Impacts of a regional drought on the productivity, dieback, and biomass of western Canadian aspen forests

E.H. (Ted) Hogg, J.P. Brandt, and M. Michaelian

Abstract: We examined the impacts of a severe, regional drought (2001–2002) on trembling aspen (*Populus tremuloides* Michx.) forests in the western Canadian interior. A total of 150 plots were established in 25 study areas as part of a regional-scale study (CIPHA). Aspen health and mortality were assessed annually during 2000–2005, and changes in stem biomass were estimated using tree-ring analysis and plot-based measurements. Net mean increment in living biomass for all plots was 2.2 t·ha^{-1}·year^{-1} during 2000–2002 but subsequently decreased to near zero. This collapse was driven by a more than two-fold increase in stem mortality and a 30% decrease in regional stem growth during and following the drought. The analysis showed that spatial variation in aspen productivity and biomass across the region was positively related to multiyear mean values of a climate moisture index and mineral soil silt content but was negatively related to levels of insect defoliation and wood-boring insects. In contrast, mortality and dieback was best correlated with minimum annual climate moisture index, which provided a measure of short-term drought severity. The results support previous studies showing that aspen forests are moisture limited in this region, which poses concerns for the future under a changing climate.

Résumé : Nous avons étudié les impacts d’une sécheresse sévère (2001-2002) à l’échelle régionale sur les forêts de peuplier faux-tremble (*Populus tremuloides* Michx.) de la région intérieure dans l’ouest du Canada. Au total, 150 parcelles ont été établies dans 25 zones d’étude dans le cadre d’une étude régionale (CIPHA). La santé et la mortalité du peuplier faux-tremble ont été évaluées annuellement de 2000 à 2005 et les changements dans la biomasse de la tige ont été estimés à l’aide de l’analyse des cernes annuels et du mesurage des parcelles. L’accroissement net moyen de la biomasse vivante pour l’ensemble des parcelles était de 2,2 t·ha^{-1}·an^{-1} de 2000 à 2002, mais il a par la suite diminué pour devenir presque nul. Cet effondrement était le résultat de la mortalité des tiges qui avait plus que doublé et d’une diminution de la croissance régionale de la tige de 30% pendant et après la sécheresse. Les analyses ont montré que la variation spatiale dans la biomasse et la productivité du peuplier faux-tremble dans la région était positivement reliée aux valeurs moyennes sur plusieurs années de l’indice d’humidité du climat et de la teneur en limon du sol minéral. Par contre, elle était négativement reliée à la sévérité des défoliations causées par les insectes et des dégâts causés par les insectes perceurs. À l’inverse, la mortalité et le dépérissement étaient le mieux corrélés au minimum annuel de l’indice d’humidité du climat qui fournit une mesure de la sévérité de la sécheresse à court terme. Les résultats concordent avec ceux des études précédentes qui montraient que l’humidité est le facteur limitant dans les forêts de peuplier faux-tremble de cette région, ce qui soulève des craintes pour l’avenir dans le contexte des changements climatiques.

[Traduit par la Rédaction]

Introduction

Trembling aspen (*Populus tremuloides* Michx.) is the most widespread tree species in North America (Perala 1990) and is especially abundant in the Canadian boreal forest, where it is important both ecologically and commercially (Peterson and Peterson 1992). Trembling aspen (hereinafter referred to as “aspen”) is also the predominant tree in the parkland zone along the northern edge of the Great Plains, where conifers are naturally absent (Hogg and Hurdle 1995). Despite the high tolerance of aspen to climatic and biotic stressors (Lieffers et al. 2001), aspen forests have declined in some areas of North America, including the southwestern United States (Bartos 2001; Di Orio et al. 2005; Worrall et al. 2008) and in northeastern Ontario (Candau et al. 2002). Commonly reported symptoms of aspen decline have included (*i*) abnormally high levels of twig and branch dieback in the crowns of living trees (hereinafter referred to as “dieback”); (*ii*) increases in aboveground mortality; and (*iii*) long-term losses of aspen forest cover arising from a combination of high mortality and poor regeneration (e.g., Bartos 2001; Frey et al. 2004).

