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Original article

Searching for thresholds in climate–radial growth relationships of Engelmann spruce and subalpine fir, Jasper National Park, Alberta, Canada

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ABSTRACT

The relationship between monthly climate predictors and radial growth of Engelmann spruce (*Picea engelmanni* Parry) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt) were explored using both a standard dendroclimatological approach and a multiple adaptive regressions splines (MARS) framework. Consistent with previous research, the radial growth of fir and spruce was related to temperature variables over the time period of the instrumental record. We identify important temporal instability in the statistical relationships between climate variables and the radial growth of both subalpine fir and Engelmann spruce. Using a 30-year running window, only four of the climate variables related to the radial growth of either spruce or fir did not show a switch in the sign of the correlation. A multiple adaptive regressions spline method was then used to gain insight into thresholds that may relate to radial growth–climate instabilities. Using MARS, we were able to identify knots and non-monotonic relationships between radial growth and climate predictors that may be indicators of ecological thresholds. This combination of dendroclimatic methods provides valuable insight into the complex nonlinear responses that both subalpine fir and Engelmann spruce have been growing under in the past centuries.

Introduction

Recent dendroclimatic studies have identified reductions in tree sensitivity and/or changes in tree responses to target climate variables as climate varies over time (Jacoby and D'Arrigo, 1995; Briffa et al., 1998a,b; Wilson and Luckman, 2003; Wilson and Elling, 2004; D'Arrigo et al., 2008; Trindade et al., 2010). The decoupling between radial growth and climate, or what is also called the 'divergence problem', has been attributed to several different causes. Generally, these explanations fall into one of three categories. Divergence has been interpreted as a result of standardization methods used to remove non-climatic variation (Cook and Peters, 1997; Melvin and Briffa, 2008; Briffa and Melvin, 2011), a threshold effect between tree growth and the limiting climatic factor where trees once limited by temperature have become more drought sensitive (Visser and Molenaar, 1988; Jacoby and D'Arrigo, 1995; Barber et al., 2000; Wilmking, 2005), or the development of non-climatic factors (LaMarche et al., 1984; Graumlich, 1991; Fenn et al., 2003; Huang et al., 2007; Brooks and Coulombe, 2009). This decoupling presents a challenge to dendrochronologist's assumptions about uniformitarianism.

Dendroclimatic reconstructions are based upon the principle of limiting factors, the idea that radial growth is conditioned by the most limiting factor (Blackman, 1905; Fritts, 1976), and uniformitarinism, which suggests that natural laws and the processes that control radial growth are constant over time (Longwell, 1965; Fritts, 1976). These tenets have allowed dendroclimatologists to model past climate from radial growth. Typically, this has been accomplished with simple linear regression because of its ease of use and the limited increase in explained variance resulting from most nonlinear applications (Hughes, 2002). However, if thresholds exist in climate–growth relationships more emphasis should likely be placed on nonlinear functions and nonlinear models capable of expressing such non-monotonic relationships.

Multiple adaptive regression splines (MARS) is a flexible form nonparametric regression analysis that automatically models nonlinearities and interactions between predictor variables (Friedman, 1991). The MARS model is composed of a series of basis functions, all which take one of three forms: (1) the intercept, defined as the mean of the response variable; (2) a hinge function of the form max (0, x – constant) or max(0, constant – x); (3) a product of 2 or more hinge functions. Hinge functions are zero for part of the predictor variable range and so can be used to partion data into

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disjunct regions (Friedman, 1991). MARS is thus particularly useful for describing non-monotonic relationships that may indicate a threshold reaction in the response of tree-radial growth to climate variables.

The purpose of this paper is to explore statistical techniques for explaining the complex climate–growth relationships of two subalpine conifers, Engelmann spruce (*Picea engelmanni* Parry) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt). Specifically, we seek to identify potential thresholds between radial growth and climate predictors by examining two single-site chronologies. Our objectives were to understand:

1. To what extent standard dendroclimatological methods (bootstrapped correlation analysis and moving correlation analysis) could be used to identify any instability in the radial growth–climate relationships that may be indicative of a climatic threshold.
2. To what degree a multiple adaptive regressions splines (MARS) framework, could be used to describe any threshold reactions in the response of tree-radial growth to climate variables.
3. To compare relationships between climate predictors and radial growth response variables, derived from MARS and standard linear bootstrapped correlation analysis.

Materials and methods

Study area

The study area is located within the southern Canadian Rockies in Jasper National Park (JNP), Alberta. Climate of the region is strongly shaped by the complex topography of the mountains. Mean monthly temperatures (1970–2000) at the Jasper town site, range from 15 °C in July to −9.4 °C in January. Precipitation peaks in the summer and averages about 399 mm per year (Meteorological Service of Canada, 2010).

