Growth and dieback of aspen forests in northwestern Alberta, Canada, in relation to climate and insects

E.H. Hogg, James P. Brandt, and B. Kochtubajda

Abstract: Trembling aspen (*Populus tremuloides* Michx.) is the most important deciduous tree in the Canadian boreal forest, with >1000 Tg of carbon stored in the aboveground biomass of this species. Since the early 1990s, aspen dieback has been noted over parts of the southern boreal forest and aspen parkland in western Canada. In this study, tree-ring analysis and forest health assessments were conducted in 18 aspen stands near Grande Prairie, Alta., to examine causes of reduced growth and dieback. Defoliation histories were reconstructed based on light-colored ("white") tree rings and records of past insect outbreaks. The results indicated that several factors contributed to the observed dieback. Defoliation by forest tent caterpillar (*Malacosoma disstria* Hbn.) and drought in the 1960s and 1980s led to reduced growth and predisposed some stands to secondary damage by wood-boring insects and fungal pathogens. Thaw–freeze events during a period (1984–1993) of unusually light snow cover in late winter may have also contributed to the observed dieback. Under global change, the severity of these stressors may increase, which would pose a serious concern for the future health, productivity, and carbon sequestration of aspen forests in the region.

Résumé : Avec plus de 1000 Tg de carbone emmagasiné dans la biomasse épigée de cette essence, le peuplier faux-tremble (*Populus tremuloides* Michx.) est l'espèce décidue la plus importante dans la forêt boréale canadienne. Depuis le début des années 1990, le dépérissement du peuplier faux-tremble a été noté dans certaines parties de la forêt boréale méridionale et les tremblaies de l'ouest du Canada. Dans cette étude, l'analyse des cernes annuels et l'évaluation de l'état de santé de la forêt ont été réalisées dans 18 peuplements de peuplier faux-tremble, près de Grande Prairie en Alberta, afin d'examiner les causes de la réduction de croissance et du dépérissement. L'historique des défoliations a été reconstitué sur la base des cernes de couleur pâle (« blanc ») et des données sur les épidémies d'insectes passées. Les résultats montrent que plusieurs facteurs ont contribué au dépérissement qui a été observé. La défoliation par la livrée des forêts (*Malacosoma disstria* Hbn.) et la sécheresse survenues au cours des années 1960 et 1980 ont entraîné une réduction de croissance et prédisposé certains peuplements aux attaques des insectes xylophages et des pathogènes fongiques. Des épisodes de dégel et gel lors d'une période (1984–1993) où la couverture de neige était exceptionnellement mince à la fin de l'hiver peuvent également avoir contribué au dépérissement. Dans le contexte d'un réchauffement global, la sévérité de ces stress pourrait augmenter, ce qui causerait une grande inquiétude dans l'avenir pour la santé et la productivité des forêts de peuplier faux-tremble dans la région et la séquestration du carbone par ces forêts.

[Traduit par la Rédaction]

Introduction

Trembling aspen (*Populus tremuloides* Michx.) is the most important deciduous tree species in the North American boreal forest, both ecologically and commercially. In Canada, the total aboveground biomass of aspen has been estimated at 2066 Tg (D.T. Price and M. Siltanen, Canadian Forest Service, personal communication), based on the Canadian Forest Inventory (Penner et al. 1997). This corresponds to about 1000 Tg of carbon, of which >700 Tg is situated within the boreal forest of the western Canadian interior. The inventory data indicate that aspen-dominated forests occupy an area of at least 200 000 km^2 in this region. Net carbon sequestration by aspen forests in western Canada may exceed 30 Tg during favourable growth years with minimal disturbance, based on a crude spatial scaling of the average carbon uptake of 157 g C·m^{-2}·year^{-1} during 4 years of eddy correlation measurements at a typical mature aspen stand in this region (Black et al. 2000). Thus, carbon sequestration by aspen forests is potentially significant to the carbon cycle at the national scale (Kurz and Apps 1999), even when compared with the ca. 130 Tg·year^{-1} of carbon emissions from Canadian fossil fuel use.

Since the early 1990s, dieback and reduced growth of aspen forests has been noted over some areas of the Canadian Prairie Provinces. A previous study showed that severe decline of aspen stands near St. Walburg, Sask. (53°45′N, 109°08′W), was initiated following several years of defoliation by forest tent caterpillar (*Malacosoma disstria* Hbn.) in the 1980s (Hogg and Schwarz 1999). During major outbreaks, as in 1988, this species can severely defoliate aspen

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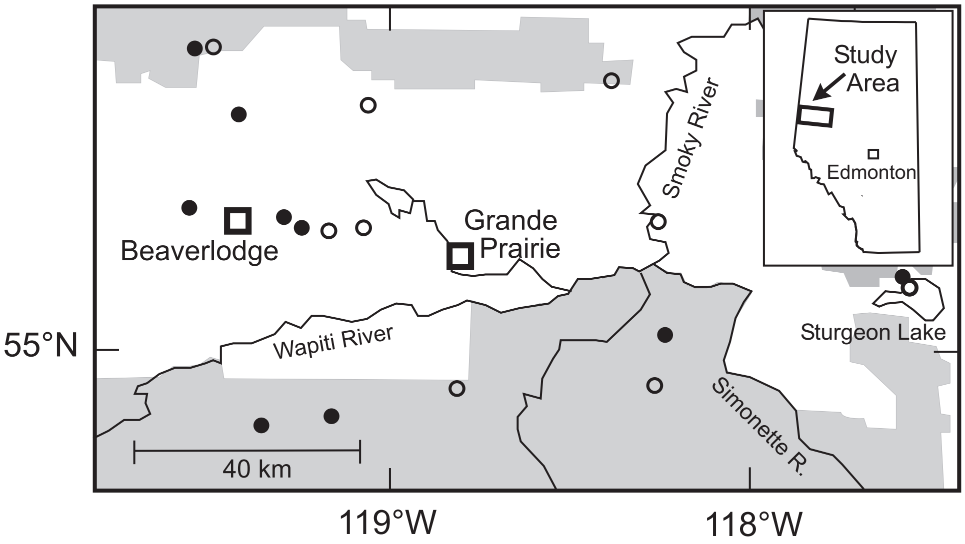
Fig. 1. Location of study area in northwestern Alberta, Canada, showing location of sites in aspen stands designated as healthy (●) and stressed (○). The shaded area is mostly continuous boreal forest (aspen and mixedwood), and the unshaded area is predominantly agricultural land with patches of aspen forest (including aspen parkland).



