

Climate and annual ring growth of black spruce in some Alberta peatlands

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The long-term relationship between climate and tree-ring growth in black spruce (*Picea mariana* (Mill.) B.S.P.) was determined in two peatland sites near Slave Lake, Alberta. At each site, 15 dominant–codominant black spruce were sampled for tree-ring growth at 30 cm height. The tree-ring indices for each site were related to precipitation and temperature data from Slave Lake. It was found that (i) tree-ring indices were positively correlated with June–August precipitation of the current year and of the 1st and 2nd years prior to the current year; (ii) June–August maximum temperatures of the current year and of the 1st and 2nd years prior to the current year were negatively correlated with tree-ring indices; (iii) tree-ring indices had a positive linear correlation with the June–August minimum temperature of the current year and polynomial correlations with June–August minimum temperatures of the 1st and 2nd years prior to the current year; and (iv) summer precipitation values greater than 325 mm probably had a negative impact upon the tree-ring growth. Maximum and minimum temperatures, however, were intercorrelated with precipitation.

Key words: dendrochronology, climate, tree rings, peatlands, mire.

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La relation à long terme entre le climat et la croissance des anneaux annuels chez l'épinette noire (*Picea mariana* (Mill.) B.S.P.) fut déterminée à deux stations d'une tourbière près du lac des Esclaves, en Alberta. A chaque station, 15 épinettes noires dominantes–codominantes furent échantillonnées à 30 cm de hauteur en vue d'observer la croissance des anneaux annuels. Les indices de croissance des anneaux à chaque station furent reliés aux données de précipitation et de température. L'on a trouvé que (i) les indices corrélés positivement à la précipitation de juin–août de l'année en cours et de la première et de la deuxième années antérieures à celle en cours; (ii) les températures maximales de juin–août de l'année en cours et de la première et de la deuxième années antérieures à l'année en cours sont corrélées négativement aux indices; (iii) les indices ont une corrélation linéaire positive avec la température minimale de juin–août de l'année en cours, et des corrélations polynomiales avec les températures minimales de juin–août de la première et de la deuxième années antérieures à l'année en cours; et (iv) les valeurs de précipitation estivale plus élevées que 325 mm ont probablement un impact négatif sur la croissance des anneaux annuels. Les températures maximales et minimales, cependant, sont intercorrélées avec la précipitation.

Mots clés : dendrochronologie, climat, anneaux annuels, tourbière, bourbier.

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Introduction

Whereas annual rings in trees in upland areas have often been related to climate (Fritts 1976; Josza et al. 1984), there is little information on the impact of yearly variation in climate on growth of trees in wetland areas. In natural peatlands, tree growth is dependent on the depth of water table (Boggie and Miller 1976; Jasieniuk and Johnson 1982; Mannerkoski 1985). Generally, root growth of peatland trees is restricted by a high water table (Boggie 1972; Boggie and Miller 1976; Lieffers and Rothwell 1987b), but it has been documented that black spruce (*Picea mariana* (Mill.) B.S.P.) and tamarack (*Larix laricina* (Du Roi) K. Koch.) will increase rooting depth and fine-root biomass when the water table is lowered (Lieffers and Rothwell 1987b). Fluctuations in the water table reduce the vertical reach of tree roots (Mannerkoski 1985).

Depth to water table in peatlands is regulated by many factors, but probably precipitation and temperature are the most important in the control of seasonal and yearly variations (Mannerkoski 1985). The water table rises after heavy rain-falls (Dai et al. 1974; Munro 1984). If a high water table depresses the growth of peatland trees, then in years with much greater than average precipitation, growth should also be reduced. Temperature regulates the water table by its influence on evapotranspiration (Mannerkoski 1985), but it also directly affects tree growth (Van Cleve et al. 1983; Tryon and Chapin 1983) and phenology (Lieffers and Rothwell 1987a).

The objectives of the present study are to examine the long-term relationship between the annual ring growth of black spruce and precipitation and air temperature.

