

Modeling Aspen Responses to Climatic Warming and Insect Defoliation in Western Canada

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Abstract— Effects of climate change at three aspen sites in Saskatchewan were explored using a climate-driven model that includes insect defoliation. A simulated warming of 4–5 °C caused complete mortality due to drought at all three sites. A simulated warming of 2–2.5 °C caused complete mortality of aspen at the parkland site, while aspen growth at two boreal sites showed little change from the present climate until after insect defoliation, when dieback was more severe under the warmer climate. The results suggest that future impacts of climate change on boreal aspen forests may not become evident until after major insect outbreaks have occurred.

Introduction

Populus tremuloides Michx., commonly known as trembling aspen by Canadian researchers, is the most important deciduous tree species in the North American boreal forest. It is especially abundant as pure and mixed wood stands in the southern boreal forest of western Canada, where it has become a major commercial species for forestry over the past 10–15 years (Peterson and Peterson 1992). Trembling aspen is also the primary native tree species in the aspen parkland, a predominantly agricultural zone located between the boreal forest to the north and the prairies to the south. Under the climatically dry conditions in the parkland, aspen forms stunted patches of forest that are prone to crown dieback following periods of drought (Zoltai et al. 1991).

The western Canadian interior is projected to experience relatively rapid warming in response to continued increases in atmospheric concentrations of CO₂ and other greenhouse gases (e.g., Watson et al. 1996). Indeed, the climate record indicates that this region has already warmed by between 0.9 and 1.7 °C between 1895 and 1992 (Environment Canada 1995). Although much uncertainty remains, most General Circulation Model (GCM) projections suggest that precipitation will not increase sufficiently to offset the higher rates of evapotranspiration expected under the expected future warming, thus leading to drier soils and potentially more severe drought (Zoltai et al. 1991). If this occurs, the southern boreal forest of western Canada could develop a future climate similar to that presently found in the parkland, which would pose a major concern for the future productivity of aspen forests in the region (Hogg and Hurdle 1995).

Since the early 1990s, crown dieback and increased stem mortality has been noted in some areas of the southern boreal forest and adjacent parkland in the Canadian provinces of Saskatchewan and Alberta. A recent study of aspen tree rings in the Bronson Forest of western Saskatchewan (Hogg and Schwarz 1999) indicated that repeated defoliation by forest tent caterpillar (*Malacosoma disstria* Hbn.) during the 1980s was the major cause of reduced growth and dieback, but that drought was also a significant contributing factor. Forest tent caterpillar and other insects are an important component of the natural functioning of boreal

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aspen ecosystems, because during major outbreaks, they periodically severely defoliate several million ha of forested landscapes across distances of > 1,000 km (e.g., Brandt 1995). Thus, the impacts of these insect defoliators needs to be considered when projecting future climate change effects on the forests of this region.

As a first step toward understanding how climate and insect defoliation affects productivity and dieback, a computer model was developed and tested against the results of tree-ring analysis at two aspen-dominated sites in Saskatchewan. These sites included the Bronson Forest (Hogg and Schwarz 1999), located at the southern edge of the boreal forest, and Batoche, a stressed aspen forest in the dry parkland zone (Hogg and Hurdle 1995). The model (Hogg 1999) is carbon-based and driven by daily climate data, with a structure similar to FOREST-BGC (Running and Coughlan 1988), but includes insect defoliation and additional features relevant to a deciduous forest canopy. Sensitivity analysis of the model indicated that simulated aspen biomass would be strongly affected by small changes in air temperature and defoliation severity; however, the combined impacts of climate change and insect defoliation were not examined.

The objective of the present study was to examine modeled aspen responses under a generalized, 2X CO₂ scenario of climate change (Hogg and Hurdle 1995) based on the Canadian Climate Centre GCM2 (Boer et al. 1992). Specifically, I examined how the presence or absence of insect defoliation may affect aspen sensitivity to this climate change scenario, in terms of aspen stem productivity, biomass accumulation, and severity of dieback. Simulations were conducted at three aspen sites located in climatically sensitive areas of Saskatchewan. These sites included the two aspen sites modeled previously (Hogg 1999), as well as a boreal aspen site. This boreal site was used for intensive measurements in BOREAS, a large, international study of forest-atmosphere interactions (Sellers et al. 1997), and is currently one of the tower sites for a longer term, subsequent study called BERMS (Boreal Ecosystem Research and Monitoring sites).

Methods

Study Sites

The three sites used for model simulations are all pure aspen stands, situated along a climatic moisture gradient from the dry parkland (Batoche site) to the southern boreal forest (BERMS site) of Saskatchewan. The Bronson Forest site, situated in the transition zone between parkland and boreal forest (Zoltai 1975), has a climate that is intermediate between the Batoche and BERMS sites (table 1). At Batoche, the aspen has a stunted growth form and stems are frequently forked, crooked or leaning (Hogg and Hurdle 1995). Stands often include two or three age classes, probably due to stand opening during previous dieback events. In the Bronson Forest, stands are taller (table 1) and generally even-aged but many clones show evidence of severe crown dieback and decline (Hogg and Schwarz 1999). At the BERMS site (Hogg et al. 1997), the aspen forest is even-aged, with straight, healthy stems and shows little evidence of crown dieback. Soil texture is sandy at Batoche and varies from sandy loam to clay loam in the Bronson Forest and BERMS sites.

Tree-Ring Analysis and Past Insect Defoliation

Tree-ring analysis was conducted on two radii per tree from increment cores or disks collected from aspen stems at 1.3 m height. Ring width measurements

Table 1—Summary of site characteristics for aspen stands used in simulations.