forests over areas greater than 500 × 300 km (Emond and Cerezke 1989), leading to reduced growth (Hildahl and Reeks 1960) and crown dieback (Batzer et al. 1954). Defoliation can also increase the susceptibility of stands to infestation by wood-boring insects and fungal pathogens, leading to further dieback and eventual forest decline (Churchill et al. 1964; Hildahl and Campbell 1975; Houston 1992). Climatic factors are also important to the productivity and height growth of aspen (Maini 1972), and drought has been implicated as a major cause of aspen dieback, especially in the climatically dry parkland zone along the northern edge of the Canadian prairies (Zoltai et al. 1991; Hogg and Hurdle 1995).

Despite the importance of trembling aspen, its responses to the combined effects of climate variation, insects, and diseases have received little attention until recently (Hogg 1999). Dendrochronology is a potentially powerful means of assessing past growth responses of forests, but it has seldom been applied to aspen. Although the tree rings of aspen are often much less distinct than those of most boreal conifers, the annual growth increments can be reliably identified and cross-dated from carefully prepared and polished stem sections or increment cores. Furthermore, the recent discovery that distinctive, pale-coloured tree rings (“white rings”) are formed in aspen stems during years with severe, early season defoliation (Hogg and Schwarz 1999) provides a potentially useful method of retrospectively assessing the impacts of insect defoliators on the growth of this species.

The present study was conducted in response to public concerns about dieback of aspen forests in the Grande Prairie area in northwestern Alberta (Fig. 1), dating back to the period 1990–1992. Subsequent aerial surveys by the Canadian Forest Service in August 1992 showed patches of aspen dieback along the valleys of the Smoky and Wapiti rivers in this area (H. Cerezke and H. Gates, unpublished report[2]). The affected area includes part of a northern outlier of the aspen parkland that is climatically drier than most other forested areas in the western Canadian interior (Hogg 1994). Records of past insect surveys also indicated that portions of this area were defoliated by forest tent caterpillar during the last major outbreak in 1988–1992 (Brandt 1995).

The overall objective of this study was to conduct tree-ring analyses and forest health assessments in healthy and stressed aspen forests over the area of concern as a means of determining the onset, magnitude, and likely causes of reduced stem growth, mortality, and crown dieback. A secondary objective was to identify factors most likely to be important in determining future impacts of climate change on the productivity of aspen forests in the region. To address these objectives, we used regression analysis to examine the relative influences of climatic factors and insect defoliation on interannual growth variation. We also examined the potential role of other stressors such as fungal pathogens, wood-boring insects, and extreme weather events that have been previously implicated as causes of forest dieback, notably winter thawing followed by severe spring frost (Cayford et al. 1959; Auclair et al. 1990, 1996).

Methods

Study area and site selection

The study area covers about 10 000 km^2 surrounding the city of Grande Prairie in northwestern Alberta, Canada (Fig. 1). The area includes portions of the mixedwood boreal forest and lower foothills of the Rocky Mountains, as well as a number of small northern outliers of the climatically drier aspen parkland zone (Moss 1952; Rowe 1972). Trembling aspen is abundant in the region and mainly forms even-aged stands with a fire origin. Pure aspen stands are common, especially at the lower elevations, and aspen is also an impor-

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[2] H.F. Cerezke and H.S. Gates. 1992. Aerial survey of aspen forest conditions near Grande Prairie, Alberta. File report, 21 Aug. 1992. Forest Insect and Disease Survey. Canadian Forest Service, Northern Forestry Centre, Edmonton, Alta.

tant component of stands mixed with white spruce (*Picea glauca* (Moench) Voss) and other conifers. At Grande Prairie (elevation 669 m), mean monthly temperatures range from –18°C in January to 16°C in July and mean annual precipitation is 453 mm, including 180 cm of snowfall (Environment Canada 1983).

A total of 18 sites were selected in pure aspen stands that were accessible by road, with a minimum stand size of 20 ha and no visible signs of human disturbance (locations shown in Fig. 1). Heavily grazed sites, sites affected by flooding, and stands located along the edges of roads, seismic lines, or crops (that may have been sprayed with herbicides) were avoided. Site characteristics were typical of aspen stands in northern Alberta (Beckingham and Archibald 1996), being well drained on level to gently sloping terrain with an understorey vegetation most frequently dominated by *Rosa acicularis* Lindl., *Viburnum edule* (Michx.) Raf., and *Epilobium angustifolium* L.