Materials and methods

The study sites were located in a large undisturbed treed fen 11 km east–northeast of Slave Lake (55°20'N; 114°34'W), central Alberta. Forests in this area consist of black spruce and scattered tamarack. Understories are dominated by *Ledum groenlandicum* Oeder, *Rubus chamaemorus* L., and *Sphagnum magellanicum* Brid. Two sites, 1 km apart, were selected. Fifteen dominant–codominant black spruce were cut from each site in the spring of 1987, before the initiation of diameter growth. The sample trees were approximately 87 years old. Three cross sections were taken from the bole of each tree at the tree base and at 30 and 130 cm height. The sections were air-dried and belt-sanded. The ring width of all the sections was measured on a computerized tree-ring measuring device (Clyde and Titus 1987). Four radii along the longest and shortest diameters were measured for each section. Ring-width data were plotted against tree age. Cross-dating was conducted to identify false and (or) missing rings (Fritts 1976). Cross-dating was done by comparing graphs of tree-ring width versus age among radii within sections, among sections within trees, and among trees (Fig. 1). Missing and (or) false rings were confirmed by careful examination of the discs. Correction was made for false or missing rings. The ring widths of different radii were averaged to get the mean width of the annual ring for a given year. This was done for the base, 30-cm sections, and 130-cm sections. The mean sensitivity (Ms) of each section was calculated using the following formula (Fritts 1976):

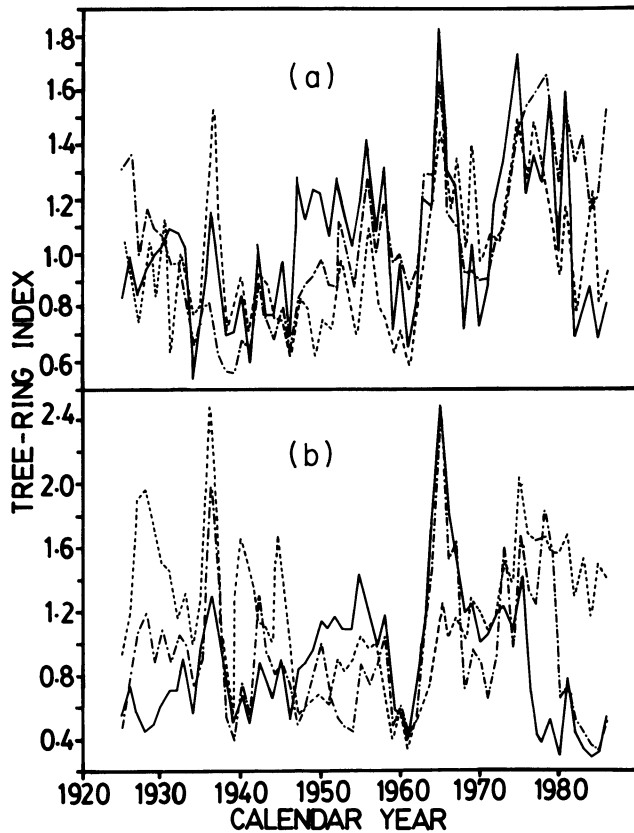


FIG. 1. Cross-dating among trees within sites and between (a) site 1 and (b) site 2. Tree-ring data shown were derived from the means of the four radii from 30 cm height discs of three randomly selected trees from each site.

$$M_s = \frac{1}{n-1} \sum \frac{2(X_{t+1} - X_t)}{X_{t+1} + X_t}$$

where X_{t+1} and X_t are the widths of two neighboring rings and n is the total number of rings. The discs at the 30 cm height had the largest average mean-sensitivity value and therefore were used in further analysis. To remove the effects of tree age on tree-ring width, the tree-ring width data from the 30 cm height were modelled using a negative exponential function, and each observed tree-ring width was divided by the corresponding value generated from the above function to give tree-ring index (Fritts 1976). This is a common standardization procedure (Fritts 1976; Till 1987). Because the climatic data were available only back to 1925, only the tree-ring data for the last 62 years of growth (when ring width decreased with tree age) were used. One-way analysis of variance showed no significant difference among the series of tree-ring indices for the 15 trees from the same site; therefore, the tree-ring indices were averaged year by year to obtain the tree-ring width chronologies of each site (Fritts 1976) for further analysis. The tree-ring width chronologies for the two sites were highly correlated ($r = 0.82$).

Temperature and precipitation data from Slave Lake Airport were obtained from the monthly records (Environment Canada 1925–1986) for the periods 1925–1962 and 1970–1986. Precipitation variables used for the analysis were pregrowing season (previous September to current May) total precipitation and total growing season (June–August) precipitation of the current year and of the 1st and 2nd years prior to the current year. Temperature variables used were growing season (June–August) mean, average maximum, and average minimum temperatures of the current year and of both the 1st and 2nd years prior to the current year.

