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Spatial climate-dependent growth response of boreal mixedwood forest in western Canada

Xinyu Jiang [a,b], Jian-Guo Huang [a,b,*], Kenneth J. Stadt [c], Philip G. Comeau [d], Han Y.H. Chen [e]

[a] Key Laboratory of Vegetation Restoration and Management of Degraded Ecosystems, South China Botanical Garden, Chinese Academy of Sciences, Guangzhou 510650, China
[b] Guangdong Provincial Key Laboratory of Applied Botany, South China Botanical Garden, Chinese Academy of Sciences, Guangzhou 510650, China
[c] Forest Management Branch, Sustainable Resource Development, Edmonton, Alberta, Canada
[d] Department of Renewable Resources, University of Alberta, Edmonton, Alberta, Canada
[e] Faculty of Natural Resources Management, Lakehead University, 955 Oliver Road, Thunder Bay, ON, Canada

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ABSTRACT

The western Canadian mixedwood boreal forests were projected to be significantly affected by regional drought. However, drought degrees were spatially different across elevations, longitudes and latitudes, which might cause different tree growth responses to climate change in different sub-regions within western Canada. In this way, regional classification of western Canadian boreal forests and understanding spatial tree growth responses to climate might be necessary for future forest management and monitoring. In this paper, tree-ring chronologies of two dominant tree species, trembling aspen (*Populus tremuloides* Michx.) and white spruce (*Picea glauca* (Moench.) Voss), were obtained from mixed forest stands distributed across western Canada to study spatial tree growth response to climate based on three regional classification schemes (a phytogeographic sub-region classification, a natural sub-region classification and non-classification). Phytogeographic sub-region classification was estimated based on tree ring samples we collected in this study, while natural sub-region classification was previously developed based on analysis of regional differences in vegetation, soil, site and climate conditions. Results showed that air temperature did not significantly increase, while drought stress became more severe between 1985 to 2010. Relationships between trembling aspen growth and temperature differed between north and south parts of the study area, resulting from spatial difference in water supply. Trembling aspen growth was influenced by temperature or moisture variables of the previous years. White spruce growth was influenced primarily by moisture variables (current or previous year), and response coefficients between white spruce and drought conditions (represented by drought code) were negative in all phytogeographic sub-regions, suggesting that white spruce was more sensitive to drought stress under climate change. As a late-successional dominant species, increasingly drought stress on white spruce might cause significant alteration in forest composition of western Canadian boreal forest.

1. Introduction

Climate changes during the past several decades have led to a variety of responses in terrestrial ecosystems, including variations in net primary productivity, forest growth, and species distributions (Zhao and Running, 2010; Liang et al., 2015; Nabeshima et al., 2015). Much progress has been made to quantify the impact of climate changes on forest growth all around the world (Bowman et al., 2014; Zhang et al., 2015). Boreal forest ecosystem contains nearly half of the global forest carbon due to the slow decomposition rate of dead biomass in cold climates, playing an important role in the global carbon cycle, and has been identified as a potential tipping element of the Earth climate system (Lenton et al., 2008). However, inconsistent effects of climate change on the boreal forest ecosystems create a challenge to accurately predict global carbon cycle and forest productivity. A previous study suggests that western Canadian boreal forest seems to be more sensitive to climate change than eastern Canadian boreal forest (Peng et al., 2011); while within vast western Canada, spatially different climate change responses of boreal forest may also be caused by elevations, longitudes, latitudes, site effects (Gewehr et al., 2014) or species composition (Coomes et al., 2014; Chen and Luo, 2015).

Climate changes are spatially different in change rates and trends. For example, the increasing trend of average surface air temperature in Arctic area is higher than those in low latitudinal regions (ACIA, 2004). Climate change can also cause spatially inconsistent effects on tree growth through different mechanisms. In high latitude or altitude, climate warming seems to be able to directly alleviate the limiting effect of cold temperature on tree growth, which is distinct from

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* Corresponding author at: Guangdong Provincial Key Laboratory of Applied Botany, South China Botanical Garden, Chinese Academy of Sciences, Guangzhou 510650, China.
E-mail address: huangjg@scbg.ac.cn (J.-G. Huang).

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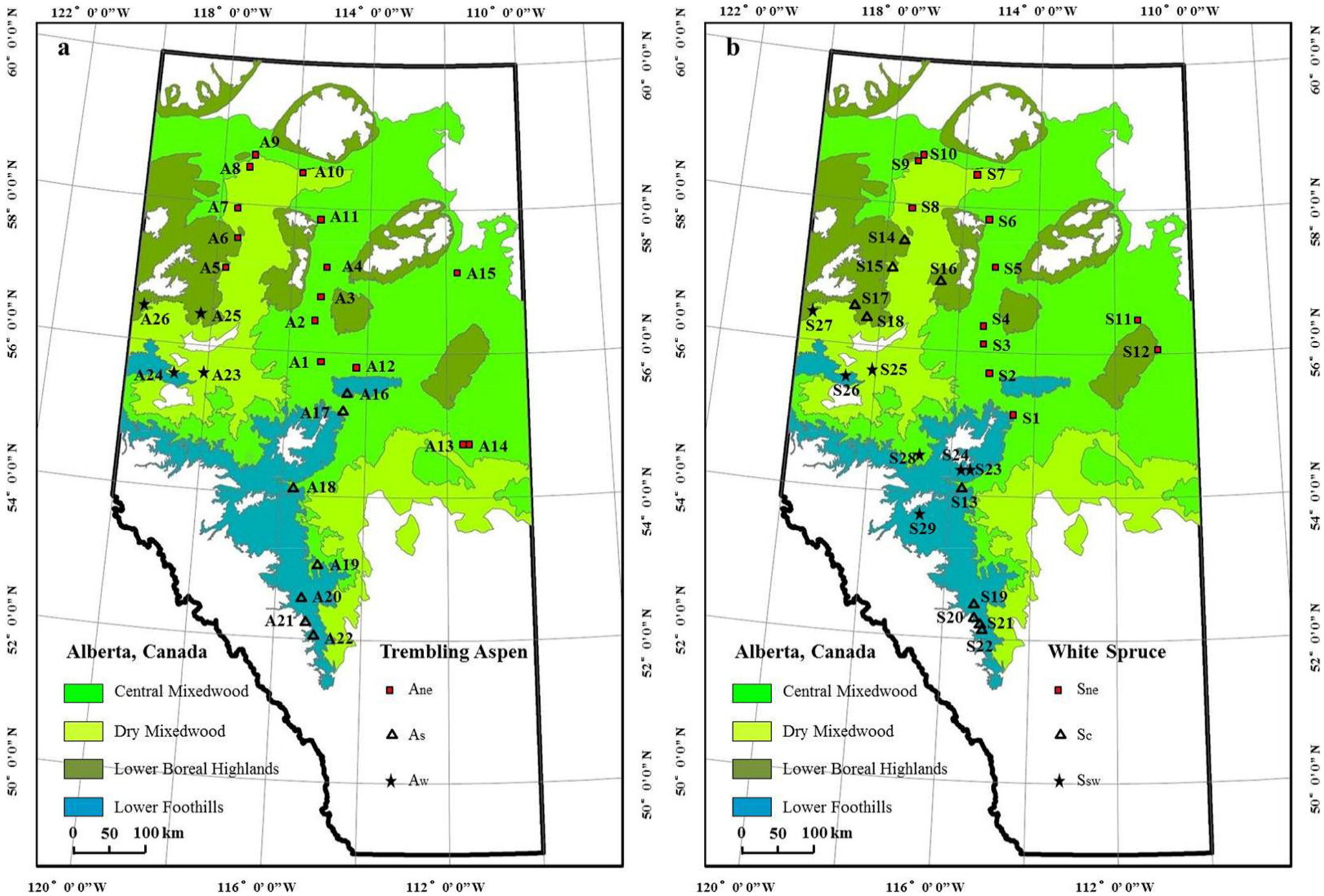