	Batoche ^a	Bronson ^b	BERMS ^c
Vegetation zone	parkland	boreal transition	boreal
Latitude	52° 44' N	53° 48' N	53° 38' N
Longitude	106° 09' W	109° 08' W	106° 12' W
Elevation (m)	500	600	600
Mean temperature ^d (°C)	1.2	0.6	-0.2
Mean July temperature ^d (°C)	18.3	16.6	16.3
Mean precipitation ^d (mm y ⁻¹)	375	400	463
Climate Moisture Index ^e	-13	0	+8
Stand age in 1995 (y)	<30–80	46–66	70–76
Height (m)	<5–14	11–21	18–22
Stem diameter (cm)	<6–23	12–31	17–27
Leaf Area Index (m ² m ⁻²)			
Observed (average)	1.4	2.1	2.3
Observed (range)	—	1.1–2.7	—
Modeled	1.3	1.8	2.7
Stem biomass (kg C m ⁻²)			
Observed (average)	1.0	3.2	4.2
Observed (range)	0.9–1.2	1.4–5.7	3.5–5.2
Modeled	1.3	2.2	3.8

^aStand measurements in 1994 (Hogg and Hurdle 1997).

^bStand measurements in 1994 (Blanken et al. 1997; Halliwell and Apps 1997).

^cStand measurements in 1995 (Hogg and Schwarz 1999).

^dFrom 1951–1980 climate normals for adjacent stations (Environment Canada 1982).

^eBased on mean annual precipitation (cm) minus estimated potential evapotranspiration (Hogg 1994).

on finely polished material were made manually using an ocular micrometer under 20X magnification, and results were expressed as annual increment in cross-sectional area (details described by Hogg and Schwarz 1999). For the model comparisons at the Bronson Forest and Batoche sites, I used the results presented earlier (Hogg 1999; Hogg and Schwarz 1999) but included 17 additional trees sampled at Batoche in 1998–99. Model simulations for the BERMS site were compared with tree-ring analysis of increment cores collected from 30 aspen at this site (two stands about 1 km apart) during 1994–1998.

Years with defoliation by insects were first determined at each site from annual insect surveys by the Canadian Forest Service (e.g., Brandt et al. 1995). However, recent studies have shown that aspen forms abnormally pale, low-density growth rings during years when severe defoliation occurs (Hogg and Schwarz 1999; Hogg et al., unpublished). These rings have been referred to as white rings and can be a good indicator of past defoliation of aspen at the stand level. Thus, I determined the year to year occurrence of white rings in the aspen cores and disks that were collected and then used the annual percentage incidence of white rings at each site as an index of defoliation severity for input to model simulations (Hogg 1999).

The Model

Simulations of aspen growth and dieback were conducted using a climate-driven model (Hogg 1999) that operates on a daily time step and has six primary state variables. These include three variables representing the stand-based carbon pools in structural components of leaves, stems, and roots; one variable representing total nonstructural carbohydrate (regardless of location); and two variables describing soil conditions in the rooting zone (temperature and moisture). There are also several derived variables, notably leaf area index of the aspen canopy (LAI), and variables that keep account of cumulative growth, mortality, and transfers of carbohydrate and water on a daily, monthly, and annual basis.

The model is designed to simulate productivity, dieback, and mortality of pure aspen stands over periods of several decades, including stands in remote areas of the Canadian boreal forest where detailed meteorological data are not available. Thus, the model requires only inputs of daily maximum and minimum temperature, daily precipitation, mean monthly solar radiation, latitude (for day length calculations), and elevation (for mean atmospheric pressure). Vapor pressure deficit is estimated by assuming a dew point that is 2.5 °C cooler than daily minimum temperature (Hogg 1997). Simulations are normally initiated with estimated values of carbon pools expected in a young, regenerating aspen stand 5 to 10 years after a stand-replacing disturbance such as fire (Hogg 1999).

The daily sequence of processes simulated by the model is summarized in table 2 and the model parameters are listed in table 3. The specific equations and details of model structure are presented by Hogg (1999). Spring development of leaf area is simulated through the transfer of carbon from the carbohydrate storage pool to the leaf carbon pool. Spring leafing is initiated on the first date when the cumulative number of growing degree days (daily mean air temperature >5 °C) has reached a certain threshold (GDD_{start}) and is completed on the date when a second, higher threshold is reached (GDD_{end}). Insect defoliation is simulated by removing leaf carbon during spring leafing; the proportion removed is calculated from the parameter $wDEFOL$ multiplied by the defoliation severity, as estimated from the proportion of white tree rings in a given year. Leaf carbon and leaf area decrease gradually over the growing season according to a minimum rate of turnover expected in healthy stands (e.g., losses from minor insect herbivory and fungi, or breakage of stems and twigs by wind and falling trees). Additional losses of leaves are simulated during frost events, and

Table 2—Summary of aspen model (Hogg 1999) showing sequence of calculations.

Input model parameters and initialize state variables.
 Input **latitude**, **elevation**, and **defoliation history** at site, and start and end years of simulation.
 Calculate **daylength** and mean **solar radiation** for each day of the year at site.

Start daily loop (for 1 January of first simulation year to 31 December of last simulation year).