Prior to sampling, we categorized the stands as “healthy” or “stressed” (nine stands in each category). Initially, we had intended to use the mean percentage of crown dieback as an indicator of forest health based on the methods of an earlier study (Hogg and Schwarz 1999); however, the level of dieback was generally less than anticipated, and it was difficult to differentiate stress-induced dieback and mortality from that induced by self-thinning during natural development of healthy stands. Thus, we defined “stressed” stands as those showing significant signs of external damage by wood-boring insects and fungal pathogens. The remaining stands were designated as “healthy”. Within each of these two categories, five stands were located in the predominantly agricultural zone with patchy forest cover (predominantly aspen), and four stands were situated within the provincial “green zone” with a more continuous cover of commercial forest (aspen and mixedwood).

Field assessments of stand characteristics

Field sampling was conducted in July 1997. At each site, a circular plot 20 m in diameter was established within pure aspen forest, at a representative location at least 50 m from stand edges or anthropogenic disturbances. The stem diameter (1.3 m height) of each live or standing dead aspen (minimum stem diameter of 5 cm) within the plot was measured, and percent crown dieback was assessed in 10% classes. For each aspen stem, incidence of the five most prevalent insects and diseases was assessed based on visual examinations for external indicators (Hiratsuka 1987; Ives and Wong 1988). Standing dead aspen were also examined destructively for evidence of *Armillaria* root rot, as indicated by the presence of white mycelial fans of this fungal pathogen in the bark and cambium of stem boles and adjacent large roots. At each site, a sample of the uppermost 30 cm of mineral soil was collected and particle-size analysis was conducted by the hydrometer method (Kalra and Maynard 1991).

Tree-ring analysis of aspen responses to climate and insects

At each site, 10 trees representing the range of size and health conditions were felled (total of 180 trees). Their heights were measured and disks were collected at stump height (30 cm from the ground, for age determination only), and at 1.3, 5, and 10 m height. Sections of dead and live branches were also collected from the crowns of trees showing dieback, for the purpose of dating when dieback occurred. Disks were dried at 50°C and prepared for tree-ring analysis by polishing with progressively finer grades of sandpaper. Tree ring widths were measured along two radii using an ocular micrometer mounted on a compound dissecting microscope at 20× magnification. Ring width measurements from the two radii were averaged and used to calculate the mean stem disk radius (R) at the end of each year’s growth. Growth was expressed as annual increment in stem cross-sectional area ($\mathrm{cm}^2\cdot\mathrm{year}^{-1}$) to help remove the temporal trend for decreasing ring widths that typically occurs with increasing stem circumference (Kolb and McCormick 1993). The annual stem area increments (I) of each disk were calculated from annual values of R using the formula for the area of a circle (Kolb and McCormick 1993; Hogg and Schwarz 1999), and mean values of I were determined from the 10 aspen stems felled at each site.

Tree rings that were abnormally pale in colour (“white” rings), indicating years when insect defoliation occurred (Hogg 1999; Hogg and Schwarz 1999), were also noted. Unlike the light-coloured rings reported in conifers (e.g., Liang et al. 1997), the appearance and structure of both early- and late-wood differs strongly from that in normal growth rings (E.H. Hogg, unpublished data). For each year during the period 1950–1997, the overall percentage incidence of white tree rings recorded from the 180 aspen stems was compared with the proportion of the study area defoliated by forest tent caterpillar, as determined from mapped outbreaks recorded during annual insect surveys by the Canadian Forest Service (Moody and Amirault 1992; Brandt 1995).

Analyses of climatic variation were conducted using daily temperature and precipitation data from the two stations (Beaverlodge and Grande Prairie) with the longest climate record in the region. Annual changes in moisture were examined using a climate moisture index (CMI) developed by Hogg (1997). The CMI was based on the quantity P minus PET, where P is the annual precipitation and PET is the annual potential evapotranspiration (i.e., expected loss of water vapor loss from the landscape under well-watered conditions) using a simplified form of the Penman–Monteith equation. Negative values of the CMI denote dry conditions typical of aspen parkland or prairie grasslands, whereas positive values indicate levels of moisture that are normally associated with the boreal forest (Hogg 1994). Monthly values of PET were calculated from the estimated vapor pressure deficit, which was in turn estimated from the average daily maximum and minimum temperature for each month. Precipitation and moisture conditions late in a calendar year (September–December) should have a negligible effect on the ring width for that year, because radial growth of aspen is normally completed by August (Ahlgren 1957; E.H. Hogg, unpublished data). Thus values of annual precipitation and the CMI were calculated for various 12-month periods (e.g., 1 September of the previous year and ending on 31 August of the current year) relevant to the assessment of aspen growth responses to changes in climatic moisture regimes. Thermal conditions for radial growth were assessed by calculating monthly sums of growing degree-days, based on positive departures of daily mean temperature from a

Table 1. Characteristics of the healthy (N = 9) and stressed (N = 9) aspen stands sampled for tree-ring analysis.