The tree community in JNP grades from full size lodgepole pine (*Pinus contorta* var. latifolia Engelm.) and Douglas-fir (*Pseudotsuga menziesii* var. glauca (Beissn.) Franco) at low elevations, to a heterogeneous forest of Engelmann spruce and subalpine fir until near treeline. At the forest limit, Engelmann spruce is typically no longer found and only subalpine fir is present at the highest elevations. The radial growth of the spruce and fir within the southern Canadian Rockies is broadly understood to vary as a function of summer growing season temperatures (Wilson and Luckman, 2003; Luckman and Wilson, 2005).

Both Engelmann spruce and subalpine fir were sampled just below treeline near the Mt. Edith Cavell meadows. In August of 2006, sampling was conducted in the continuous forest below the meadows at 52 41.221′N, 118 03.086′W. The elevation at the site was 2014 ± 30 m asl.

Data collection and processing

Monthly temperature and precipitation data were obtained from the nearest meteorological station located in Jasper, AB for the complete period of record (1916–2006; Climate Station ID 3053519 combined with Climate Station ID 3053520; Meteorological Service of Canada, 2010). These data were acquired from the Adjusted Homogenized Canada Climate Data website (Environment Canada, 2010). Missing data were replaced with long-term monthly average values.

Tree ring chronologies were established using standard dendrochronology techniques (Stokes and Smiley, 1968). Two cores were taken at ca. 1.3 m height from each tree using a 5.1 mm increment borer. Cores were taken at 180° to one another on a cross slope position to acquire samples that were used to derive the average radial growth of each tree species. To ensure adequate replication, twenty trees were sampled for both subalpine fir and Engelmann spruce from the site.

All cores were air dried, and glued into slotted mounting boards. The cores were then sanded to a 600-grit polish to allow for the visualization of annual rings (Stokes and Smiley, 1968). Ring widths were measured using WinDendro computer software and a high-resolution flatbed scanner to allow for the extraction of the growth trends (Guay et al., 1992). Ring-width patterns for each species were crossdated visually and then statistically using the computer program COFECHA (Holmes, 1983). COFECHA correlations were determined by comparing segments of a tree-ring series to the COFECHA master chronology using 50-year segments lagged successively by 25 years at a one-tailed 99% confidence level (Grissino-Mayer, 2002). Trees that exhibited growth patterns deemed anomalous to the group signal were removed from the data set.

All possible steps to reduce the potential bias of standardization effects introducing artificial divergence were taken in the construction of our master tree-ring chronologies. Raw ring-widths were first transformed using an adaptive power transformation to stabilize the variance of each ring-width series through time (Cook and Peters, 1997). To remove age related and localized disturbance related trends, raw ring-width series were then detrended using a cubic smoothing spline (Cook and Peters, 1981) that preserved 50% of the amplitude over a wavelength of 67% of the series length in R (R Development Core Team, 2010) using the package dplR (Bunn, 2008). Index values for each series were then calculated by subtracting the spline predicted value from the transformed ring-widths (Cook and Peters, 1997). This method has shown to account for the inflation of end values that can arise when using standard ratio detrending (Cook and Peters, 1997). An autoregressive model was then used to remove autocorrelation present in each tree ring chronology, available from the dplR package (Bunn, 2008). Chronologies were then calculated using a robust estimate of the mean to account for outliers (Cook and Kairiūkštis, 1990). The site chronology variance was then temporally stabilized using techniques outlined in Osborn et al. (1997) to ensure that no variance was introduced due to changes in interseries correlation or sample depth. Finally, persistent chronology autocorrelation was removed using a low order autoregressive model in program R (R Development Core Team, 2010).

Expressed population signal (EPS) values were then calculated for each chronology. EPS is a statistic that expresses the degree to which the chronology signal is given when series are averaged. EPS value greater than 0.85 indicate enough agreement between the tree-ring series and the chronology signal to allow for dendroclimatological analysis (Wigley et al., 1984). For each chronology we calculated the exact year at which the EPS value dropped below 0.85 using in R using package dplR (Bunn, 2008; R Development Core Team, 2010)

Linear correlation climate analysis

Tree-ring chronologies were compared with both the monthly precipitation and temperature time series. Monthly climate data from the previous-year June through to September of the current year of growth were used to represent the climate conditions that affect the growing season (Cook and Kairiūkštis, 1990). Bootstrapped correlation coefficients were calculated between each monthly climate predictor and each tree ring index in R (R Development Core Team, 2010) using the package bootRes (Zang, 2009). Correlation analysis is more easily reproduced and tends to

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Table 1
Average tree ring series statistics for each species.