Input **daily weather** (maximum and minimum temperature, precipitation).
 If **climate change scenario**, then apply changes to inputs of temperature and precipitation.
 Calculate mean, daytime, nighttime air temperature, and soil temperature.
 Calculate growing degree days (GDD).
 If **spring** (based on cumulative GDD since 1 January) then **grow leaves** from stored carbohydrate, if year with **insect defoliation**, then remove leaf carbon.
 If **frost** then kill leaves.
 If autumn based on photoperiod, then start **leaf fall**.
 Calculate **Leaf Area Index** (LAI) from leaf carbon and specific leaf area.
 Calculate **light interception** by trees and understory (based on LAI and solar radiation).
 Calculate **vapor pressure deficit** (VPD) based on maximum and minimum air temperature.
 Calculate **canopy conductance** (based on VPD and LAI with reductions for dry soils and frost).
 Calculate **transpiration** (based on canopy conductance, VPD and daylength).
 Calculate **interception** of rainfall, **evaporation**, **soil moisture** and **runoff**.
 Calculate **light** levels on leaves based on solar radiation and LAI.
 Calculate **mesophyll conductance** to CO₂ (based on light and temperature).
 Calculate **photosynthesis** (based on LAI, daylength and overall conductance to CO₂).
 Calculate **respiration** of leaves, stems and roots.
 Calculate net photosynthesis and allocate to **carbohydrate storage** versus growth.
Grow stems and roots.
 Calculate carbohydrate status.
Kill stems, roots, and leaves: normal turnover plus additional mortality if carbohydrates are low.
 Translocate recoverable carbohydrate from dead stems to living stems.
 If year end, then **output** annual summary.

End daily loop.

Table 3—Parameters used in model simulations. Values in bold have been modified from those used in the simulations reported by Hogg (1999).

Parameter	Value	Description (units)
GDD_{start}	120	Cumulative growing degree days at start of spring leafing ($^{\circ}\text{C}$)
GDD_{end}	200	Cumulative growing degree days at end of spring leafing ($^{\circ}\text{C}$)
$DAYL_{min}$	12	Day length inducing autumn leaf fall (h d^{-1})
$wFALL$	0.15	Daily rate of autumn leaf fall ($\text{g g}^{-1} \text{d}^{-1}$)
$wDEFOL$	0.7	Proportional leaf loss from insect defoliation
k	0.5	Canopy light extinction coefficient
SLA	0.0225	Specific leaf area ($\text{m}^2 \text{g}^{-1}$ carbon)
$CO2grad$	11.7	CO_2 diffusion gradient (mmol m^{-3})
gM_{max}	2.5	Maximum mesophyll conductance, gM (mm s^{-1})
T_{opt}	20	Daytime temperature optimum for gM ($^{\circ}\text{C}$)
B	4	Coefficient for temperature response of mesophyll conductance ($^{\circ}\text{C}$)
RAD_{half}	250	Coefficient for radiation response of mesophyll conductance (W m^{-2})
$wMResp_{leaf}$	0.01	Leaf maintenance respiration rate, 10°C ($\text{g g}^{-1} \text{d}^{-1}$)
$wMResp_{stem}$	0.0002	Stem maintenance respiration rate, 10°C ($\text{g g}^{-1} \text{d}^{-1}$)
$wMResp_{root}$	0.002	Root maintenance respiration rate, 10°C ($\text{g g}^{-1} \text{d}^{-1}$)
$Q10$	2.3	$Q10$ for temperature response of maintenance respiration
$wGResp$	0.3	Growth respiration (g g^{-1})
wC_{leaf}	0.5	Proportion of stored carbohydrate (C_{TNC}) used for leaf growth
wC_{stem}	0.7	Stem growth as proportion of total growth
$wTNC_{loss}$	0.5	Proportional loss of C_{TNC} during senescence
$wTNC_{use}$	50	Coefficient for use of C_{TNC} during growth
$wTurn_{leaf}$	0.6	Minimum rate of leaf turnover ($\text{g g}^{-1} \text{y}^{-1}$)
$wTurn_{stem}$	0.01	Minimum rate of stem turnover ($\text{g g}^{-1} \text{y}^{-1}$)
$wTurn_{root}$	0.1	Minimum rate of root turnover ($\text{g g}^{-1} \text{y}^{-1}$)
$FROST_{max}$	400	Coefficient for frost damage to leaves ($^{\circ}\text{C}$) ²
$pTNC_{min}$	0.05	C_{TNC} threshold for increased mortality (g g^{-1})
$wKILL$	0.5	Coefficient for mortality during low C_{TNC}
$SOILCAP$	150^a	Soil water holding capacity, rooting zone (mm)
$SOILDY$	75^a	Minimum soil water before canopy conductance is reduced (mm)
gW_{max}	10	Maximum canopy conductance (mm s^{-1})
VPD_{crit}	1	Maximum VPD before canopy conductance is reduced (kPa)
$wVPD_{min}$	0.333	Coefficient of canopy conductance response to VPD
$wICEPT$	0.2	Coefficient of canopy interception of precipitation

^aParameter values for loam soils used in simulations of Bronson forest and BERMS site. For simulations of Batoche site, $SOILCAP$ and $SOILDY$ were set at 100 mm and 50 mm, respectively, for sandy soils (De Jong et al. 1992).

in autumn, the loss of remaining leaves is driven by the seasonal decrease in photoperiod. Changes in soil moisture are simulated from the daily inputs of precipitation (less that intercepted and evaporated by the canopy) and daily losses by transpiration and runoff. Simulated photosynthesis of the aspen canopy is determined as a function of leaf area, solar radiation and temperature, and is reduced by dry soils and high vapor pressure deficit. Daily net production of photosynthate is allocated either to the structural growth of stems and roots, or to storage as nonstructural carbohydrate; the proportion used for growth increases as a function of the ratio between net daily photosynthesis and root biomass (Hogg 1999).

Simulated aspen mortality includes two components: (a) a minimum rate of ongoing stem and root turnover that reflects natural processes in the development of healthy stands, e.g., competition and self thinning; and (b) additional mortality and dieback resulting from climatic or biotic stressors such as frost, drought, and insect defoliation. In the model, stem and root mortality normally proceeds at the minimum rates of turnover, and mortality increases only when the level of nonstructural carbohydrate (expressed as a proportion of total stem and root biomass) falls below a certain threshold ($pTNC_{min}$). Thus, stress-induced increases in mortality are simulated as being largely an indirect consequence of reduced net photosynthesis (e.g., following defoliation or

drought), which can eventually lead to exhaustion of the carbohydrate reserves necessary to the tree's survival.