	Healthy stands		Stressed stands	
Stand characteristics	Mean	Range	Mean	Range
Altitude (m)	787	650–930	729	580–850
Age (years in 1997)	64	53–90	67	43–99
Diameter at 1.3 m height (cm)	15.4	11–23	15.3	11–21
Height (m)	18.7	15–26	16.5	11–24
Total basal area ($m^2 \cdot ha^{-1}$)	45	32–62	35	23–48
Total stems per plot	78	35–134	60	29–103
Dead or damaged stems (%)	28	16–46	69.9	51–97
Insect and disease damage (%)[a]	4.1	0–14	44.8	15–97
Live with other damage (%)[b]	7	0–22	12.5	0–35
Live with moderate dieback (%)	20.1	2–39	28	14–43
Live with severe dieback (%)	2.2	0–7	5.7	2–12
Dead (%)	17.3	6–24	32.9	18–47
Mineral soil texture				
Sand (%)	33	18–74	33	19–66
Silt (%)	42	16–60	33	17–54
Clay (%)	26	10–50	34	16–61

[a] Percentage of stems with poplar borers and (or) fungal pathogens but excluding current-year defoliation.
[b] Includes frost cracks, stem breaks, and other damage caused by wind and wildlife.

base of 5°C. A dynamic regression approach using Forecast Pro software (Business Forecast Systems, Inc.) was used to examine the combined influences of climatic factors and insect defoliation events on aspen stem growth for the period from 1950 to 1996. The dependent variable describing stem growth was determined from annual values of mean area increment from the tree-ring analysis of disks at 1.3 m height. The independent variable describing insect defoliation intensity each year was determined based on two methods: (*i*) the proportion of the study area defoliated annually based on past insect surveys and (*ii*) the proportion of trees having white rings for each year (Hogg 1999). The following climatic factors were also tested as independent variables: mean temperature, growing degree-days, total precipitation, the CMI for various consecutive periods up to 12 months prior to September of each growth year, and snow depth (recorded annually on 28 February and 31 March at Beaverlodge). Regression analyses were tested using both untransformed and $\log_e$-transformed values of the dependent variable describing aspen growth (I). A preliminary analysis of the tree-ring records indicated significant ($P < 0.001$) serial autocorrelation in the dependent variable (r^2 values of 0.463 for I and 0.366 for $\log_e(I)$ based on all 180 stems). The autocorrelation was removed by differencing the tree-ring chronologies to produce a stationary time series, so that regression analysis could be appropriately applied for assessment of factors affecting interannual variation in aspen growth (Hogg 1999). Differencing of the $\log_e$-transformed growth variable ($\log_e(I) - \log_e(I_{-1})$) is mathematically equivalent to generating a time series of $\log_e(I/I_{-1})$, which thus expresses the proportional change in the current year's growth (I) relative to that in the previous year (I_{-1}).

In the analysis, the best fitting regression equation was obtained after stepwise inclusion of independent variables with coefficients that were statistically significant at the 5% level. Delays in growth responses were also examined by testing the inclusion of each independent variable with a 1-, 2- or 3-year time lag in the regression equations. The sensitivity of stem area increment to each significant factor was assessed using a sensitivity index, calculated by multiplying the regression coefficient for each factor by the standard deviation of observed values of that factor for the period of interest (1950–1997). The potential impact of other climatic factors such as thaw–freeze events, that are difficult to quantify for regression modelling, were also examined.

Results

Stand characteristics

Dates of stem origin from the basal disks indicated that the 18 aspen stands ranged in age from 43 to 99 years (Table 1). The stands were mostly evenly aged, with a mean age range of 5 years for stems sampled within stands. The means and ranges of stem age and diameter were similar between stands designated as "healthy" and "stressed," while height, density, and basal area tended to be greater in the healthy stands. Soil texture was highly variable among the 18 stands, with a similar range of percent content of sand, silt, and clay among the nine stands in each category (Table 1).

By definition, the nine stressed stands had a greater percent incidence of stems showing damage by wood-boring insects and fungal pathogens (15–97%) relative to that in the nine healthy stands (0–14%; Tables 1 and 2). When all forms of stem damage are included, including stem breakage and cracks by wind and frost, more than half (51–97%) of the standing stems were damaged or dead in each of the stressed stands, whereas fewer than half (16–46%) of the stems were damaged or dead in each of the stands classed as healthy (Table 1). The incidence of moderate (10–40%) and severe (>40%) crown dieback among living stems was highly variable but tended to be greater in the stressed stands than in the healthy stands.

Table 2. Mean percent incidence of stems (total live and dead, except where noted) showing visible signs of external damage by major species of wood-boring insects and fungal pathogens in healthy (N = 9) and stressed (N = 9) stands.

	Healthy stands	Stressed stands
Wood-boring insects		
Saperda calcarata	<1% (3)	12% (5)
Agrilus liragus	0% (0)	2% (2)
Fungal pathogens		
Armillaria spp.[a]	<1% (1)	40% (7)
Phellinus tremulae	2% (5)	10% (8)
Venturia macularis	<1% (1)	10% (2)
Hypoxylon mammatum	0% (0)	1% (1)
Peniophora polygonia	0% (0)	<1% (1)

Note: The number of stands affected by each species is given in parentheses.

[a] Percentage incidence for *Armillaria* based on dead trees only.

Insect defoliation history

Past surveys by the Canadian Forest Service indicated that defoliation by forest tent caterpillar occurred in the study area during two major periods: 1958–1964 and 1979–1990. The overall mean percent incidence of white tree rings (Hogg and Schwarz 1999) at the 18 sites showed a strong positive correlation (r^2 = 0.732, t = 11.2, df = 46, P < 0.001) with the percentage of the study area where defoliation was recorded during these insect surveys over the period 1950–1997 (Fig. 2). The incidence of white rings in disks collected at the 5- and 10-m heights was nearly always the same as that recorded in the disks from the 1.3-m height (data not shown). Although the mean total number of white rings per stem tended to be slightly greater in stressed stands (3.6) than in healthy stands (3.0), high variation in white ring incidence among the 18 stands (range 1.0–6.0) precluded the detection of any statistical difference (t = 0.66, df = 16, P > 0.5).