Fig. 1. Natural sub-regions and phytogeographic sub-regions for a) trembling aspen and b) white spruce in our study area. Different colors represent the natural sub-regions, including central mixedwood (green), dry mixedwood (yellow), lower boreal highlands (olive), and lower foothills (light blue). A_{ne} (hollow square), A_s (hollow triangle), and A_w (solid asterisk) represent three phytogeographic sub-regions for trembling aspen; while S_{ne} (hollow square), S_c (hollow triangle), and S_{sw} (solid asterisk) represent phytogeographic sub-regions for white spruce. A_{ne}, A_s, and A_w covered northeast, south, and west of the study area; while S_{ne}, S_c, and S_{sw} covered northeast, central, and southwest of the study area, respectively. Words next to different symbols represent site numbers. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

situations in lower latitude or altitude (Reich and Oleksyn, 2008; Zhang et al., 2012). In some regions, such as North America, climate warming may induce regional drought, which reduce biomass carbon of boreal forests (Ma et al., 2012; Chen and Luo, 2015). Even for the same climatic variable, induced effects on tree growth may also vary across large spatial scales. For instance, changes in precipitation can significantly influence tree growth in low latitudes, but have less effect in high latitudes (Helama et al., 2005; Henttonen et al., 2014).

Effects of climate changes on tree growth are also dependent on tree species, especially in the same eco-region with similar spatial climatic change trends (Luo and Chen, 2011; Messaoud and Chen, 2011). Species effect further complicates modeling efforts; therefore, it is necessary to include species specific responses to climate change in tree growth studies. Tree growth is dependent on biomass of neighbors as a result of asymmetric competition (Huang et al., 2013). Unlike shade-intolerant species, shade-tolerant species commonly obtain a net carbon gain to create thicker bark and higher wood densities under species competition or shaded environments because of their lower plant respiration rates (Niinemets and Valladares, 2006); therefore, shade-tolerant species are more resistant to disturbance agents (Poorter et al., 2010). In western Canada, boreal mixedwood forests, dominated by trembling aspen (canopy and shade-intolerant species) and white spruce (understory and shade-tolerant species), distribute across large latitudes and longitudes. This area also covers an elevation range of 210 m in the northeast to 3700 m in the western Rocky Mountains, and has some of the most diverse terrain in North America. Climate change forecasting indicates substantial warming and increased drought stress over the next century in this region (Price et al., 2013; Wang et al., 2014). A previous study has also reported the spatially different mortality response of trembling aspen to environmental stressors in southeastern part of this region (Michaelian et al., 2011).

Given that there may be a heterogeneity in spatial climate dependent tree growth response, it is necessary to achieve regional classification based on spatial difference in tree growth response to climatic variables across a large spatial scale. But how to achieve the regional classification is still a challenge. Some ecological sub-region classification schemes have been developed, for example in western Canada a natural sub-region classification scheme has been developed based on analysis of regional differences in vegetation, soil, site, climate conditions and forest productivity information (Beckingham et al., 1996). This sub-regional classification is thus a logical place to start. However, tree species ecotypes may cross these boundaries; trees that are in geographic proximity but in different natural sub-regions may be more similar than more distant trees of the same species in the same natural sub-region.

In this study, another classification scheme called phytogeographic sub-regions classification will be developed based on tree-ring data collected directly in field. In this way, tree-ring data were collected from different boreal mixedwood forest stands in western Canada to 1) identify the main climatic variables affecting growth in different sub-regions for different tree species, and 2) illustrate the mechanisms that caused spatial dependent tree growth response to climate variables for different tree species. It was hypothesized that variations in climate variables, ecophysiological characteristics of different sub-regions, and tree species would result in spatially contrasting response of tree growth to climate changes.

2. Materials and methods

2.1. Study area

In the current natural sub-region classification, the forested area was divided into four natural sub-regions: central mixedwood, dry mixedwood, lower boreal highlands, and lower foothills (Beckingham et al., 1996), and our study area included the four major forested natural sub-regions of boreal mixedwood forest in Alberta, western Canada (110°W–120°W, 51°N–59°N) (Fig. 1). Following the longitudinal and latitudinal gradients, mean annual temperature (*T*) decreases from south to north and east to west, while annual total precipitation (*W*) shows a rising trend from northeast to southwest with the drier areas in the southeast and northwest (Environment Canada, 2012). Our study area is primarily affected by dry continental polar air masses from the north in the winter and regular incursions by cool, moist Pacific air from the west all year. Occasionally, warm and moist Atlantic air masses bring heavy precipitation from the southeast. Trembling aspen (*Populus tremuloides* Michx.) and white spruce (*Picea glauca* (Moench.) Voss) are the major tree species on upland sites in the boreal forests, and occur in both pure and, more often, in mixed stands (Stadt et al., 2007). This region is dominated by a typically dry continental climate, with cold winters and warm summers. Mean annual *T*, growing degree-days (*Gdd*), and *W* were 2.0 °C, 1306, and 487 mm with 30% in the form of snow. Dominant soil types in this region include orthic gray luvisols, clays and brunisolic loams.