The values of parameters used in the present study (table 3) were mostly the same as those used previously (Hogg 1999). However, a subsequent evaluation suggested that the earlier version of the model underestimates the growth of aspen biomass under optimal conditions. This was addressed by increasing the rate of maximum mesophyll conductance, and reducing the values for minimum rate of stem and root turnover; the latter change also necessitated an increase in the proportion of carbon allocated to stem growth to achieve model stability. The cumulative number of growing degree days associated with the end of spring leafing was also increased to more closely correspond with observations at the BERMS site (A. Barr, personal communication). Finally, parameters describing soil water holding capacity were modified (table 3) to correspond more closely to the observed differences in soil texture at each site.

Weather Data and Climate Change Scenarios

Records of daily maximum and minimum temperature and daily precipitation were assembled from climate stations adjacent to each site for the periods 1930–1995 (Batoche), 1940–1995 (Bronson), and 1930–1996 (BERMS). The start of these periods corresponds to when the main (or oldest) age class of aspen in these stands would have been about 5 to 10 years old (table 1). The climate data for simulations at Batoche and Bronson are the same as those used by Hogg (1999), while the climate record for the BERMS site was estimated using weather data from Waskesui Lake and Prince Albert, Saskatchewan, respectively located about 30 km N and 60 km SE of the site.

For simulations of aspen sensitivity to climate change impacts, the inputs of the observed daily weather record were modified according to the projected changes for the western Canadian interior under a doubling of atmospheric CO₂ levels. In this preliminary investigation, I applied a generalized climate change projection for the region based on mean regional differences between the 2X and 1X CO₂ scenarios of the Canadian Climate Centre GCM2 (Boer et al. 1992), which gives a 4.2 °C increase in daily maximum temperature, a 4.9 °C in daily minimum temperature, and an 11% increase in daily precipitation. This is the same scenario used by Hogg and Hurdle (1995) in an earlier analysis of possible impacts of climate change on vegetation zonation in this region.

Results and Discussion

Observed and Modeled Aspen Growth (Current Climate)

The occurrence of white tree-rings at the three sites showed a good correspondence with the years when major defoliation events were recorded during past insect surveys, considering that these surveys were conducted over a large geographic area with limited spatial resolution (Hogg 1999; table 4). In terms of percentage incidence of white rings, 1980 was the year with the most severe defoliation by forest tent caterpillars at all three sites. Severe defoliation also occurred at the Bronson and BERMS sites in the early 1960s, especially 1964. These major defoliation events were accompanied by severe reductions in aspen growth, based on the results of tree-ring analysis (figure 1). However, it should also be noted that 1964 was also a major drought year at all three sites,

Table 4—Percentage of radii with light-colored (white) tree rings during years with insect defoliation, as recorded in aspen stems (1.3 m height). Numbers in bold denote years with records of extensive defoliation by forest tent caterpillar based on surveys by the Canadian Forest Service (excludes records of sporadic outbreaks or defoliation in areas adjacent to each site).

	Site		
	Batoche (47 trees)	Bronson (102 trees)	BERMS (30 trees)
1953	35	0	0
1956	0	9 ^a	0
1962	0	19	0
1963	0	52	32
1964	0	87	96
1965	0	2	0
1979	81	8	65
1980	85	97	99
1981	0	1	0
1982	0	1	0
1983	0	12	0
1985	0	37	0
1986	0	69	0
1987	0	82	0
1988	0	64	0
1989	0	6	0
1990	0	8	0
1992	0	0	72 ^a

^aDefoliation by large aspen tortrix (*Choristoneura conflictana*).

and 1980 was a major drought year at the Batoche and Bronson sites (climate data not shown). Situations like this, when drought and defoliation occur during the same year, can pose challenges when attempting to separate the impacts of these factors on aspen growth and dieback.

Aspen growth at the Bronson forest was severely reduced by forest tent caterpillar defoliation during several successive years in the mid and late 1980s, and this also appears to be the major cause of the observed crown dieback at this site (Hogg and Schwarz 1999). The other two sites have been apparently free of defoliation since 1980, except for an outbreak by large aspen tortrix (*Choristoneura conflictana* [Walker]) in 1992, which caused a transient reduction in growth at the BERMS site.

The results of the simulations for the three sites showed a good correspondence between the year-to-year pattern of modeled stem biomass increment and the observed stem area increment based on tree-ring analysis (figure 1). The values of r^2 were 0.522 and 0.682 for the Batoche and Bronson sites, similar to those reported from previous simulations for these sites (Hogg 1999), while a much lower r^2 of 0.185 was obtained at the BERMS site. However, such comparisons are of limited value because the expression of annual stem growth differs between the modeled (stand-based biomass) and observed (tree-based area increment) growth. A more appropriate basis of comparison is to express both series in terms of relative interannual changes, so that the influence of longer-term stand dynamics (height growth, recruitment, and mortality) are minimized in the pattern obtained from tree-ring analysis. With both series detrended in this way by differencing of log-transformed growth (Hogg 1999), the revised values of r^2 were slightly less for the Batoche and Bronson sites (0.491 and 0.591, respectively) but increased substantially for the BERMS site ($r^2 = 0.376$).