Species	Time span	Mean RW	Sens-1[a]	Ar-1[b]	Interseries correlation[c]	EPS[d]
Fir	1745–2006	0.53	0.21	0.56	**0.42**	1907
Spruce	1640–2006	0.59	0.21	0.68	**0.41**	1907

[a] Sensitivity coefficient following equation 1 in Biondi and Qeadan (2008).
[b] The first order coefficient from an autoregressive model fit to the tree ring series.
[c] Mean average correlation between all series and the master chronology determined using 50-year blocks, significant correlations are shown in bold.
[d] The year each chronology exhibited a 0.85 expressed population signal statistic following (Wigley et al., 1984).

be more stable than response function analysis, another common dendroclimatic technique (Blasing et al., 1984). The stationarity of the linear relationships between radial growth and climate were then analyzed using moving correlation analysis (Biondi, 1997; Wilson and Elling, 2004). Correlation coefficients between radial growth and climate were calculated using a 30-year running correlation implementing a 1-year lag in R (R Development Core Team, 2010).

MARS climate analysis

Radial growth–climate relationships were also examined by modeling radial growth as a function of each of the monthly climate variables (previous-year January through to current-year September) using a MARS framework in R (R Development Core Team, 2010) using the package earth (Milborrow, 2009). Models were built by first successfully adding the new basis function, which consists of a term already in the model (e.g. the intercept or a knot) multiplied by a new hinge function, that gives the greatest reduction in the sum of squares residual error. Terms were added to the model until the change in residual error is insignificant. Terms were then stepwise removed from the model to prevent overfitting until the submodel with the highest penalized generalized cross-validation (GCV) score, an approximation of the cross validation score obtained using a leave-one-out strategy, was obtained. The GCV scores were penalized for each additional knot to create the most parsimonious model (Milborrow, 2009).

Results

Tree ring results

The oldest subalpine fir sampled in the continuous forest was found to be 262 years old (Table 1). Using 50-year segments lagged successively by 25 years, the COFECHA correlation derived from the subalpine fir set was found to be statistically significant ($r = 0.42$) at a one tailed 99% confidence level (Table 1). Two cores were deemed anomalous and were removed from the set, thus a total of 38 cores were used to express the overall radial-growth relationship of the subalpine trees at the site (Fig. 1).

The oldest Engelmann spruce sampled was found to be 367 years old (Table 1). Engelmann spruce displayed a significant COFECHA correlation of 0.41 using 50-year segments lagged successively by 25 years (Table 1). Five cores were removed from this set bringing the total number of cores down to 35 (Fig. 1). The mean measurement of Engelmann spruce was found to be slightly wider than subalpine fir (Table 1) and both chronologies exhibited significant autocorrelation in their original data sets (fir = 0.56; spruce = 0.68; Table 1). Under further analysis, significant autocorrelation persisted at greater lags in the spruce chronology where a

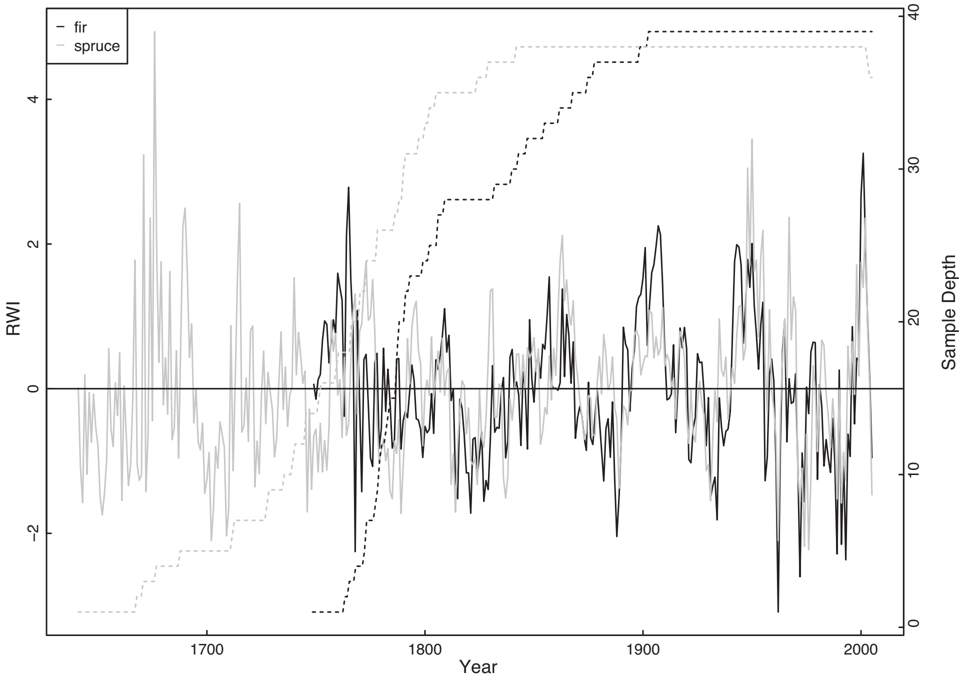

Fig. 1. Tree ring chronologies displayed with sample depth. Gray corresponds with Engelmann spruce radial growth. Black indicates subalpine fir.