Linear and polynomial regressions were used to determine the

TABLE 1. Regression analysis of tree-ring index and precipitation in growing season

Time lag (years)	Site 1				Site 2			
	a_0	a_1	r^2	n	a_0	a_1	r^2	n
0	0.70	0.0014	0.18**	53	0.73	0.0013	0.15**	53
1	0.67	0.0015	0.23**	51	0.72	0.0013	0.17**	51
2	0.68	0.0014	0.20**	49	0.79	0.0011	0.10*	49

NOTE: The model used was $I = a_0 + a_1P$, where I is the tree-ring index, P is precipitation, and a_0 and a_1 are coefficients of the linear equation. Time lags of 0, 1, and 2 years represent the current year, the 1st year prior to the current year, and the 2nd year prior to the current year, respectively. *, $p < 0.05$; **, $p < 0.01$.

relationship between the tree-ring index and each of the climatic variables. The intercorrelations among climatic variables were explored by principal component analysis (PCA) using the correlation matrix of the climatic variables (Dixon et al. 1985). Response function analysis, which uses PCA as a primary step (Fritts and Wu 1986), could not be completed because the first principal component did not have a linear relationship with tree-ring index.

Results

Tree-ring growth and precipitation

The tree-ring index was correlated with growing-season precipitation of the current year and growing-season precipitation of both the 1st and 2nd years prior to the current year for both sites (Table 1). Most of the precipitation data were within the range of 71–325 mm, with the exception of years with 410 and 424.7 mm. These points appeared to be outliers and were eliminated from the regression analysis. Within the range of 71–325 mm, tree-ring index increased with precipitation for both sites (Table 1; Fig. 2). For both sites, the precipitation of the previous year was the most strongly correlated with tree-ring growth. The two data points that were eliminated were generally below the regression lines (Fig. 2); this suggests that there was a reduction in growth in years with very high summer precipitation and in the following 2 years.

There was no significant relationship between pregrowing-season precipitation and tree-ring index.

Tree-ring growth and air temperature

For both sites, tree-ring index was not significantly correlated with average growing-season temperature, but was correlated with maximum and minimum temperatures (Figs. 3, 4; Tables 2, 3). The maximum temperatures of the current year and of the 1st and 2nd years prior to the current year were all negatively correlated with tree-ring index (Fig. 3; Table 2). Tree-ring growth decreased linearly as maximum temperature increased. There was little variability in slopes and intercepts of regression lines between the two sites and among the current year and the 1st and 2nd years prior to the current year. The maximum temperatures of the current year and the previous year were more strongly correlated with tree-ring index than that of the 2nd year prior to the current year.

Minimum temperature of the current year was positively correlated with tree-ring index for site 1, but the correlation was not significant for site 2 (Table 3). For both sites the minimum temperatures of the 1st and 2nd years prior to the current year were more strongly correlated with tree-ring index than that of the current year (Table 3).

The relationship between tree-ring index and minimum temperatures of the 1st and 2nd years prior to the current year

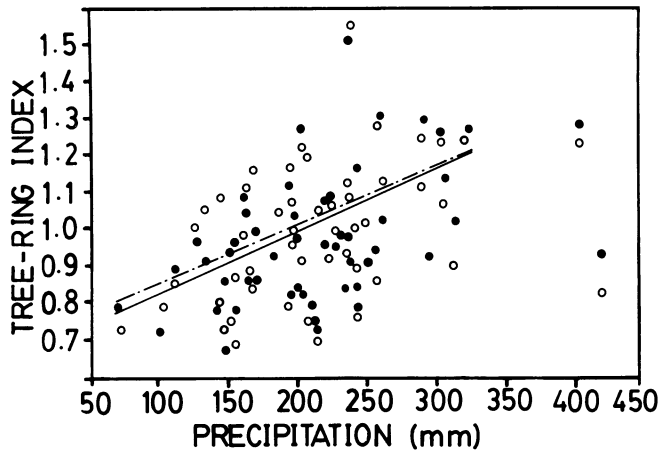


FIG. 2. Tree-ring index of black spruce in relation to June–August precipitation of the previous year for site 1 (●, —) and site 2 (○, - - -).

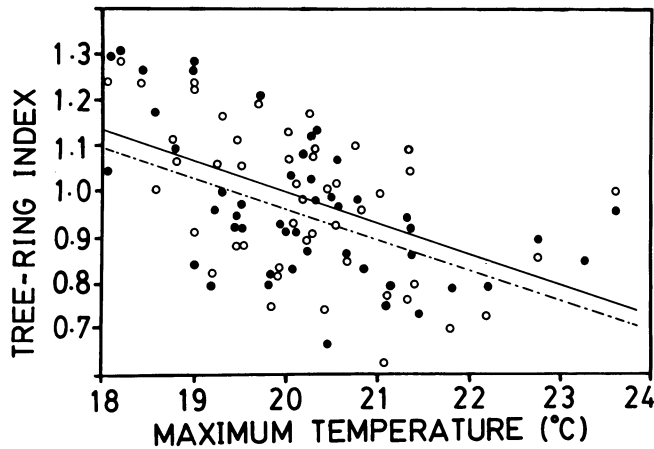


FIG. 3. Tree-ring index of black spruce in relation to mean maximum air temperature (June–August) of the previous year for site 1 (●, —) and site 2 (○, - - -).

