximum growth reduction was observed in the 1980s although the magnitude and duration of the drought were not at their peak values. A previous study reported that an outbreak of forest tent caterpillar in the 1980s contributed to severe decline in western Canadian aspen forest (Hogg & Schwarz, 1999). Consequently, in addition to the main driver of drought, it is very likely that a variety of factors such as insects and resource competition have been, more or less, related to this growth reduction and declination in aspen growth (DeByle *et al*., 1987; Hogg *et al*., 2002; Parry *et al*., 2003; Allen *et al*., 2010; Luo & Chen, 2013; Bretfeld *et al*., 2015).

Relationship between growth and spatial variability of drought indices

Responses of radial growth to drought indices varied along latitudes with extreme values at approximately 56°N (Fig. 8), which agrees with the boundary of the two subregions based on the PC analysis. This indicates that the spatial variability of drought indices could be useful to explain the spatial variation in the response of radial growth to drought indices. The response curves were generally consistent with a U-shaped trend (Fig. 8). In the study area, the values of GDD showed a decreasing trend from 1300 °C at 54°N, 115°W to 1100 °C at 55°N, 115°W and finally increased to around 1300 °C at 58°N, 115°W (Appendix S5). This suggested that the GDD might in part explain the spatial variability of radial growth response to SPI and SPEI, which can explain the significant variation in the response of radial growth to drought indices with GDD (Appendices S7 and S8). Furthermore, PC analysis also indicates that the GDD could account for the spatial variability of drought indices (Figs 5 and 6). Therefore, we believe that it is important to include temperature data in drought indices to better quantify the impacts of drought in western Canada.

Understanding the impacts of droughts on forest ecosystems is not only useful to provide guidance for developing strategies to mitigate drought stress and maintain forest productivity (Assal *et al*., 2016), but it is also vital toward a comprehensive clarification of the effects of global climate change on forest structure and function (Luo & Chen, 2015). Research has predicted more severer droughts with higher frequency, due to ongoing global warming and the predicted increasing temperatures, will occur in western Canada (Bonsal *et al*., 2013). Thus, we conclude that, to better quantify the impacts of drought on boreal forests, drought indices can be a powerful tool to monitor the potential effects of increased drought stress, develop or improve the current classification of eco-regions and effective mitigation strategies to maintain western Canadian boreal forests.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. (a) Annual mean temperature (T_{mean}), minimum temperature (T_{min}), and maximum temperature (T_{max}); and (b) total precipitation for the 40 trembling aspen sites.
Appendix S2. Temporal variation of annual mean temperature and annual total precipitation from 1930 to 2010 in the study area.
Appendix S3. Statistical information of the residual chronologies of trembling aspen.
Appendix S4. The Standard Deviation (STD), Proportion of Variance (POV) and Cumulative Proportion (CPR) of first six Principal Components (PCs).
Appendix S5. Spatial variability of (a) mean annual total precipitation from May to September, and (b) the growing degree-days (GDD > 5 °C).
Appendix S6. Variation of correlations between radial growth and monthly total precipitation of (a) previous May and (b) current May with growing degree-days (GDD > 5 °C); (c) previous April and (d) current May with different elevations.
Appendix S7. Variation of correlations between radial growth and 6-month (a) SPI at the end of January; (b) SPI at the end of February; (c) SPEI at the end of January; (d) SPEI at the end of February with growing degree-days (GDD > 5 °C).
Appendix S8. Variation of correlations between radial growth and 12-month SPI at the end of January-August (a–h); (i) SPEI at the end of June with growing degree-days (GDD > 5 °C).