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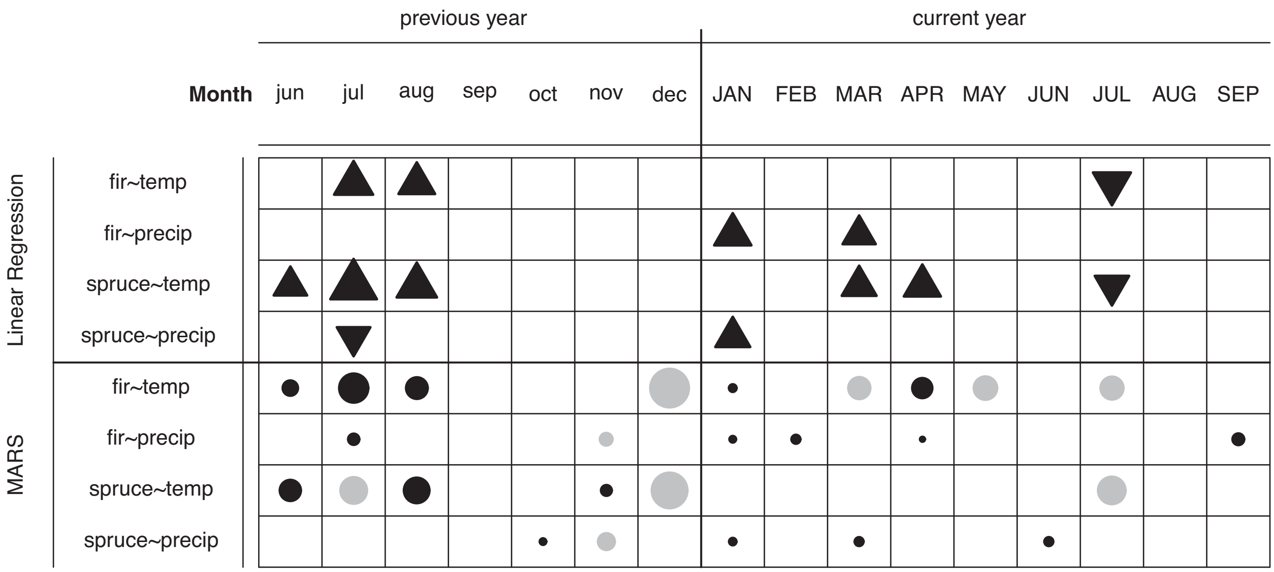


Fig. 2. Coefficient of explanation in each model (generalized *R*-square in MARS models and *R*-square in simple linear model). Black indicates a monotonic relationship and gray indicates a non-monotonic relationship. Volume corresponds to the strength of the relationship. For linear analysis, relationship direction is indicated by triangle direction (pointed up indicates positive correlation and pointed down means a negative relationship).

Table 2
Chronology autoregressive model statistics calculated using a simple autoregressive model fit using a Yule-Walker method in R (R Development Core Team, 2010).

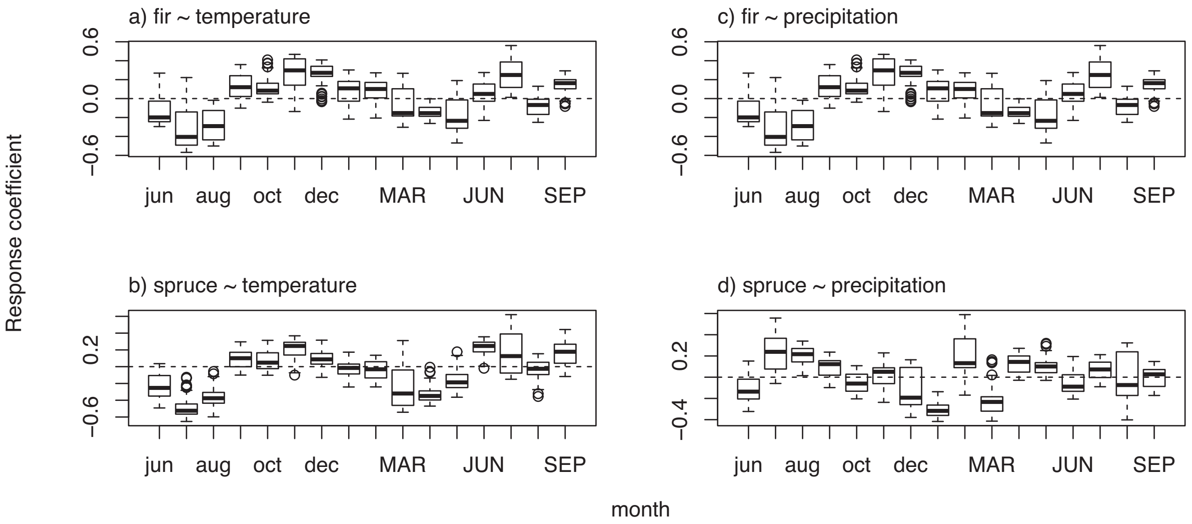
Species	Lagged year coefficient					
	1	2	3	4	5	6
Fir	0.64					
Spruce	−0.31	0.27	0.11	−0.15	0.12	−0.12