2.2. Tree-ring data

Field tree-ring sampling was conducted within the study area in 2007, 2008, 2010 and 2011. In Alberta, mixed trembling aspen and white spruce stands were randomly sampled in four forested natural sub-regions, which ranged from 25 to 100 years according to the Phase 3 forest inventory database (AESRD, 2012). Stands where the trembling aspen cohort was clearly uneven-aged or stands with indications of ground fires or insect outbreaks were not included. In each stand, a belt transect (average area was 415 m^2) was employed to identify sample trees and estimate density. The transect size depended primarily on tree density (low numbers of tree required larger areas to obtain an adequate sample). Within each transect, 20 live white spruce or trembling aspen were randomly chosen. Two 5.1 mm diameter increment cores from each of these trees were collected at diameter at breast height (1.3 m above root collar) for annual ring-width measurement done later in the laboratory. Two cores of each tree were taken from opposite orientation of tree, and also were taken parallel to the slope. In total, 29 stands for white spruce and 26 stands for trembling aspen were used for statistical analysis.

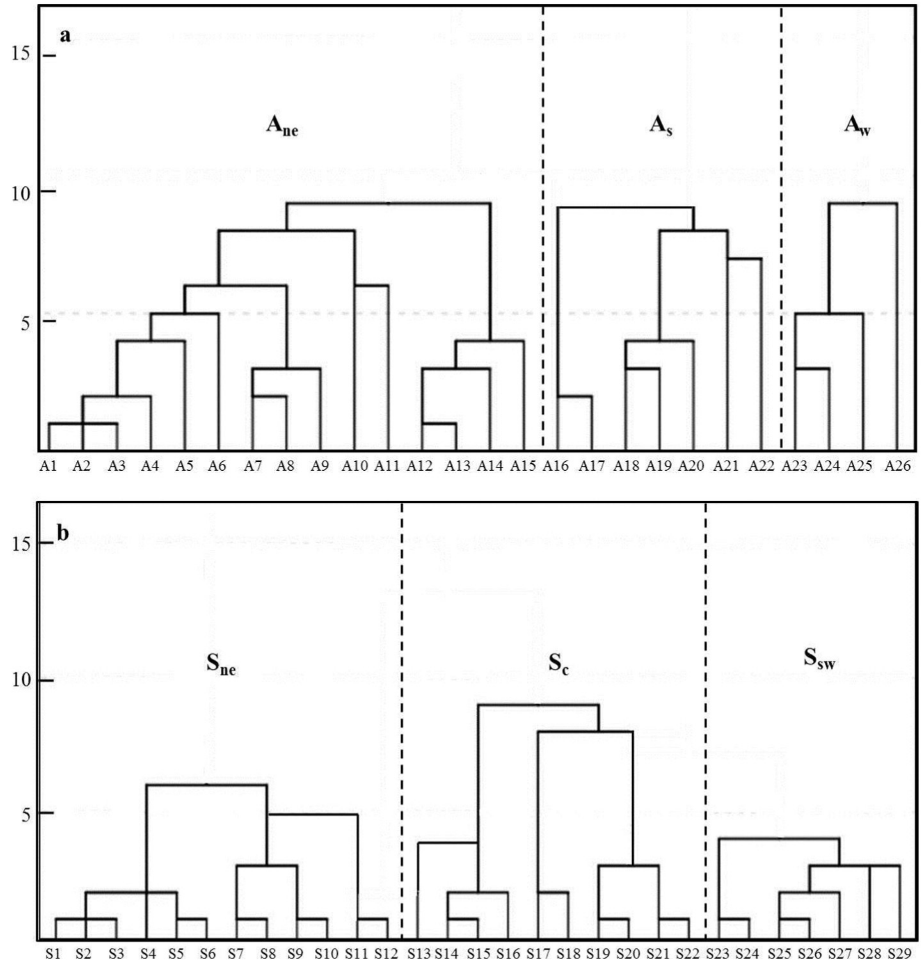


Fig. 2. Cluster analysis results of all sampling site chronologies in the period 1985 to 2010 for a) trembling aspen and b) white spruce. A_{ne}, A_s, and A_w represent three phytogeographic sub-regions for trembling aspen; while S_{ne}, S_c, and S_{sw} represent phytogeographic sub-regions for white spruce. A1 to A26 and S1 to S29 represent site numbers of trembling aspen and white spruce, respectively.

Table 1
Characteristics of climates (mean ± SE) of phytogeographic sub-regions for trembling aspen (A_{ne}, A_s, and A_w) and white spruce (S_{ne}, S_c, and S_{sw}). Phytogeographic sub-regions A_{ne}, A_s, and A_w covered northeast, south, and west parts of the study area; while S_{ne}, S_c, and S_{sw} covered northeast, central, and southwest parts of the study area, respectively.

Phytogeographic sub-regions	Annual climate variables					
	Minimum temperature (°C)	Maximum temperature (°C)	Mean temperature (°C)	Total precipitation (mm)	Growing degree-days (°C)	Drought code (June–July)
A_{ne}	−24.72 ± 3.20	22.65 ± 1.22	0.65 ± 0.99	456 ± 73	1298 ± 114	465 ± 130
A_s	−19.97 ± 3.55	21.95 ± 1.19	2.30 ± 1.05	544 ± 81	1224 ± 104	316 ± 96
A_w	−23.34 ± 3.64	22.04 ± 1.28	1.19 ± 1.07	451 ± 82	1193 ± 117	462 ± 138
S_{ne}	−24.31 ± 2.95	22.56 ± 1.21	0.59 ± 0.93	451 ± 72	1286 ± 115	467 ± 130
S_c	−22.93 ± 3.56	22.31 ± 1.15	1.38 ± 1.04	497 ± 66	1225 ± 108	405 ± 96
S_{sw}	−21.57 ± 3.55	21.87 ± 1.21	1.74 ± 1.04	511 ± 70	1177 ± 109	385 ± 104

All cores were carefully polished with fine grit sandpaper in the laboratory after air drying. Prior to sanding, cores were mounted on grooved wooden platforms. Visual cross-dating of each core was conducted under a binocular microscope. The dated cores were measured using a Velmex measuring system interfaced with the 'Times Series Analysis Program' (TSAP; Frank Rinntech, Heidelberg, Germany) to a precision of 0.001 mm. Visual cross-dating was verified using COFECHA (Holmes, 1983). Tree age was also determined according to the method of Denneler et al. (2008).