Tree-ring analysis

The aspen stands showed high interannual variation in growth, based on mean stem area increments (I) in the disks from the 1.3-m height (Fig. 3). In both the healthy and stressed stands, growth was strongly reduced during years with defoliation by forest tent caterpillar, especially 1962–1963, 1979, and 1984–1985, which are the years when the incidence of white tree-rings in the 180 stems exceeded 20%. The pattern and magnitude of growth was similar in healthy and stressed stands during the period 1950–1965 but was chronically reduced in stressed stands after this period. The relative difference was largest in 1981–1983, when there was a strong recovery of growth in the healthy stands but not in the stressed stands. Overall growth was especially favourable during 1971–1978; however, during 1979–1986, mean I was reduced by 34% in the healthy stands and by 50% in the stressed stands, relative to that in the preceding 8-year period. In general, growth tended to increase slightly during the late 1980s and 1990s, especially during the year when sampling was conducted (1997); however, values of I were still smaller than in most of the years in the 1970s (Fig. 3).

Fig. 2. Annual incidence of defoliation by forest tent caterpillar based on (*i*) estimated percentage of study area where defoliation was recorded during insect surveys by the Canadian Forest Service, and (*ii*) percentage of aspen stems (N = 180) showing white tree rings in disks collected at 1.3-m height.

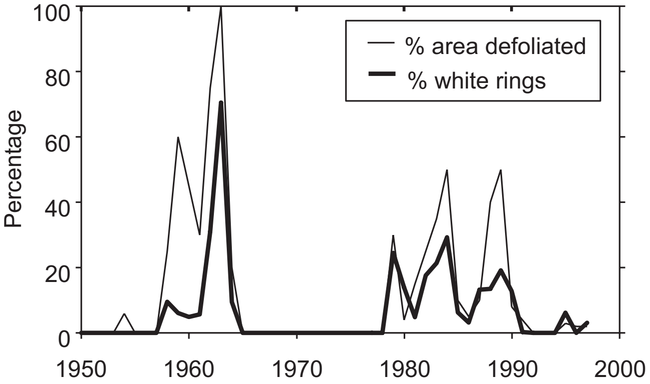
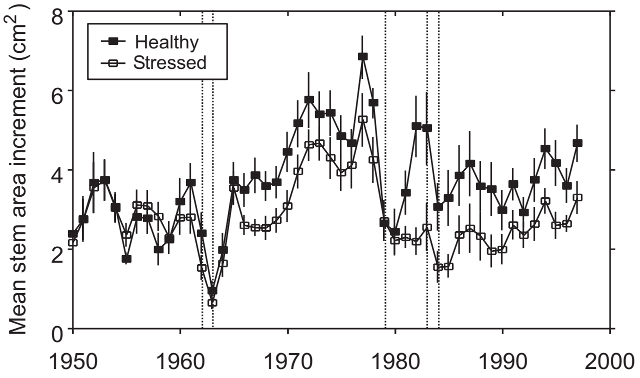


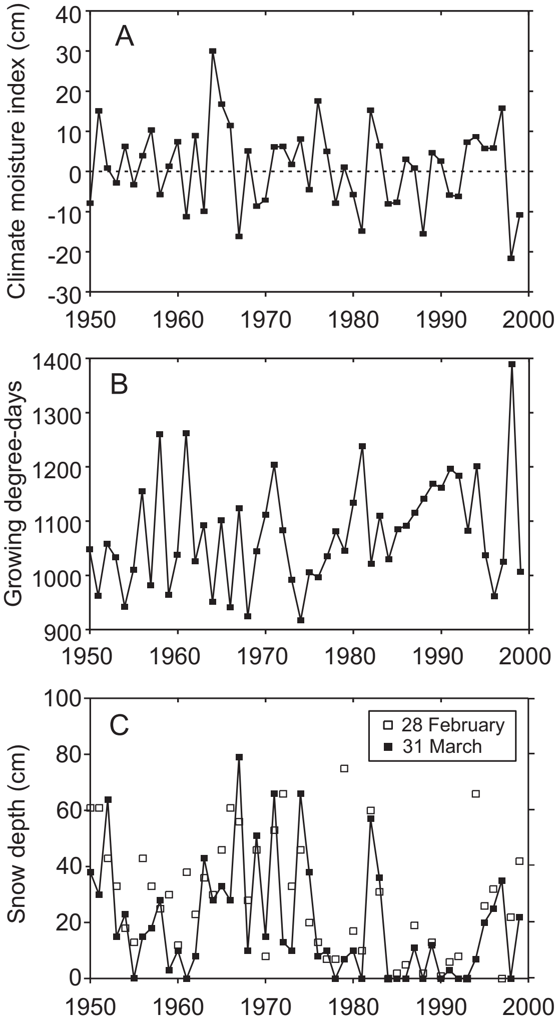
Fig. 3. Trends in mean stem area increment per tree in aspen stands designated as healthy (N = 9) and stressed (N = 9) in the Grande Prairie area of northwestern Alberta, based on tree-ring analysis of disks collected at 1.3-m height (total of 180 trees). Error bars are SEs, based on the variation recorded among stands. Broken vertical lines indicate years with severe defoliation by forest tent caterpillar based on >20% incidence of white tree rings.



The temporal variation in I was similar, with a synchronous growth pattern, at the three heights sampled (data not shown). For the period 1950–1997, annual values of I at the 1.3-m height showed a strong positive correlation (r^2 = 0.916, t = 22.4, P < 0.001) with those at 5 m and a moderate positive correlation (r^2 = 0.645, t = 9.1, P < 0.001) with those at 10 m. The latter relationship, however, was affected by the smaller number of sites represented at the start of this period (1950), when only 5 of the 18 stands had reached the 10-m height.