6-year lag was still a significant predictor in radial growth, versus only a 1-year lag in subalpine fir (Table 2).

Linear correlation climate analysis

Bootstrapped correlation analysis revealed both chronologies to be significantly related to monthly climate variables (Fig. 2). Although neither of the chronologies were exceptionally well correlated with a monthly climate variable. The highest absolute correlation coefficients obtained for fir and spruce were only $r = -0.33$ (previous July temperature) and $r = -0.47$ (previous July temperature), respectively. Both chronologies exhibited statistically stronger relationships with temperature variables than precipitation relationships. The predominant signal exhibited by both the Engelmann spruce and subalpine fir chronology was a negative relationship with summer temperature (June–August) of the previous year (Fig. 2).

Using moving correlation analysis we found considerable variability in the relationship between climate predictors and tree growth. Most of the climate predictors illustrated both positive and negative relationships with tree growth (Fig. 3). Although previous summer temperature had the strongest relationship with both fir and spruce radial growth over the entire time period, we found over shorter 30-year time periods, previous summer growth was often not a great predictor of radial growth (Fig. 3).


a) fir ~ temperature

c) fir ~ precipitation

b) spruce ~ temperature

d) spruce ~ precipitation

Fig. 3. Boxplots illustrating the variability in response coefficients calculated by comparing each climate predictor and the radial growth response variables over moving 30-year windows.

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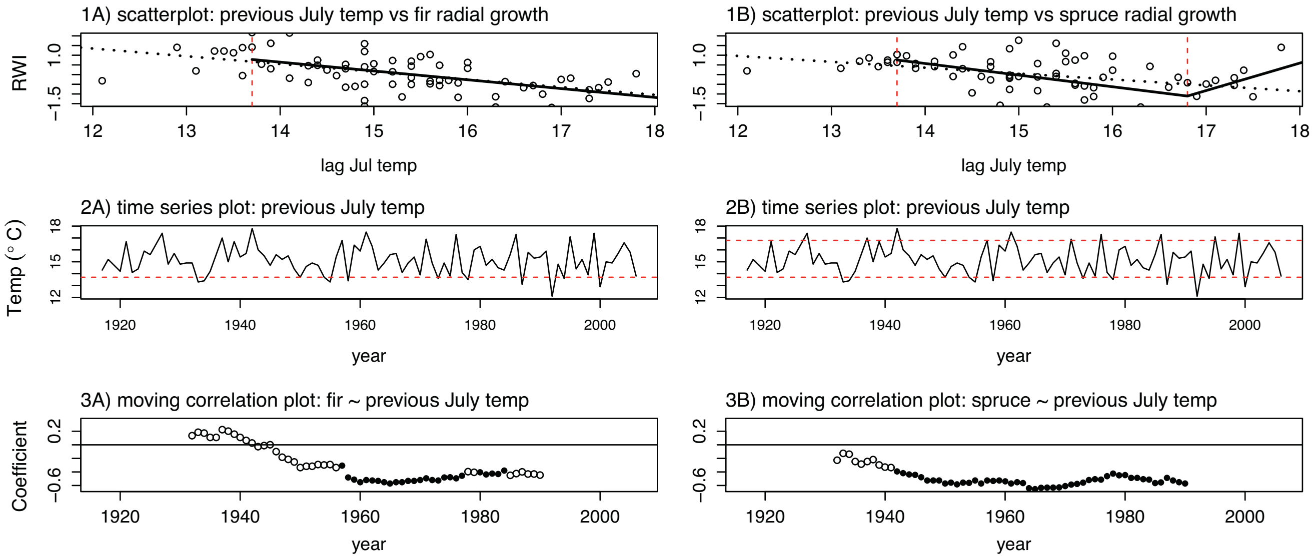

Fig. 4. (Panels 1A and 1B) Scatterplots of the previous July temperature versus radial growth. Regression lines from both MARS and linear regressions are displayed with solid and dashed lines respectively. (Panels 2A and 2B) Time series plots of monthly climate predictors. Horizontal lines indicate knot positions. (Panels 3A and 3B) Plots of moving correlation analysis. Each point indicates the Pearson Product Moment correlation coefficient between tree growth and the climate predictor variable calculated using data from 15 years of data on either side of the point. Filled in points indicated correlations significant at the 95% confidence level; empty points indicate insignificant correlations.