2.3. Chronology construction for each sampling sites

Chronology construction was carried out using the ARSTAN software (version 4.0a). The negative exponential detrending method (Cook, 1985) was conducted to remove the age and size-related variances in tree growth, while retaining climate-related variances. This process involved transforming the ring-width measurements into dimensionless indices by dividing the observed ring-width measurements by those estimated using the negative exponential function. Temporal autocorrelation was removed from each standardized series using an autoregressive model (AR) to enhance the common signal. To further eliminate the effect of endogenous stand disturbances and enhance the common signal, all residual series were averaged by site using a biweight robust mean. For all sampling sites, the length of trembling aspen chronologies varied from 29 to 89 years, while white spruce chronologies spanned 26 to 89 years. For each sampling site, 20 trembling aspen or white spruce were included in the chronologies.

2.4. Spatial classification of phytogeographic sub-regions based on chronologies

Hierarchical clustering analysis was conducted to develop phytogeographic sub-region classifications for both trembling aspen and white spruce using chronologies from each sampling site. Trees in some sites were young (<30 years); therefore, in order to include all sampling sites, chronologies for the common period from 1985 to 2010 were used to develop the phytogeographic sub-region classification. Squared Euclidean distance was used to judge the similarity of tree growth between different sampling sites and to divide sampling sites.

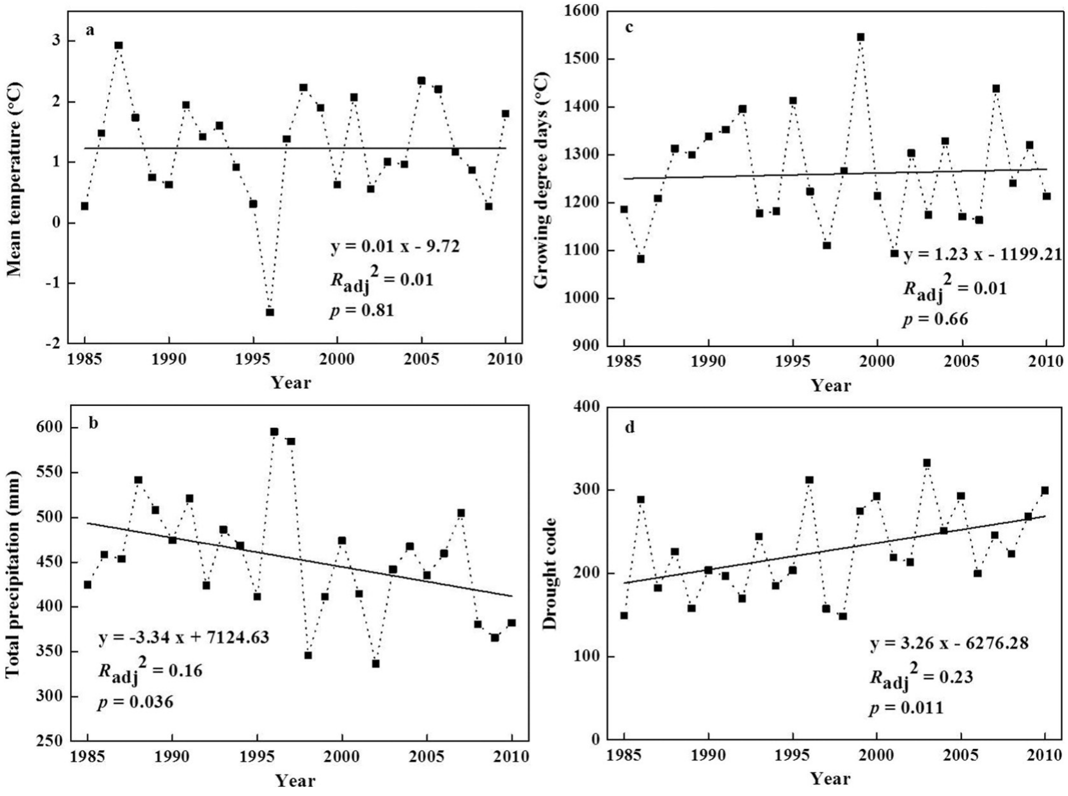


Fig. 3. Patterns of a) mean temperature (°C), b) total precipitation (mm), c) growing degree days (°C), and d) drought code of the entire study area from 1985 to 2010. Linear regression results were listed on the figure.

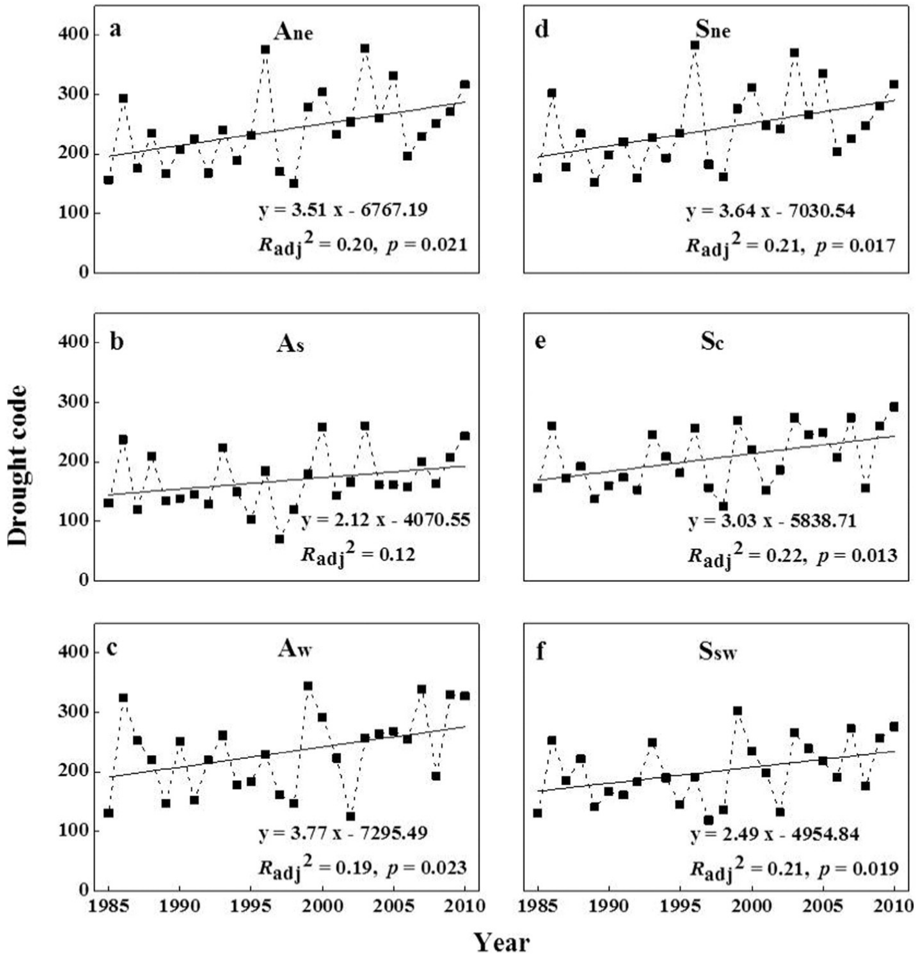


Fig. 4. Patterns of drought code from 1985 to 2010 in the phytogeographic sub-regions for trembling aspen (a for A_{ne}; b for A_s; c for A_w) and white spruce (d for S_{ne}; e for S_c; f for S_{sw}) in our study area. Linear regression results were listed on the figure.