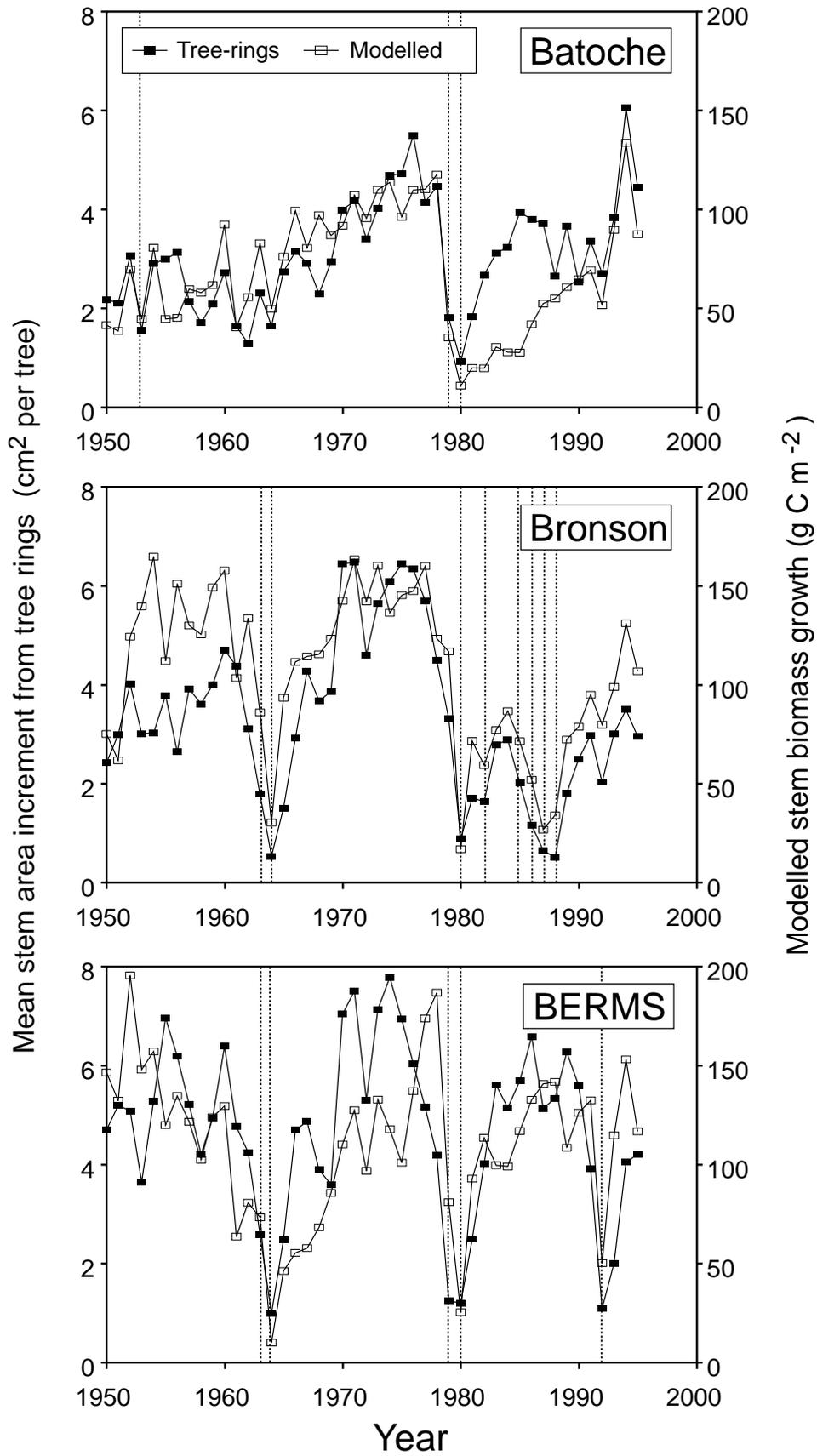


Figure 1—Interannual variation in stem growth at three aspen sites in Saskatchewan, Canada, based on (a) radial growth from tree-rings, expressed as mean stem area increment from cores or disks collected at 1.3 m height, and (b) modeled growth in stem biomass carbon at the stand level. Major defoliation events at each site (table 4) are indicated by dotted vertical lines.

Long-term, permanent sample plot data are not available from any of the three sites. However, a comparison of measured versus simulated aspen biomass and leaf area index in 1994–1995 (table 1) indicates that the model performed reasonably well, considering that it is a very simple model that does not include site-specific factors such as soil nutrient status.

Climate Change Scenarios of Aspen Responses

Simulated changes in aspen stem biomass carbon under the observed conditions of climate and defoliation history (indicated by an asterisk for each site in figure 2) show that modeled dieback occurred during and following major insect outbreaks. The most severe dieback occurred following the 1979–1980 outbreak at Batoche and following the 1963–1964 outbreak at the BERMS site, while at the Bronson site, repeated defoliation during the 1980s caused a more gradual but sustained decline in stem biomass during this period. A major contributing factor to the modeled dieback was drought, which accompanied the severe defoliation events at the Bronson and BERMS sites in 1964, and at the Batoche and Bronson sites in 1980. However, when insect defoliation was “turned off” in the simulations (figure 2), dieback was minimal following these drought events. This suggests that under the current climate, drought is not a major cause of aspen mortality except in combination with insect defoliation and other stresses, at least in the boreal forest.

Under the 2X CO₂ climate change scenario (4–5 °C warming), the modeled aspen at all three sites died during the first decade of simulations, despite the 11% increase in precipitation. In the model, stem and root mortality can only increase when nonstructural carbohydrates fall below a critical minimum. Because there was no defoliation during this initial period of the simulation, the modeled stand death can be attributed to (1) a combination of reduced photosynthesis under the drier conditions (high VPD and low soil moisture) and (2) depletion of carbohydrates through temperature-induced increases in respiration rates.