MARS climate analysis

MARS analysis also revealed that both chronologies are significantly related to monthly climate variables (Fig. 2). Again, both chronologies exhibited stronger relationships with temperature than precipitation. Nine of the radial growth–climate relationships were identified as non-monotonic. The predominant radial growth–climate signal identified using a MARS approach was still the relationships with previous summer temperature (June–August). Relationships with summer temperature were predominantly non-monotonic, although the relationship between July temperature and spruce radial growth was non-monotonic. The most explanatory non-monotonic variable related to the radial growth of both subalpine fir and Engelmann spruce was mean December temperature of the previous year. Mean summer temperatures (June–August) of the previous year had the highest monotonic explanatory coefficients for both spruce and fir.

Moving correlation analysis between lagged July temperature and the radial growth of fir highlighted a stronger relationship from the late 1950s to the mid 1970s (Fig. 4-2A). MARS analysis of fir growth with lagged July temperature revealed one knot, suggesting that only values warmer than 13.7 °C were negatively related to tree growth (Fig. 3-1A). In general, values less than the threshold are infrequent and spread throughout the time series (Fig. 3-1B). The first period of insignificant correlation (1930s through the late 1950s) occurs during a period of the instrumental record where temperature values are predominantly over the threshold. A few extremely low values occur in the 1990s, potentially resulting in a loss of significance during this time period (Fig. 3-1B and -1A).

MARS analysis of spruce growth with lagged July temperature revealed two knots. Temperature values between 13.7 °C and 16.8 °C were negatively related to growth and values greater than 16.8 °C were positively related to growth (Fig. 3-3A). Moving correlation analysis between lagged July temperature and the radial growth of Engelmann spruce showed a significant relationship after the 1940s (Fig. 3-3C). Temperature values less than the 13.7 °C threshold are scattered throughout the historical climate record.

Discussion

In general, there was some commonality between the results of the two modeling procedures. Both exhibited that temperature was more important to growth of the two tree species than precipitation, and current and previous growing season temperatures were the key to radial growth. We identify a negative relationship between summer temperatures of the previous summer and the radial growth of both Engelmann spruce and subalpine fir, consistent with work conducted in the Pacific Northwest (Ettl and Peterson, 1995; Peterson et al., 2002). Higher-than-average summer temperatures can cause increased evapotranspiration and water loss, decreased nutrient storage and foliage efficiency, and initiate cone production earlier, all of which decrease cambial activity and reduce radial growth in the following growth year (Rossi et al., 2006; Thibeault-Martel et al., 2008).

Using MARS, we found the relationship between both tree-ring chronologies and previous summer temperatures was strong only in years that were not exceptionally cold (Fig. 3-1A and -1B). Ecologically this suggests that only summers that are warmer than the species-specific threshold can cause enough detrimental effects to decrease cambial activity and reduce radial growth in the following year. However we also identified a threshold in the response of spruce radial growth to previous July temperature, where very warm temperatures positively affected the next year's growth. Warmer temperatures during summer result in earlier needle maturation and increased photosynthesis (Schmidt and Lotan, 1980). In addition, high early summer temperatures may melt lingering snow, thereby increasing the length of the growth season. Exceptionally warm summer temperatures may result in the production of more carbohydrates and other substances that may then be stored for the next year's growing season.

When comparing the results of our classic dendroclimatic analysis with our MARS approach, we found that not all knots could be explained by examining the moving correlation analysis plots. In some cases, such as the relationship between previous-July temperature and the radial growth of spruce (Fig. 3-2A), MARS knots could not easily explain the changes in correlation coefficients

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through time (Fig. 3-2A). In these cases, there is a high likelihood that the two-dimensional relationship breaks down, and instead knots that the MARS relationship finds signifies a series of complex interactions between temperatures and precipitation variables that adds to the complexity of the trees response to the changing climate.

Conclusion

Most previous dendroclimatological studies of subalpine conifers in southern Alberta have relied on simple linear examinations of radial growth–climate relationships (Luckman et al., 1985; Colenutt and Luckman, 1996; Luckman and Wilson, 2005). The linear methods employed here suggest that important temporal instability exists in the relationships of climate variables with the radial growth of both subalpine fir and Engelmann spruce. In more northern locations such as Alaska, where unstable annual growth–climate relationships have exhibited a clear trend with time, researchers have suggested that climatically driven thresholds may exists between climate predictors and radial growth (D'Arrigo et al., 2008).