Examination of tree rings in dead and live branches of aspen crowns suggested that most of the recent dieback occurred during the period 1990–1995. However, reliable dates could be obtained from a total of only 15 dead crowns from 8 of the stressed stands, because of fungal decay or an insufficient number of tree rings for cross-dating of dead and live branches.

Fig. 4. Trends in annual climatic characteristics for the study area, used as inputs for regression analysis: (A) the climate moisture index, calculated for 12-month periods ending 31 August of the indicated year, using the simplified Penman–Monteith method (Hogg 1997); (B) growing degree-days, calculated as the annual cumulative sum of positive departures of daily temperature from 5°C for 1 April to 31 August; and (C) snow depths recorded annually on 28 February and 31 March.



Regression modelling of growth responses to climate variation and defoliation

The results of regression modelling indicated that most of the interannual variation in stem area increment (I) for the period 1950–1997 could be explained by the following factors: forest tent caterpillar defoliation (D) based on the proportion of white tree rings; the climatic moisture index from 1 September of the previous year to 31 August of the current year (CMI); growing degree-days from 1 April to 31 August (GDD); and snow depth on 31 March (S). Annual values of these two climatic variables are plotted in Fig. 4 for the period of analysis (1950–1997) and for the subsequent 2 years (1998–1999).

Initially, we conducted regression analysis separately for the healthy (N = 9) and stressed (N = 9) aspen stands, but the resultant regression equations (not shown) were nearly identical for the two groups of stands. For all 18 sites combined, the strongest overall relationship ($r^2 = 0.758$, df = 41) was obtained using following equation, in which the $\log_e$ transformation was used to represent interannual changes in stem area increment:

$$[1] \qquad \log_e(I/I_{-1}) = -1.244 - 0.0172D + 0.0078D_{-1} + 0.0049D_{-2} + 0.0117\mathrm{CMI} + 0.001\,13\,\mathrm{GDD} + 0.0293S$$

where D_{-1} and D_{-2} are defoliation by forest tent caterpillar for 1 and 2 years prior to the current year's growth, respectively. Each of the regression coefficients in this equation was statistically significant, based on the respective t values of –8.73, 3.57, 2.40, 4.34, 3.90, and 2.81 for D, D_{-1}, D_{-2}, CMI, GDD, and S ($P < 0.001$ for all coefficients except those for D_{-2}, $P = 0.021$; and S, $P = 0.008$). The corresponding respective values of the sensitivity index for these independent variables (see Methods) were –0.214, 0.097, and 0.061 for the defoliation variables (D, D_{-1}, and D_{-2}) and 0.112, 0.099, and 0.061 for the climate variables (CMI, GDD, and S). These results indicate temporal variation in stem-area increment was more strongly related to insect defoliation in the current year (strongly negative impact on growth) than to any of the variables describing climate variation. The positive, but smaller total magnitude of the sensitivity indices for defoliation during the previous 2 years reflects a trend for partial recovery of aspen growth during the 2 years after the end of defoliation events.

The same general results, but with smaller r^2 values (0.686–0.755), were obtained using alternative variables for moisture in eq. 1, including the use of 12-month periods ending on 31 July rather than 31 August for the CMI or using annual precipitation (same periods) instead of the CMI. Testing of total precipitation or mean temperature for each month separately (in place of the CMI or GDD in eq. 1), revealed a significant influence only for the current-year precipitation in June ($t = 2.28$, $P = 0.028$) or July ($t = 2.56$, $P = 0.014$), but the overall r^2 values of 0.686 and 0.695 were again smaller than for eq. 1. Similar results were also obtained using untransformed values of I or using insect survey records (mapped proportion of study area with forest tent caterpillar) as an alternative measure of D (log-transformed or untransformed I); however, values of r^2 for these regression equations (0.355–0.520) were considerably lower than for eq. 1. In all equations tested, growth variation was found to be more sensitive to defoliation than to climate variables.

Figure 5 shows the observed pattern of temporal variation in stem area increment (all sites), and that described by the best-fitting regression model (eq. 1). Although the regression model described much of the observed variation in stem-area increment, the model did not capture the pronounced growth increase in 1977 and also failed to explain observed decreases in growth in several instances, e.g., in 1966, 1990, and 1992.

Biotic factors associated with crown dieback and mortality

No significant relationships were detected in correlation analyses of relationships between mean number of white rings (insect defoliation) and the percent incidence of crown dieback and stem mortality at the 18 sites. However, the total percent incidence of wood-boring insects and fungal pathogens at each site showed a weak, but statistically significant, positive correlation with the mean number of white rings over the period 1979–1997 ($r^2 = 0.207$, $t = 2.05$, df = 16, $P < 0.05$). A stronger positive correlation ($r^2 = 0.426$, $t = 3.71$, df = 16, $P < 0.002$) was found between the total percent incidence of wood-boring insects and fungal pathogens and the total percentage of stems that were either dead or affected by crown dieback (>10%).

Extreme events during late winter

Examination of the climate record revealed that winter conditions in the study area were unusually warm and dry over consecutive years, from 1983–1984 to 1992–1993. During these years, snow depth on 28 February at Beaverlodge was only 6 cm, compared with a long-term mean snow depth of 30 cm (Fig. 4). Two of the winters during this period had exceptionally severe thaw–freeze events during late winter. In 1990, the mean temperature in March (0.3°C) was the fourth warmest on record but was followed by a cold period with a minimum temperature of –14°C on 10 April. Conditions were even more extreme in 1992, when the March mean temperature (3.0°C) was the warmest since records began in 1918. Soil thawed to a depth of 50 cm by mid-March, 1 month earlier than normal, and flowering of aspen was recorded at the end of March (E. Beaubien, personal communication). These events were followed by a period of severe frost during 7–10 April, with a minimum temperature of –16°C.