2.5. Climatic data

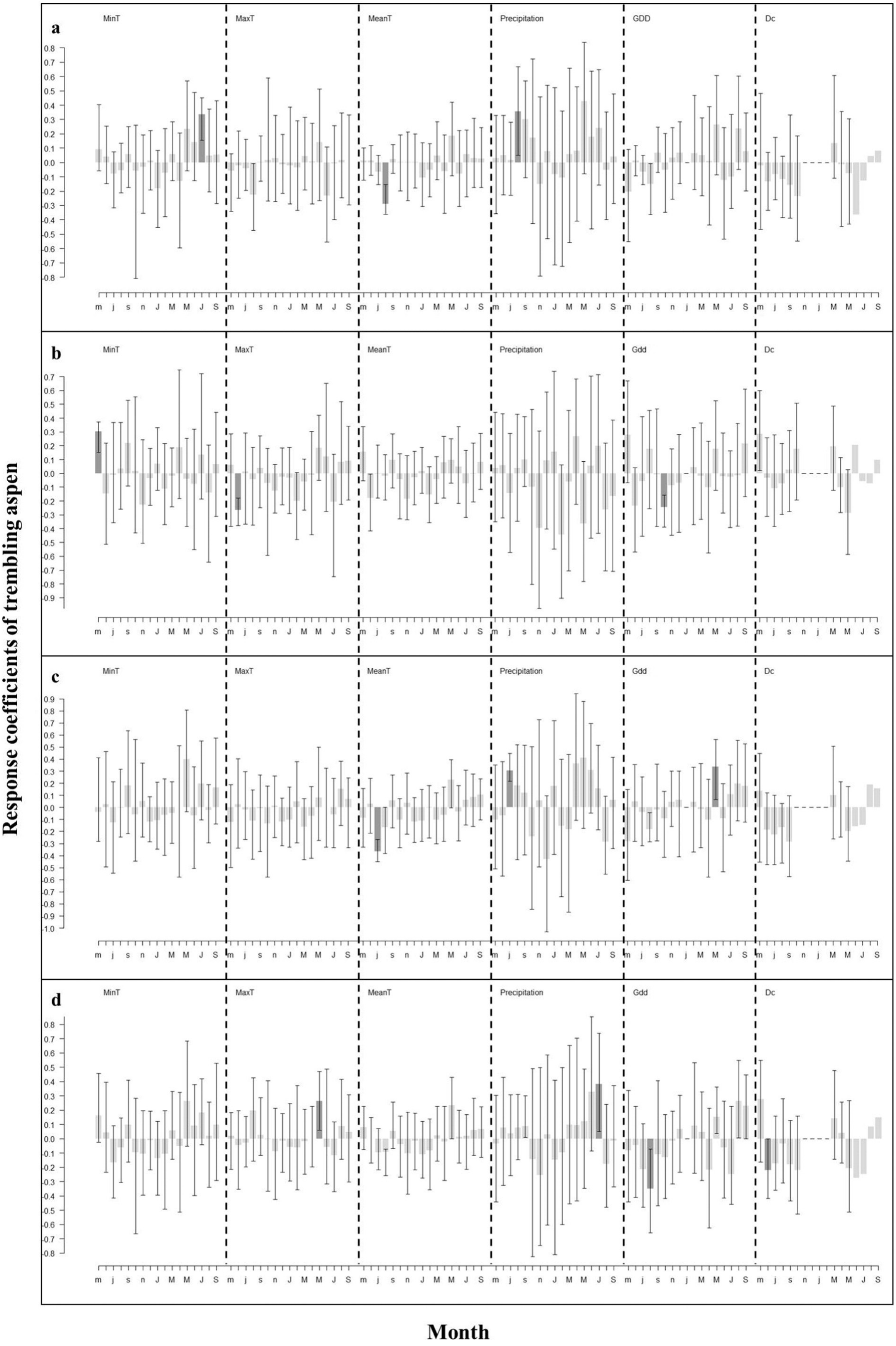
Climatic data used for analysis was generated from ANUSPLIN (version 4.3) (Hutchinson, 2004). We calculated monthly, seasonal, and annual climate variables for each sampling site from 1985 to 2010. Climatic variables included maximum temperature (T_{max}), T, minimum temperature (T_{min}), W, and Gdd (McKenney et al., 2006). Drought code (D), which was used to investigate soil moisture impact on tree growth, was calculated from T_{max} and W according to the method of Girardin and Wotton (2009). Repeated measure ANOVA was used to test the difference in climatic variables (annual T, Gdd, W, and D of each sampling site) from 1985 to 2010 between different sub-regions with year and phytogeographic sub-regions as fixed factors. In order to understand change trends of climate variables in the past several decades, linear regression methods were used to fit annual T, W, Gdd, and D with years from 1985 to 2010 for the entire study area and each phytogeographic sub-region. Annual T_{max}, T_{min}, T, W, Gdd, and D of the entire area or each phytogeographic sub-region were calculated by average of all sampling sites within that area. Statistical analyses mentioned above were all conducted using SPSS 18.0 statistical software.

Table 2
Statistical results of response function analysis between tree-ring width indices (G) and climate variables for trembling aspen (phytogeographic sub-regions A_{ne}, A_s, and A_w) and white spruce (phytogeographic sub-regions S_{ne}, S_c, and S_{sw}). A_{ne}, A_s, and A_w correspondingly referred to northeast, south, and west parts of the study area; while S_{ne}, S_c, and S_{sw} represented northeast, central, and southwest parts of the study area, respectively.