Simulations were repeated by reducing the simulated magnitude of climate change by 50%, i.e., a 2.1 and 2.45 °C increase, respectively, in daily maximum and minimum daily temperatures, and a 5.5% increase in precipitation. Such a scenario might thus correspond approximately to climate change expected under a 50% increase in atmospheric CO₂ levels, which at the current rate of increase would occur by the middle of the 21st century. Even with this modest warming scenario, the modeled aspen at Batoche did not survive. This result is consistent with the observation that aspen is absent from the prairies near the Montana-Saskatchewan border, where the climate is about 2 °C warmer, with up to 15% more precipitation, compared to Batoche (e.g., Estevan, Saskatchewan, with mean annual temperature of 3.4 °C and annual precipitation of 434 mm).

At the two boreal sites, the modest warming scenario had very little effect on aspen productivity during the early part of the simulations (i.e., prior to the early 1960s). However, dieback increased following drought and defoliation in 1964, especially at the BERMS site where almost all of the stem biomass had died by the following year (figure 2). At the Bronson forest, the warming led to increased dieback during the 1980s compared to that under the current climate. As a result of these dieback events, the simulated climate change caused about a 50% decrease in the modeled, final biomass of aspen at both boreal sites. When insect defoliation was “turned off” in the climate change simulations, dieback severity was reduced but it was still sufficient to cause a decrease of about 20% in the final, modeled biomass at these sites.

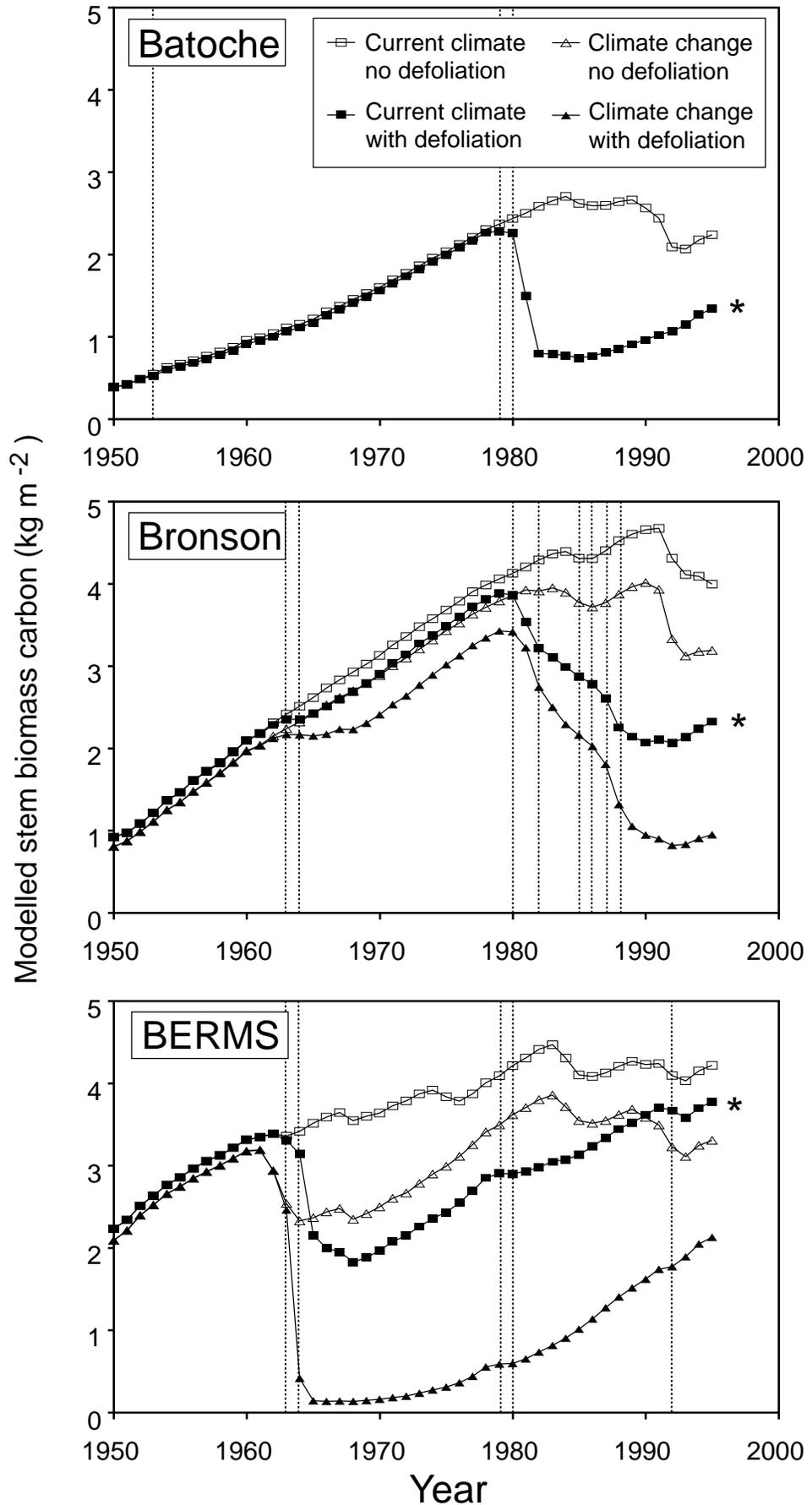


Figure 2— Simulated changes in stem biomass carbon at three aspen sites under the observed climate, and also under a future climate change scenario with a modest warming of about 2–2.5 °C that results in drier soils (details in text). These two climate scenarios were each applied in combination with the observed insect defoliation at each site (“with defoliation”) or with insect defoliation “turned off” in the model (“no defoliation”). Major defoliation events are indicated by dotted vertical lines. The simulations corresponding to the estimated stem growth at each stand for the period 1950–1996 (figure 1) are denoted by an asterisk.