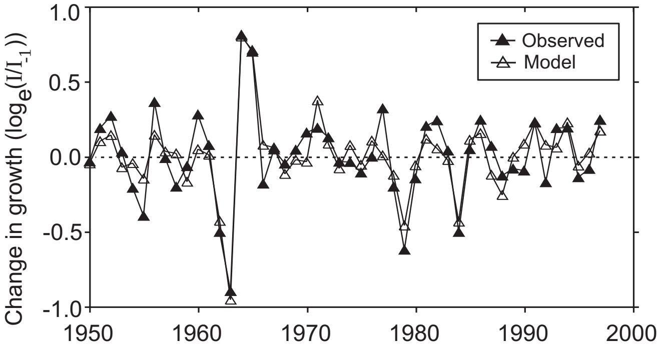
Discussion

Factors influencing interannual variation in aspen growth

The tree-ring analysis indicated that defoliation by forest tent caterpillar was the most important factor causing interannual variation in mean stem growth of the 180 aspen trees sampled in the Grande Prairie area of northwestern Alberta. The incidence of abnormally pale-coloured (white) tree rings showed a good correspondence to survey records of defoliation by forest tent caterpillar in the study area, thus supporting previous evidence that white rings can be a useful indicator of past insect defoliation of aspen at the stand level (Hogg and Schwarz 1999). White rings were recorded in each of the 18 stands sampled, indicating that most, if not all, aspen stands in the study area were defoliated at least once by insects during 1950–1997, the period covered by this study.

The tree-ring record showed two periods of strongly reduced growth of aspen, both of which coincided with major defoliation events in the study area (Figs. 2 and 3). The first was between 1961 and 1963, when mean stem area increment decreased by 75%, and the second occurred between 1977 and 1980, when a mean decrease of 64% was recorded. Similar growth patterns were observed from a previous study of declining aspen stands in western Saskatchewan (Hogg and Schwarz 1999), where severe defoliation and drought led to an 84% decrease over the period 1977–1980. Based on the large size of insect outbreaks, synchronous growth reductions may be expected over vast areas of aspen forests in the western Canadian boreal forest, adjacent parklands, and elsewhere. According to Sterner and Davidson (1982), moderate to severe insect defoliation of aspen was mapped over a total aggregate area of 20×10^6 ha in the Canadian Prairie Provinces during 1977–1981. Thus, interannual variation in net primary productivity of aspen forests, especially that caused by insect defoliation, is likely to be a significant contributor to the year-to-year variation in the uptake (or release) of CO_2 by the forested ecosystems of this region.

Fig. 5. Observed and modelled variation in stem growth of aspen (mean of all 18 sites) expressed as $\log_e(I/I_{-1})$, where I and I_{-1} are annual increments in stem area for the current and previous year, respectively. Observed growth is based on tree-ring analysis of disks collected at 1.3-m height (Fig. 3), and modelled growth was obtained using regression analysis (eq. 1).



Based on the regression analysis, climate played a significant, but secondary, role in its influence on year-to-year variation in aspen growth. Variation in moisture, as reflected by annual values of the CMI (Hogg 1997), appeared to be slightly more important than variation in temperature, as reflected by the cumulative number of growing degree-days. The relative importance of moisture may be a consequence of the generally dry climate of the study area compared with that found in other areas of the Canadian boreal forest (Hogg 1994). In addition to the direct impacts of dry soils, the high atmospheric vapour pressure deficits that occur during regional-scale drought events would have caused reduced stomatal conductance and photosynthesis of aspen, even in sites where soils may have been locally moist (Hogg and Hurdle 1997; Hogg et al. 2000*b*). The regression analysis also indicated a significant positive influence of early spring (31 March) snow depth on aspen growth, even though the moisture contributed by the previous winter's snowfall was already included in calculation of the CMI (annual periods from 1 September to 31 August). This may indicate that in addition to its role in providing moisture to soils during the spring, snow has other benefits for aspen growth, such as protection of roots from exposure to thaw–freeze events and dessication in late winter.

Factors affecting aspen health and crown dieback

The most distinctive difference between the aspen stands classified as "healthy" or "stressed" (Table 1) was that the stressed stands had a greater proportion of stems that had been damaged by wood-boring insects, fungal pathogens, and other factors. However, no single factor could directly explain this difference. The stressed stands tended to have a slightly greater number of white rings and were situated at a slightly lower mean elevation relative to healthy stands. Thus, stressed stands should have had a slightly warmer and drier climate, on average, than the healthy stands (Hogg 1994). For both of these factors, the difference in mean values was small relative to the variation within each of the two stand categories, but the combined effects of the three factors might have contributed to the observed differences between the healthy and stressed stands. For example, the tree-ring analysis indicated that following the collapse in stem growth during 1977–1980, the healthy stands showed a stronger and more rapid recovery than the stressed stands (Fig. 3). Climatic conditions were dry in 1980–1981, and drought was probably more severe, on average, in the stressed stands. This might have increased the likelihood of subsequent infestations by wood-boring insects and fungal pathogens in these stands, as suggested by several previous studies of forest decline in eastern North America (Houston 1992). Several early studies concluded that forest tent caterpillar defoliation causes reduced growth (Duncan and Hodson 1958; Hildahl and Reeks 1960) and twig dieback (Rose 1958) in trembling aspen but no significant impact on stem mortality. In a subsequent study, however, Churchill et al. (1964) showed that severe insect defoliation of aspen for three consecutive years led to an increase in fungal pathogens and insect borers, with a significant increase in stem mortality during the period 6–10 years after the defoliation had occurred. This interpretation is supported by our results, in which we found that among the 18 stands, the incidence of wood-boring insects and fungal pathogens in 1997 was significantly correlated with (*i*) the cumulative number of white rings during the previous 18 years and (*ii*) the proportion of stems that were either dead or affected by crown dieback. One of the unexpected results of this study, however, was that the most recent dieback in the study area was not reported until 1990–1992, during a period of generally increasing growth in both stressed and healthy stands following the defoliation and drought events of the 1980s. If wood-boring insects and fungal pathogens were already playing a major role during this period, then stem growth should have shown a gradual decline, especially in the most strongly affected, stressed stands (but see Mallett and Volney 1999). This points to the possibility that additional factors contributed to this dieback event.