The MARS nonparametric method we used presented a flexible way of detecting such thresholds between climate predictors and tree growth in our study. What also becomes paramount in interpreting these MARS results is that all relationships identified should be understood ecologically. Knots should be considered to be estimates of potential thresholds in radial growth–climate relationships, and thus the results presented here, should be interpreted with care.

Our combination of dendroclimatic methods provides valuable insight into the complex nonlinear responses that both subalpine fir and Engelmann spruce have shown with climate over the past 60 years. The identification of these types of relationships are increasingly important for both reconstruction of past climate and an increased understanding of the possible responses of ecological systems to the wide array of future changes that might be occurring within the growing environments of the forests of the future.

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References

Barber, V.A., Juday, G.P., Finney, B.P., 2000. Reduced growth of Alaskan white spruce in the twentieth century from temperature-induced drought stress. Nature 405, 668–673.

Biondi, F., 1997. Evolutionary and moving response functions in dendroclimatology. Dendrochronologia 15, 139–150.

Biondi, F., Qeadan, F., 2008. Inequality in paleorecords. Ecology 89, 1056–1067.

Blackman, F.F., 1905. Optima and limiting factors. Annals of Botany XIX.LXXIV, 281–295.

Blasing, T.J., Solomon, A.M., Duvick, D.N., 1984. Response functions revisited. Tree Ring Bulletin (USA) 44, 1–15.

Briffa, K.R., Melvin, T.M., 2011. A closer look at regional curve standardization of tree-ring records: justification of the need, a warning of some pitfalls, and suggested improvements in its application. In: Hughes, M.K., Swetnam, T.W., Diaz, H.F. (Eds.), Dendroclimatology: Progress and Prospects. Spinger Verlag, New York, NY, pp. 133–145.

Briffa, K.R., Schweingruber, F.H., Jones, P.D., Osborn, T.J., Harris, I.C., Shiyatov, S.G., 1998a. Trees tell of past climates: but are they speaking less clearly today? Philosophical Transactions: Biological Sciences, 65.

Briffa, K.R., Schweingruber, F.H., Jones, P.D., Osborn, T.J., Shiyatov, S.G., Vaganov, E.V., 1998b. Reduced sensitivity of recent tree-growth to temperature at high northern latitudes. Nature 391, 678–682.

Brooks, J.R., Coulombe, R., 2009. Physiological responses to fertilization recorded in tree rings: isotopic lessons from a long-term fertilization trial. Ecological Applications 19, 1044–1060.

Bunn, A.G., 2008. A dendrochronology program library in R (dplR). Dendrochronologia 26, 115–124.

Colenutt, M.E., Luckman, B.H., 1996. Dendroclimatic characteristics of alpine larch (*Larix lyallii* Parl.) at treeline sites in western Canada. In: Dean, J.S., Meko, D.M., Swetnam, T.W. (Eds.), Tree Rings, Environment and Humanity. Department of Geosciences, The University of Arizona, Tucson, pp. 143–154 (Radiocarbon Spec. Issue).

Cook, E.R., Peters, K., 1981. The smoothing spline: a new approach to standardizing forest interior tree ring width series for dendroclimatic studies. Tree Ring Bulletin 41, 45–54.

Cook, E.R., Peters, K., 1997. Calculating unbiased tree ring indices for the study of climatic and environmental change. The Holocene 7, 361–370.

Cook, E., Kairiūkštis, L., 1990. Methods of Dendrochronology. Springer, Boston, MA.

D'Arrigo, R., Wilson, R., Liepert, B., Cherubini, P., 2008. On the "Divergence Problem" in Northern Forests: a review of the tree ring evidence and possible causes. Global and Planetary Change 60, 289–305.

Environment Canada, 2010. Adjusted and Homogenized Canadian Climate Data.

Ettl, G.J., Peterson, D.L., 1995. Extreme climate and variation in tree growth: individualistic response in subalpine fir (*Abies lasiocarpa*). Global Change Biology 1, 231–241.

Fenn, M.E., Baron, J.S., Allen, E.B., Rueth, H.M., Nydick, K.R., Geiser, L., Bowman, W.D., Sickman, J.O., Meixner, T., Johnson, D.W., 2003. Others. Ecological effects of nitrogen deposition in the western United States. BioScience 53, 404–420.

Friedman, J.H., 1991. Multivariate adaptive regression splines. The Annals of Statistics 19, 1–67.

Fritts, H.C., 1976. Tree Rings and Climate. Academic Press, NY.

Graumlich, L.J., 1991. Subalpine tree growth, climate, and increasing CO_2: an assessment of recent growth trends. Ecology 72, 1–11.