Carbon Dioxide Fertilization

One of the major factors that was not included in these preliminary simulations is the effect of elevated CO₂ on photosynthesis, which might reduce—or even reverse—the negative impacts on aspen productivity that would otherwise be expected under a warmer and drier future climate. For example, photosynthesis of *Betula pendula* was enhanced by 33% after four years of field exposure to doubled CO₂ levels (Rey and Jarvis 1998). However, ecosystem responses under elevated CO₂ levels are complex, so that the long-term benefits of CO₂ on plant productivity are often much less than would be predicted from simple physiological models (e.g., Ward and Strain 1999). Interactions with other human-induced changes in air quality could also be significant in this respect. For example, preliminary results from a free carbon dioxide enrichment (FACE) experiment in Wisconsin indicate that artificially elevated concentrations of ground level ozone completely eliminated the benefits of CO₂ fertilization on aspen growth (J. G. Isebrands, personal communication).

As a preliminary means of exploring how CO₂ fertilization might affect aspen responses to climatic warming, the simulations (with defoliation) were repeated under the same climate change scenarios using various percentage increases in modeled photosynthesis rates. Under the modest (2–2.5 °C) warming scenario, corresponding to a roughly 50% increase in atmospheric CO₂, photosynthesis rates had to be increased by 31% to achieve the same final stem biomass at Batoche as that simulated under the current climate. The corresponding figures for the Bronson and BERMS sites were 9 and 12%, which indicates that if photosynthesis rates increase by more than these percentages, aspen biomass would increase. However, with the original scenario for 2X CO₂ (4–5 °C warming), much greater increases in photosynthesis would be needed to offset the modeled climate change impacts: the Batoche site would require an unrealistic tripling of photosynthesis rates to achieve the same final biomass, whereas photosynthesis would need to increase by 30 and 47% at the Bronson and BERMS sites. The latter percentage increases in photosynthesis might reasonably be expected under CO₂ fertilization, so that biomass of boreal aspen forests may show little change under a warmer climate; but it appears that aspen biomass in the parkland would be reduced, even under the most optimistic assumptions.

Model Limitations and Knowledge Gaps

Although the model performed reasonably well in simulating interannual changes in aspen stem growth based on tree-ring analysis, the model projections under climate change should be interpreted with caution for several reasons. First, the model outputs of growth, dieback, and mortality need to be more rigorously validated at the stand level, preferably through model comparisons with annual measurements and health assessments in aspen stands exposed to various stresses. Second, other than drought and defoliation, the model does not include many of the factors that can reduce aspen productivity and biomass—e.g., fungal pathogens and wood-boring insects, spring thaw-freeze events, competition with conifers in mixed wood stands, and cold soils (Lieffers et al., this proceedings). Another limitation is that for some of the key physiological processes being simulated, there is little published information available for developing functionally realistic algorithms with reliable estimates of model parameters. These processes include, for example, the allocation of carbohydrate to growth versus storage, and the relationship between whole-tree carbohydrate levels and mortality.

Given the importance of defoliation to aspen stand dynamics, another critical knowledge gap for the future is to understand how forest tent caterpillar and other insects may respond to future climate change. Forest tent caterpillar is favored by warm, dry summers (Ives 1981). For the first time in 1995, a major outbreak was recorded at a latitude $>60^{\circ}$ N in the Canadian Northwest Territories (Brandt et al. 1996), suggesting that the climatic warming observed to date may be facilitating the northward expansion of this species. Thus, be expected to increase—leading to even greater impacts on the growth and dieback of aspen in the region.

Another important consideration is the reliability of future climate projections based on General Circulation Models such as the one used in this study. These models have a very coarse spatial resolution, and until recently, they were very poor at characterizing feedbacks of terrestrial vegetation on regional climate. Indeed, a recent study indicates that seasonal leafing of aspen and other deciduous vegetation may exert a significant influence on the climate patterns of the western Canadian interior (Hogg et al., in press). Thus, even the projections of future climate change could ultimately be improved through a greater understanding of aspen ecosystem processes and their interactions with the atmosphere and regional climate.

Conclusions

The results from the model simulations indicate that future climate change impacts on boreal aspen forests in western Canada may not become apparent until after major defoliation events occur. However, it is not currently possible to predict with any confidence how aspen productivity will be affected, if the climate of this region becomes warmer and drier as projected by most General Circulation Models. Under a warmer and drier future climate, drought and defoliation are expected to increase, leading to reduced growth and dieback of aspen; however, these impacts may be reduced or even reversed in some areas by the benefits of CO₂ fertilization and warmer soils. There are also many knowledge gaps, including limitations of understanding of a large variety of interacting factors that operate over a wide range of spatial and temporal scales. Nevertheless, climate change poses a serious risk for the future productivity and health of aspen forests in western Canada, especially in the drier climate zones that include much of the southern boreal forest. Given the importance of aspen forests, both ecologically and commercially, there is a need for regional-scale monitoring as an “early warning” indicator of how these forests may be responding to the warming trend that is already apparent in the western Canadian interior.