In the more detailed examination of the climate record, we noted that late winter snow cover was unusually light during the period 1984–1993. Two of those years, 1990 and 1992, exhibited extreme thaw–freeze events in March and April that should have been sufficiently severe to cause damage to aspen stands in the study area, especially at the lower elevations. A tendency for modest, transient reductions in stem growth was observed during these 2 years, especially 1992, that was not reflected in the regression model of growth responses to defoliation, drought and growing degree-days (Fig. 5). Although the impact of these extreme weather events is difficult to assess in our retrospective analysis, Cayford et al. (1959) documented reduced growth, bud injury, and abnormal leaf development in trembling aspen and other species, following a similar sequence of weather events in Manitoba and eastern Saskatchewan during the winter and spring of 1958. Unusual, late winter thaw–freeze events have also been implicated as a major cause of various episodes of extensive forest dieback in areas throughout North America and Europe (Auclair et al. 1990, 1992, 1996; Braathe 1995). In addition to frost injury of buds and leaves, it has been shown experimentally that such thaw–freeze events can lead to dieback in birch as a result of xylem cavitation (Cox and Malcolm 1997), although comparable experiments have not been conducted on aspen.

Based on the results of this study, it appears that the combined impacts of several factors have contributed to dieback, increased mortality, and reduced growth of aspen stands in the study area and elsewhere in western Canada. These factors include insect defoliation, drought, and thaw–freeze events, as well as the impacts of fungal pathogens and wood-boring insects. Similar conclusions, involving synergistic influences of climatic and biotic stresses, have been made in explaining the causes of dieback in many tree species (Houston 1992), including the decline of sugar maple in eastern North America during the 1980s (Kolb and McCormick 1993; Payette et al. 1996).

Although natural factors appeared to explain the observed responses, aspen forests in the study area are also subject to a wide variety of localized impacts from human activity, including cattle grazing, cultivation, and industrial development. The aspen stands included in this study were chosen to be relatively free of these influences, but we cannot rule out possible influences of air pollutants such as ozone (Greitner et al. 1994), SO_2 (Lieffers and Campbell 1984), and elemental sulfur deposition (Maynard et al. 1994) on the observed patterns of growth and dieback.

Future impacts of climate change

The tree-ring analysis indicated that there was a general recovery of aspen growth in the study area during the 1990s. In 1997, when sampling was conducted, mean stem area increment peaked at its greatest value since the early 1980s (Fig. 3). This growth recovery coincided with a period of generally cool, moist conditions during the mid-1990s, when very little insect defoliation was recorded (Figs. 2 and 4). The major El Niño year of 1998, however, was unusually warm and dry, and severe drought continued during 1999. Furthermore, large areas of aspen forests were defoliated in northern Alberta, including portions of the study area, by a major outbreak of large aspen tortrix (*Choristoneura conflictana* (Walker)) during the summer of 2000 (J.P. Brandt and E.H. Hogg, unpublished data). Thus, aspen growth in the study area is likely to have decreased since 1997, and the incidence of crown dieback may be expected to increase again in the near future.

The western Canadian interior had already warmed by between 0.9 and 1.7°C between 1895 and 1992 (Environment Canada 1995), and temperatures are projected to increase even more rapidly as concentrations of CO_2 and other greenhouse gases continue to rise during the 21st century (Intergovernmental Panel on Climate Change 1996). One of the major concerns for this region is that warming might result in a drier future climate similar to that presently found at the northern edge of the prairies, where aspen stands are stunted and prone to severe dieback during periods of drought (Hogg and Hurdle 1995). Forest tent caterpillar is generally favoured by warm, dry summers (Ives 1981); therefore, its impacts on aspen, in combination with drought, might be expected to increase under climate change. Thus, process-based model projections of future increases in net primary productivity of boreal forests under global change (e.g., Peng and Apps 1999; Price et al. 1999; Grant and Nalder 2000) could be highly optimistic for aspen, unless the impacts of insect defoliation are included (Hogg 1999). Other factors such as fungal pathogens and impacts of thaw–freeze events are more difficult to characterize quantitatively in simulation models, but they are also likely to play a fundamental role in determining future responses of aspen forests under global change. Furthermore, it has been postulated that aspen forests exert significant feedbacks on the seasonal climate patterns of this region (Hogg et al. 2000*a*). Given the complexity of these interacting factors, there is a need for large-scale research and monitoring to determine how aspen and other boreal tree species are responding under the climatic warming that is already evident in this region.

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