were modelled by a quadratic polynomial (Table 3). As the minimum temperature of the 1st year prior to the current year increased, tree-ring index increased at first, then leveled off and began to decline at about 8.5°C for both sites (Fig. 4). The relationship between tree-ring index and minimum temperature of the 2nd year prior to the current year was different for the two sites. For site 1, tree-ring index increased with minimum temperature over the temperature range studied. Tree-ring index for site 2, however, increased at first and began to decline after the temperature exceeded 8.4°C. For both sites, the minimum temperatures of the 1st and 2nd years prior to the current year were more strongly correlated with tree-ring index than that of the current year (Table 3).

Intercorrelations among climatic variables

PCA of the weather data yielded three principal components with eigenvalues greater than one (Table 4). The first principal component indicated that maximum summer temperatures of the current year and the previous year were negatively related to summer precipitation of the corresponding years. The second principal component indicated that minimum temperature and summer precipitation were positively correlated. Cur-

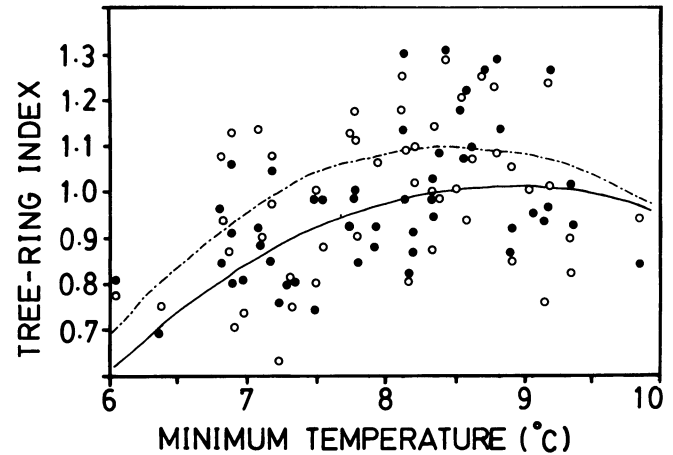


FIG. 4. Tree-ring index of black spruce in relation to mean minimum air temperature (June–August) of the previous year for site 1 (●, —) and site 2 (○, - - -).

TABLE 2. Regression analysis of tree-ring index and maximum temperature

Time lag (years)	Site 1				Site 2			
	a_0	a_1	r^2	n	a_0	a_1	r^2	n
0	2.45	-0.071	0.22**	50	2.64	-0.080	0.25**	50
1	2.65	-0.081	0.29**	50	2.61	-0.077	0.25**	50
2	2.36	-0.067	0.18**	49	2.55	-0.075	0.21**	49

NOTE: The model used was $I = a_0 + a_1 T_m$, where I is tree-ring index and T_m is maximum temperature. See Table 1 for time-lag and coefficient definitions. **, $p < 0.01$.

rent year precipitation and maximum temperature, however, were relatively independent of those of the 2nd year prior to the current year. These interrelationships were used as guides in interpreting the relationships between tree-ring index and individual climatic variables (see Fritts and Wu 1986 for discussion of the importance of intercorrelations among climatic variables).

Discussion

Most studies of tree growth in peatlands indicate that growth is limited by a high water table (Boggie 1972; Boggie and Miller 1976; Jasieniuk and Johnson 1982; Mannerkoski 1985; Lieffers and Rothwell 1987b). Data from the present study, however, suggest that tree growth was greatest in years with relatively high summer precipitation; these presumably are years with a high water table. In virgin peatlands, the vertical reach of tree roots depends more on the usual seasonal maximum than the average water level (Mannerkoski 1985). Therefore, roots are usually restricted to positions above the usual upper limit of water-table fluctuation (Boggie and Miller 1976). Black spruce in natural peatlands have shallow spreading roots (Strong and LaRoi 1983), and roots are usually confined to hummock positions (Lieffers and Rothwell 1987b). Average productivity in peatlands is low for various reasons, including the fact that tree roots occupy a small volume of substrate. In relatively wet years, the water table may stay close to the surface (Munro 1984) near these roots; the roots then have opportunities to absorb water and minerals. In dry years, the water table is much lower and trees may be under water