Grissino-Mayer, H.D., 2002. Research report evaluating crossdating accuracy: a manual and tutorial for the computer program COFECHA. Tree ring Research 57, 205–221.

Guay, R., Gagnon, R., Morin, H., 1992. A new automatic and interactive tree ring measurement system based on a line scan camera. The Forestry Chronicle 38, 138–141.

Holmes, R.L., 1983. Computer-assisted quality control in tree ring dating and measurement. Tree Ring Bulletin 43, 69–78.

Huang, J.G., Bergeron, Y., Denneler, B., Berninger, F., Tardif, J., 2007. Response of forest trees to increased atmospheric CO_2. Critical Reviews in Plant Sciences 26, 265–283.

Hughes, M.K., 2002. Dendrochronology in climatology – the state of the art. Dendrochronologia 20, 95–116.

Jacoby, G.C., D'Arrigo, R.D., 1995. Tree ring width and density evidence of climatic and potential forest change in Alaska. Global Biogeochemical Cycles 9, 227–234.

LaMarche, V.C., Graybill, D.A., Fritts, H.C., Rose, M.R., 1984. Increasing atmospheric carbon dioxide: tree ring evidence for growth enhancement in natural vegetation. Science 225, 1019.

Longwell, C.R., 1965. Is uniformitarianism necessary? A discussion. American Journal of Science 263, 918–919.

Luckman, B.H., Hamilton, J.P., Jozsa, L.A., Gray, J., 1985. Proxy climatic data from tree rings at Lake Louise Alberta: a preliminary report. Géographie Physique et Quaternaire 39, 127–140.

Luckman, B.H., Wilson, R.J.S., 2005. Summer temperatures in the Canadian Rockies during the last millennium: a revised record. Climate Dynamics 24, 131–144.

Melvin, T.M., Briffa, K.R., 2008. A signal-free approach to dendroclimatic standardisation. Dendrochronologia 26, 71–86.

Meteorological Service of Canada, E.C., 2010. Canadian Climate.

Milborrow, S. Derived from mda: mars by Hastie, T., Tibshirani, R., 2009. Earth: multivariate adaptive regression spline models. R package version 3.2-3. http://CRAN.R-project.org/package=earth

Osborn, T.J., Briffa, K.R., Jones, P.D., 1997. Adjusting variance for sample-size in tree ring chronologies and other regional-mean time-series. Dendrochronologia 15, 89–99.

Peterson, D.W., Peterson, D.L., Ettl, G.W., 2002. Growth responses of subalpine fir to climatic variability in the Pacific Northwest. Canadian Journal of Forest Research 32, 1503–1517.

R Development Core Team, 2010. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Rossi, S., Deslauriers, A., Anfodillo, T., Morin, H., Saracino, A., Motta, R., Borghetti, M., 2006. Conifers in cold environments synchronize maximum growth rate of tree-ring formation with day length. New Phytologist 170, 301–310, http://dx.doi.org/10.1111/j.1469-8137.2006.01660.x.

Schmidt, W.C., Lotan, J.E., 1980. Phenology of common forest flora of the Northern Rockies – 1928 to 1937. U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experimentation Station, pp. 1–20.

Stokes, M.A., Smiley, T.L., 1968. An Introduction to Tree Ring Dating. University of Chicago Press, Chicago, IL.

Thibeault-Martel, M., Krause, C., Morin, H., Rossi, S., 2008. Cambial activity and intra-annual xylem formation in roots and stems of *Abies balsamea* and *Picea mariana*. Annals of Botany 102, 667–674.

Trindade, M., Bell, T., Laroque, C., 2010. Changing climatic sensitivities of two spruce species across a moisture gradient in Northeastern Canada. Dendrochronologia 29, 25–30.

Visser, H., Molenaar, J., 1988. Kalman filter analysis in dendroclimatology. Biometrics 44, 929–940.

Wigley, T.M.L., Briffa, K.R., Jones, P.D., 1984. On the average value of correlated time series, with applications in dendroclimatology and hydrometeorology. Journal of Applied Meteorology. 23, 201–213.

Wilmking, M., 2005. Increased temperature sensitivity and divergent growth trends in circumpolar boreal forests. Geophysical Research Letters, 32.

Wilson, R.J.S., Luckman, B.H., 2003. Dendroclimatic reconstruction of maximum summer temperatures from upper treeline sites in Interior British Columbia, Canada. The Holocene 13, 851–861.

Wilson, R., Elling, W., 2004. Temporal instability in tree-growth/climate response in the Lower Bavarian Forest region: implications for dendroclimatic reconstruction. Trees – Structure and Function 18, 19–28.

Zang, C., 2009. bootRes: Bootstrapped Response and Correlation Functions.

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