Phytogeographic sub-regions	Climate variables	R^2_{adj}
A_{ne}	Current July minimum temperature (T_{min7}) Previous August mean temperature (T_{8p}) Previous August total precipitation (W_{8p})	0.51
A_s	Previous May minimum temperature (T_{min5p}) Previous June maximum temperature (T_{max6p}) Previous October growing degree-days (Gdd_{10p})	0.33
A_w	Previous July mean temperature (T_{7p}) Previous July total precipitation (W_{7p}) Current May growing degree-days (Gdd_5)	0.46
S_{ne}	Previous August mean temperature (T_{8p}) Previous August total precipitation (W_{8p}) Current June drought code (D_6)	0.56
S_c	Previous May minimum temperature (T_{min5p}) Current April total precipitation (W_4) December growing degree-days (Gdd_{12})	0.45
S_{sw}	Current April total precipitation (W_4) Current July drought code (D_7)	0.49

2.6. Climate–growth relationships

Climate data sets for each phytogeographic sub-region, natural sub-region and the entire study area were used for analysis. Tree growth during the current year could be also affected by carbohydrates reserved in the previous year (Huang et al., 2010), suggesting that tree growth in current year can be affected by climatic condition in the previous growing season. In this way, all correlations were calculated on a 17-month basis from May of the previous year to September of the current year. To quantify climate–growth relationships between tree-ring width indices and monthly climate data, response coefficients and


Response coefficients of trembling aspen
Month
a
b
c
d
MinT
MaxT
MeanT
Precipitation
GDD
Gdd
Dc
m j s n J M M J S
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
-0.1
-0.2
-0.3
-0.4
-0.5
-0.6
-0.7
-0.8
-0.9
-1.0
0.9

climate-related variance explained (R^2_{adj}) were calculated using response function analysis with “bootRes” package in R software (Zang and Biondi, 2012).

3. Results

3.1. Spatial phytogeographic sub-region classification and tree growth

For both species, cluster analysis indicated that all sampled chronologies could be clustered into three groups, each with different radial tree growth behavior (Figs. 1 & 2). As a result, we divided our study area into three phytogeographic sub-regions for trembling aspen and white spruce, respectively. For trembling aspen, three phytogeographic sub-regions were northeast (A_{ne}), south (A_s), and west (A_w) sub-region. For white spruce, three phytogeographic sub-regions were northeast (S_{ne}), central (S_c), and southwest (S_{sw}) sub-region. Annual climate variables of all phytogeographic sub-regions were listed in Table 1.

Repeated measure ANOVA analysis showed that annual *T*, *Gdd*, *W*, and *D* (from 1985 to 2010) were all significantly different between different phytogeographic sub-regions ($P < 0.05$), but only *W* and *D* were significantly affected by time. Based on average values of all sampling sites, linear regression results showed that drought stress significantly increased from 1985 to 2010 for the entire study area ($P < 0.05$, Fig. 3). Slopes of *D* linear regression were 3.64, 3.03, and 2.49 for S_{ne}, S_c, and S_{sw}, respectively, which showed a decreasing trend from northeast to southwest of study area (Fig. 4). Changes of *T* and *Gdd* were insignificant for the entire study area or each sub-region from 1985 to 2010. A_{ne} and S_{ne} were similar for trembling aspen and white spruce, which both occupied portions of dry mixedwood and the large central mixedwood in the northern and eastern parts. Coverage between A_s and S_c was different, in which A_s only contained the southern end of the lower foothills, while S_c also included some parts of the lower boreal highlands in the middle of study area. A_w and S_{sw} both located in the west; however, S_{sw} not only occupied western potions of the dry mixedwood, but also included some portions of the lower foothills. Phytogeographic sub-regions were related to spatial climate differences across our study area, with the northeast section being colder and drier, and the southwestern part of the sampled area being warmer and wetter. For trembling aspen, *T* and *W* of A_{ne} and A_w were lower than those of A_s; whereas *D* of A_{ne} and A_w were higher than that of A_s. *T* and *W* of S_{ne} were also lower than those of S_c and S_{sw}, but *D* of S_{ne} was the highest. Annual climatic variables between S_c and S_{sw} were similar.