TABLE 3. Regression analysis of tree-ring index and minimum temperature

Time lag (years)	Site 1					Site 2				
	a_0	a_1	a_2	r^2	n	a_0	a_1	a_2	r^2	n
0	0.41	0.07	—	0.14**	50	0.67	0.04	—	0.05	50
1	-2.77	0.86	-0.049	0.30**	50	-3.45	1.07	-0.063	0.21**	50
2	-0.21	0.20	-0.007	0.25**	49	-2.54	0.84	-0.050	0.14*	49

NOTE: For time lag 0, the model used was $I = a_0 + a_1T_n$, where I is tree-ring index and T_n is minimum temperature. For time lags of 1 and 2 years, the model used was $I = a_0 + a_1T_n + a_2T_n^2$. See Table 1 for time-lag and coefficient definitions; however, note the third coefficient a_2 for the quadratic model. *, $p < 0.05$; **, $p < 0.01$.

TABLE 4. Loadings for principal component analysis of climatic variables

Variable (lag time) ^a	Component 1	Component 2	Component 3
T_m (0)	0.856	-0.020	-0.224
T_n (0)	-0.107	0.845	-0.014
T_m (1)	0.855	-0.044	-0.159
T_n (1)	0.056	0.829	0.360
T_m (2)	0.160	-0.319	-0.701
T_n (2)	-0.387	0.410	0.324
P (0)	-0.483	0.610	-0.193
P (1)	-0.533	0.370	0.148
P (2)	-0.221	-0.107	-0.860
Eigenvalue	3.401	1.486	1.127

NOTE: The climatic variables are those of the growing season (June–August). T_m , maximum temperature; T_n , minimum temperature; P , precipitation.
^aLag time is given in years.

stress; Scholander pressure-bomb readings of black spruce twigs from a peatland during a hot and dry period were as low as -2300 kPa (Q. L. Dang, V. J. Lieffers, R. L. Rothwell, and S. E. Macdonald, unpublished data). It is also interesting, however, that in the 2 years with very high summer precipitation (>400 mm) tree-ring growth was reduced in the current year and for the next 2 years (Fig. 2). We speculate that heavy rainfalls in those years caused root dieback. Thus, the shallow roots of these trees may be relatively ineffective at water uptake in dry years, but are stressed or killed by high water levels in very wet years.

There is little information in the literature to suggest that high air temperature limits the productivity in boreal forest ecosystems. Indeed, the reverse is usually the case (see Van Cleve et al. 1983; Mannerkoski 1985). The fact that tree-ring index decreased with increasing maximum temperature (Fig. 3) is therefore also contradictory. Even though many days would have a higher maximum temperature, a mean maximum temperature of 23°C (Fig. 3) should not have directly limited tree growth. The phenomenon of reduced growth in years with high maximum temperature probably also relates to the shallow root system and water stress under warm conditions. It is also noteworthy that years with higher maximum temperatures usually had lower precipitation (Table 4, component 1).

In contrast to the relationship between tree-growth responses and maximum temperatures, there was generally an increase in tree growth associated with higher minimum temperatures. Low nighttime air temperatures, and presumably cool substrate, may be directly detrimental to growth because of a reduction in biochemical activity and water uptake (Running and Reid 1980; Lopushinsky and Kaufmann 1984). Also,

since low summer precipitation was associated with years of low minimum temperatures (Table 4), it is possible that the significant relationship between minimum temperature and growth is another expression of water stress. The most likely reason for slow growth in years with low minimum temperatures, however, probably relates to summer frosts. Mean minimum temperatures in peatlands ranged from 3.2 to 7.4°C lower than at adjacent upland weather stations, and frost was recorded in all months of the year (Rothwell and Lieffers 1988). Low minimum temperatures (including frost) during summer months have a negative impact upon conifer growth (Cannell and Smith 1984).

The lag effects of climate on tree-ring growth may have been partially caused by the autocorrelation of tree growth itself. The needles of black spruce, for example, are formed in the bud the previous year and remain on the trees for several years. The climate of a given year influences the needle formation and growth and consequently affects photosynthesis and carbon accumulation in following years. Indeed, the preceding year's climate was the most strongly related to tree-ring growth. In upland forests, the previous year's rainfall was also as important to tree-ring growth as current year rainfall (Tryon and True 1958; Zahner and Stage 1966).

Central Alberta has low total precipitation and frequency of precipitation, yet it has high evapotranspiration rates relative to other peatland areas of Canada (Treidl 1978). Based upon climate alone, trees in central Alberta should have a higher probability of water stress. For this reason, it is uncertain if the trends for tree growth observed in the present study could be extrapolated to peatlands in more humid regions.

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