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References

- Blanken, P.D.; Black, T.A.; Yang, P.C.; Neumann, H.H.; Nestic, Z.; Staebler, R.; den Hartog, G.; Novak, M.D.; Lee, X. 1997. Energy balance and canopy conductance of a boreal aspen forest: partitioning overstory and understory components. *Journal of Geophysical Research* 102 (D24): 28915–28928.
- Boer, G.J.; McFarlane, N.A.; Lazare, M. 1992. Greenhouse gas-induced climate change simulated with the CCC second-generation general circulation model. *Journal of Climate* 5:1045–1077.
- Brandt, J.P. 1995. Forest insect- and disease-caused impacts to timber resources of west-central Canada: 1988–1992. Canadian Forest Service, Northern Forestry Centre, Edmonton, Alberta. Information Report NOR-X-341. 28 p.
- Brandt, J.P.; Knowles, K.R.; Larson, R.M.; Ono, H.; Walter, B.L. 1996. Forest insect and disease conditions in west-central Canada in 1995 and predictions for 1996. Canadian Forest Service, Northern Forestry Centre, Edmonton, Alberta. Information Report NOR-X-347. 53 p.
- De Jong, R.; Bootsma, A.; Dumanski, J.; Samuel, K. 1992. Characterizing the soil water regime of the Canadian prairies. Agriculture Canada Research Branch, Technical Bulletin 1992-2E, Ottawa.
- Environment Canada. 1982. Canadian climate normals 1951–80. Temperature and precipitation, prairie provinces. Canadian Climate Program, Environment Canada, Ottawa. 429 p.
- Environment Canada. 1995. The state of Canada's climate: monitoring variability and change. A State of the Environment Report No. 95-1, Environment Canada, Ottawa. 52 p.
- Halliwell, D.H.; Apps, M.J. 1997. Boreal ecosystem-atmosphere study (BOREAS) biometry and auxiliary sites: overstory and understory data. Canadian Forest Service, Northern Forestry Centre, Edmonton, Alberta. 254 p.
- Hogg, E.H. 1994. Climate and the southern limit of the western Canadian boreal forest. *Canadian Journal of Forest Research* 24: 1835–1845.
- Hogg, E.H. 1997. Temporal scaling of moisture and the forest-grassland boundary in western Canada. *Agricultural and Forest Meteorology* 84: 115–122.
- Hogg, E.H. 1999. Simulation of interannual responses of trembling aspen stands to climatic variation and insect defoliation in western Canada. *Ecological Modelling* 114: 175–193.
- Hogg, E.H.; Black, T.A.; den Hartog, G.; Neumann, H.H.; Zimmermann, R.; Hurdle, P.A.; Blanken, P.D.; Nestic, Z.; Yang, P.C.; Staebler, R.M.; McDonald K.C.; Oren, R. 1997. A comparison of sap flow and fluxes of water vapor from a boreal deciduous forest. *Journal of Geophysical Research* 102 (D24): 28915–28928.
- Hogg, E.H.; Hurdle, P.A. 1995. The aspen parkland in western Canada: a dry-climate analogue for the future boreal forest? *Water, Air, and Soil Pollution* 82: 391–400.
- Hogg, E.H.; Hurdle, P.A. 1997. Sap flow in trembling aspen: implications for stomatal responses to vapour pressure deficit. *Tree Physiology* 17: 501–509.
- Hogg, E.H.; Price, D.T.; Black, T.A. [In press]. Postulated feedbacks of deciduous forest phenology on seasonal climate patterns in the western Canadian interior. *Journal of Climate*.
- Hogg, E.H.; Schwarz, A.G. 1999. Tree-ring analysis of declining aspen stands in west-central Saskatchewan. Canadian Forestry Service, Northern Forestry Centre, Edmonton, Alberta. Information Report NOR-X-359. 25 p.
- Ives, W.G.H. 1981. Environmental factors affecting 21 forest insect defoliators in Manitoba and Saskatchewan, 1945–69. Canadian Forestry Service, Northern Forestry Centre, Edmonton, Alberta. Information Report NOR-X-233. 142 p.
- Lieffers, V.J.; Landhäuser, S.M.; Hogg, E.H. [In press]. Is the lower productivity of aspen compared to other poplar species a result of higher stress tolerance?
- Peterson, E.B.; Peterson, N.M. 1992. Ecology, management, and use of aspen and balsam poplar in the Prairie Provinces, Canada. Forestry Canada, Northern Forestry Centre, Edmonton, Alberta. Special Report 1. 252 p.

- Rey, A.; Jarvis, P.G. 1998. Long-term photosynthetic acclimation to increased atmospheric CO₂ concentration in young birch (*Betula pendula*) trees. *Tree Physiology* 18: 441–450.
- Running, S.W.; Coughlan, J.C. 1988. A general model of forest ecosystem processes for regional applications. I. Hydrologic balance, canopy gas exchange and primary production processes. *Ecological Modelling* 42: 125–154.
- Sellers, P.J., et al. 1997: BOREAS in 1997: Experiment overview, scientific results, and future directions. *Journal of Geophysical Research* 102 (D24): 28731–28769.
- Ward, J.K.; Strain, B.R. 1999. Elevated CO₂ studies: past, present and future. *Tree Physiology* 19: 211–220.
- Watson, R.T.; Zinyowera, M.C.; Moss, R.H. 1996. Climate change, 1995—impacts, adaptations and mitigation of climate change: scientific-technical analyses, contribution of Working Group II to the Second Assessment Report of the Intergovernmental Panel on Climate Change, Cambridge University Press, Cambridge: 95–131.
- Zoltai, S.C. 1975. Southern limit of coniferous trees on the Canadian prairies. Canadian Forestry Service, Northern Forest Research Centre, Edmonton, Alberta. Information Report NOR-X-128.
- Zoltai, S.C.; Singh, T.; Apps, M.J. 1991. Aspen in a changing climate. In: S. Navratil and P.B. Chapman, eds. *Aspen Management for the 21st century*. Proceedings of Symposium, 20–21 November 1990, Edmonton, Alberta. Forestry Canada, Northwest Region and Poplar Council of Canada, Edmonton, Alberta: 143–152.