3.2. Tree growth response to climatic variables

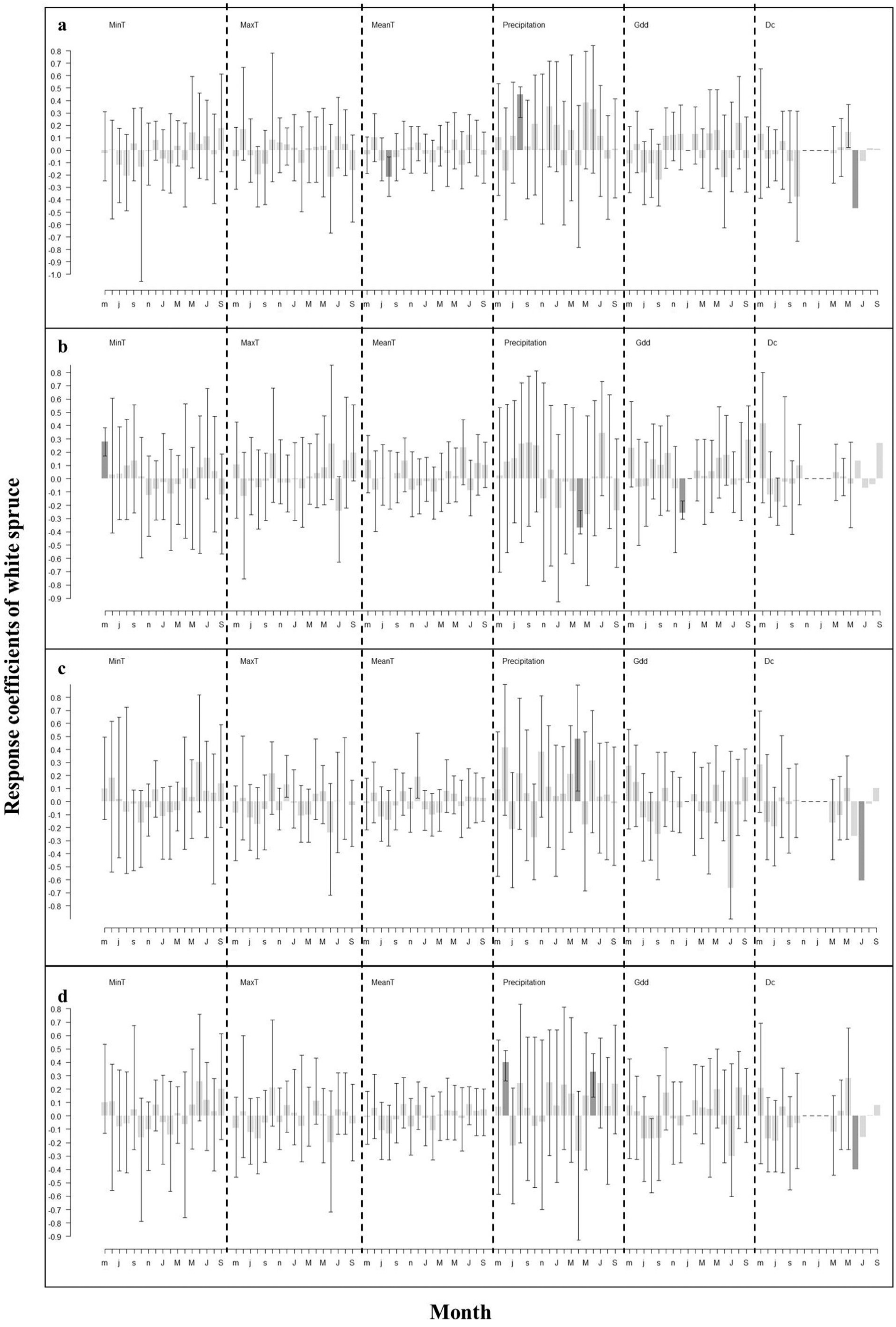
Relationships between tree-ring width indices and climatic variables showed spatial differences among three phytogeographic sub-regions, regardless of tree species (Table 2). According to response function analysis, growth of trembling aspen in A_{ne} was significantly affected by *T* and *W* of the previous August, and $T_{\min}$ of July in the current year (Fig. 5). In A_s, climatic variable of previous year was the most important factors controlling growth. Effects of *W* on trembling aspen growth in A_s was less important compared to other sub-regions, while annual *W* of A_s was the highest among all phytogeographic sub-regions. Growth of white spruce in S_{ne} were significantly affected by June *D* in the current year and *T* and *W* of August in the previous year; while in S_{sw}, *D* of July in the current year was the most significant climatic variable (Fig. 6). In S_c, *Gdd* of December and current April *W* were the most important climatic variable affecting white spruce growth. For trembling aspen, previous year variables were more important compared to current year variables in response function analysis results, especially in A_s, which indicated that trembling aspen growth was affected by climate of previous year. For white spruce, moisture-related variables (*D* and *W*) showed more notable effects on growth in S_{ne} and S_{sw}; while growth conditions in S_c was similar to trembling aspen. Results showed that climate-related variance explained (R^2_{adj}) based on natural sub-region classification were commonly lower than those explained based on phytogeographic sub-region classification, except for the central mixedwood (Tables 2 & 3). For trembling aspen, R^2_{adj} were 0.51, 0.33, and 0.46 for A_{ne}, A_s, and A_w, respectively. For white spruce, R^2_{adj} were 0.56, 0.45, and 0.49 for S_{ne}, S_c, and S_{sw}, respectively. White spruce R^2_{adj} were generally higher than those of trembling aspen, suggesting that there were more non-climatic factors controlling trembling aspen growth than white spruce.

4. Discussion

Results of response function analysis indicated that the unclassified ecoregion system would cause information loss compared to phytogeographic sub-region. For instance, results from the unclassified system only indicated positive relationship between $T_{\max}$ and growth for trembling aspen; however, negative temperature–growth relationships were common phenomena for trembling aspen in three phytogeographic sub-regions (Fig. 5). It might conclude positive feedback of temperature on trembling aspen growth if unclassified ecoregion system was involved in tree growth studies, however this conclusion was irresponsible. The R^2_{adj} between tree growth and climatic variables based on natural sub-regions were lower than that based on phytogeographic sub-regions, except for the central mixedwood. Exception on the central mixedwood was due to similar coverage among central mixedwood, A_{ne}, and S_{ne}. Since same tree-ring data were used in analysis, lower R^2_{adj} of natural sub-regions suggested that it was less suitable using natural sub-region classification to study spatial tree growth relations with climatic variables. These phenomena suggested that estimate of future forest productivity, based on prediction models that defined uniform tree growth sensitivity to climate changes on global scale, could be less certain.

Significant decrease in *W* and increase in *D* were detected in our study area for the past several decades (Fig. 3), suggesting that drought stress would be a more and more important factor influencing tree growth in different phytogeographic sub-regions. Recent studies had indicated that forest mortality increased and growth declined significantly in some western Canadian boreal forests due to drought stress (Peng et al., 2011; Worrall et al., 2013; Chang et al., 2014), while the summer water deficit was considered to be the dominant factor controlling tree growth in western Canadian boreal forest (Hogg et al., 2008; Michaelian et al., 2011). Our results were consistent to previous studies, while positive relationships between tree growth and *W* were common for all phytogeographic sub-regions, suggesting that water demand of tree was positive feedback on growth. In our study, analysis showed that warming trend was not significant for the past several decades, which indicated that increased drought stress was caused by decline in *W*. Result showed that slopes of *D* increased rates were different between three phytogeographic sub-regions (Fig. 4); therefore, influential degrees of drought stress on tree growth were different. For instance, growths of white spruce in northeastern (higher latitude) and southwestern (higher altitude) parts of Alberta were more intensely affected by drought stress, suggesting that effects of drought stress on white spruce growth might be elevated in higher latitude or higher altitude regions.

Fig. 5. Response coefficients of trembling aspen obtained by relating tree-ring width indices and monthly climatic data, such as minimum temperature (MinT), maximum temperature (MaxT), mean temperature (MeanT), precipitation, growing degree days (Gdd), and drought code (Dc), for a) A_{ne}, b) A_s, c) A_w, and d) the whole Alberta. Indices of trembling aspen are related to monthly climatic data from the previous year (months abbreviated by lowercase letters, start from May) up to the year of tree-ring formation (months abbreviated by uppercase letters, end in September). The bars with darker color indicate significant ($P < 0.05$) response coefficients.


a
b
c
d
MinT
MaxT
MeanT
Precipitation
Gdd
Dc
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
-0.1
-0.2
-0.3
-0.4
-0.5
-0.6
-0.7
-0.8
-0.9
-1.0
m j s n J M M J S
Response coefficients of white spruce
Month

Significant temperature effects were found for trembling aspen in northern phytogeographic sub-regions with higher latitudes (A_{ne} and A_w), but all these relationships were negative. This result was conflict with previous study conducted in far north of Europe (higher latitude, >62°N), in which relationship between temperature and tree growth was positive because higher temperature alleviated the cold temperature effect on tree growth (Reich and Oleksyn, 2008). The distinct result between far north of Europe and northern sub-regions in our study area might be associated with different dominate climates between two regions. Our study area was strongly influenced by continental climate; in this way, water supply for tree growth would be less sufficient compared to far north of Europe, and drought stress would be further induced when air temperature increased. In contrast to northern sub-regions, relationship between minimum temperature and trembling aspen growth was positive in southern phytogeographic sub-region with lower latitude (A_s). The divergent growth responses to climate between northern and southern sub-regions in our study were likely a result of physiological processes and biogeographically varying limitations to growth. These phenomena suggested two opposite mechanisms of climate change effects on aspen growth between northern and southern phytogeographic sub-regions. In the north, water supply was limited and higher temperatures increased vapor pressure deficits and further enhanced trembling aspen water demand (Subedi and Sharma, 2013), which further increased drought stress. Meanwhile, higher temperatures promoted trembling aspen respiration and increased consumption of carbohydrates reserved for the next year, which decreased carbon source used for growth (Huang et al., 2010). Whereas in the south, water supply was more sufficient compared to the north, and higher temperatures could not cause serious drought stress but could enhance growth in trembling aspen due to higher photosynthetic rates (Rickebusch et al., 2007). Another tree growth study conducted in eastern Canada (north of 47°N) reported that tree growth could benefit from higher temperatures, because that region was dominated by maritime air masses and water supply was therefore sufficient during the growing season (Huang et al., 2010). Previous study reported that the dominant contributor of tree growth was regional warming in western United States (van Mantgem et al., 2009); while in our study the dominant contributor should be regional drought.

Table 3
Statistical results of response function analysis between tree-ring width indices (G) and climate variables for the entire study area (no classification) and each natural sub-region (central mixedwood, dry mixedwood, lower boreal highlands, and lower foothills) for trembling aspen and white spruce).

Species	Region	Climate variables	R^2_{adj}
Trembling aspen	The entire study area	Current May maximum temperature (T_{max5}) Current July total precipitation (W_7) Previous August growing degree-days (Gdd_{8p}) Previous June drought code (D_{6p})	0.44
	Central mixedwood	Current June drought code (D_6) Previous May growing degree-days (Gdd_{5p}) Previous September growing degree-days (Gdd_{9p})	0.48
	Dry mixedwood	Previous July total precipitation (W_{7p}) Previous August mean temperature (T_{8p})	0.30
	Lower boreal highlands	Current June drought code (D_6) Previous July total precipitation (W_{7p})	0.25
	Lower foothills	Previous May mean temperature (T_{5p}) Previous June mean temperature (T_{6p})	0.28
White spruce	The entire study area	Previous June total precipitation (W_{6p}) Current June total precipitation (W_6) Current June drought code (D_6)	0.34
	Central mixedwood	Current June drought code (D_6) Previous August total precipitation (W_{8p})	0.53
	Dry mixedwood	Current June drought code (D_6) Previous September growing degree-days (Gdd_{9p})	0.29
	Lower boreal highlands	Previous June maximum temperature (T_{max6p}) Previous May total precipitation (W_{5p})	0.21
	Lower foothills	Current September maximum temperature (T_{max9}) Current June drought code (D_6) Previous August total precipitation (W_{8p})	0.35

Tree species-specific climate response might further influence forest composition and successional process in the future. Trembling aspen was a shade-intolerant species, while white spruce was a shade-tolerant species (Cortini et al., 2012). These two species formed the major species composition in western Canadian boreal mixedwood forests. It had been reported that adaptive capacity of shade-tolerant species to climate changes should be stronger than that of shade-intolerant species (Niinemets and Valladares, 2006). Previous studies had reported that the exceptional drought of 2001–2002 was still the major factor of sudden aspen decline 4 years later (2005–2006) in North American forest (Worrall et al., 2010; Michaelian et al., 2011). But our study showed that white spruce, as a shade-tolerant species, was also and even more sensitive to drought stress, which might be due to competition of other tree species on soil water supply (Filipescu and Comeau, 2007). This higher sensitivity on drought suggested that white spruce in this region also suffered serious survival stress as trembling aspen. In contrast to white spruce, trembling aspen growth was more significantly affected by climatic variables of previous years. This result suggested that carbohydrates reserved for the next year was an important influenced factor controlling aspen growth, and previous year damage might cause a persistent effect on aspen growth. Trembling aspen belonged to early-successional species, whereas white spruce belonged to late-successional species (Chen and Popadiouk, 2002). Over the past decade, widespread increase in mortality of trembling aspen had been documented in west-central Canada and the southwestern United States (Ganey and Vojta, 2011; Michaelian et al., 2011), but white spruce growth would also be significantly depressed by drought stress according to our results. In this way, forest successional process and regional forest species composition might be continuously affected by regional drought under climate changes, and more attention should be payed on drought issue in western Canadian boreal forest. Climate was one of the main drivers shaping forest composition, structure and community in terrestrial forest ecosystems. Tree growth responses to climate were spatially dependent due to spatial heterogeneity such as high variability in topography, site conditions, and species interactions (e.g. competition). Within the context of global climate change, it was important to better understand spatially dependent growth responses of trees to climate, and to further quantify the potential relations between tree growth and climate in sub-regions over broad spatial scale, which might help to better assess the effects of climate change on forest ecosystems.

5. Conclusions

Based on tree-ring data analysis in mixedwood boreal forest of Alberta, western Canada, we found that sub-regions classification helped improve understanding tree growth response to climate, and regional

Fig. 6. Response coefficients of white spruce obtained by relating tree-ring width indices and monthly climatic data, such as minimum temperature (MinT), maximum temperature (MaxT), mean temperature (MeanT), precipitation, growing degree days (Gdd), and drought code (Dc), for a) S_{ne}, b) S_c, c) S_{sw}, and d) the whole Alberta. Indices of white spruce are related to monthly climatic data from the previous year (months abbreviated by lowercase letters, start from May) up to the year of tree-ring formation (months abbreviated by uppercase letters, end in September). The bars with darker color indicate significant ($P < 0.05$) response coefficients.

classification was tree species dependent. Drought stress showed different changed rates in different phytogeographic sub-regions, which significantly caused spatial tree growth responses to climatic changes. We revealed that white spruce, a late-successional dominant species in western Canadian boreal mixedwood forest, suffered more strongly with increasingly drought stress under climate changes, which would in turn alter forest composition in the future. For further research, spatial dependent response of tree growth to climatic variables for different tree species should be considered in estimates of future forest productivity, and prediction models hypothesized uniform sensitivity to global scale climate changes could be inadequate. This finding might contribute to an improved prediction of forest ecosystem for sustainable forest development and better forest management.

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