In the prairie provinces of western Canada, a regional assessment showed that boreal aspen forests were generally healthy in the early 1990s (Brandt et al. 2003), but since then, levels of aspen dieback and mortality have increased across parts of Saskatchewan and Alberta. This has raised concerns from both the forest industry and the general public as to the causes of this dieback. Previous studies (Hogg and Schwarz 1999; Hogg et al. 2002*a*) showed that drought,

Received 20 September 2007. Accepted 19 December 2007. Published on the NRC Research Press Web site at cjfr.nrc.ca on 24 April 2008.

E.H. Hogg,[1] J.P. Brandt, and M. Michaelian. Northern Forestry Centre, Canadian Forest Service, Natural Resources Canada, 5320-122 Street, Edmonton, AB T6H 3S5, Canada.

[1] Corresponding author (e-mail: thogg@nrcan.gc.ca).

doi:10.1139/X08-001

insect defoliation, thaw–freeze events, and fungal pathogens were major factors causing dieback, mortality, and reduced growth of aspen in affected areas of western Canada.

The finding that aspen forests are sensitive to drought has posed additional concerns for the future, based on model projections of future warming that may lead to drier climates in this region over the next few decades (Hogg and Hurdle 1995; Schindler and Donahue 2006). To address these concerns, we established a large-scale study in 2000, entitled Climate Impacts on Productivity and Health of Aspen (CIPHA) that includes annual tree-based monitoring of health and dieback in a network of long-term research plots across the western Canadian interior. In a previous investigation (Hogg et al. 2005), tree-ring analysis was conducted to retrospectively determine the factors governing temporal variation in basal area increment of aspen stems in the CIPHA plots over the period 1951–2000. Most of the temporal variation in stem growth was explained by interannual changes in moisture, as reflected by a climate moisture index (CMI) in combination with insect defoliation, primarily caused by forest tent caterpillar (*Malacosoma disstria* Hbn.).

Subsequent to the establishment of the CIPHA study, the region was affected by a period of drought that was exceptionally severe during 2001–2002 (Bonsal and Wheaton 2005). We observed browning of aspen leaf margins in the parkland of east-central Alberta during the summer of 2002 and noted widespread dieback of aspen and other trees during the spring of 2003. Aerial surveys were conducted in 2004, and moderate to severe levels of mortality (estimated >35%) were mapped within a substantial proportion of the aspen stands within a 100 000 km^2 area of parkland in western Saskatchewan and eastern Alberta (M. Michaelian, unpublished data).

The establishment of the CIPHA plot network prior to the 2001–2002 drought provided an opportunity to quantify relationships between drought severity and its impact on aspen forests. Such relationships are needed for risk assessments of future impacts under a changing climate (cf. Volney et al. 2005). However, forest decline can be a complex process involving several interacting factors, as elucidated by the model of Manion (1991). In particular, drought may lead to rapid dieback and mortality through a catastrophic loss of the tree's capacity for water uptake (xylem cavitation) or may operate in combination with other stressors to cause a gradual decline in tree growth and vigour through decreased photosynthesis and exhaustion of carbohydrate reserves (Frey et al. 2004; Hogg et al. 2006). Thus, a major objective of this study was to identify which factors (including drought) are most important in determining regional-scale, spatial variation in aboveground mortality, dieback, and the growth and accumulation of stem biomass in aspen forests across the west-central Canadian interior. Specifically, we examined aspen responses over a 5 year period (2000–2005) in relation to regional-scale gradients in climatic moisture regimes, in combination with other factors including insect defoliation, damage by wood-boring insects, stand age, and site characteristics. In this study, we conducted tree-level measurements and health assessments within the network of CIPHA monitoring plots and used tree-ring analysis and allometric equations (Lambert et al. 2005) to scale up to the stand level.

Materials and methods

Field measurements and sampling

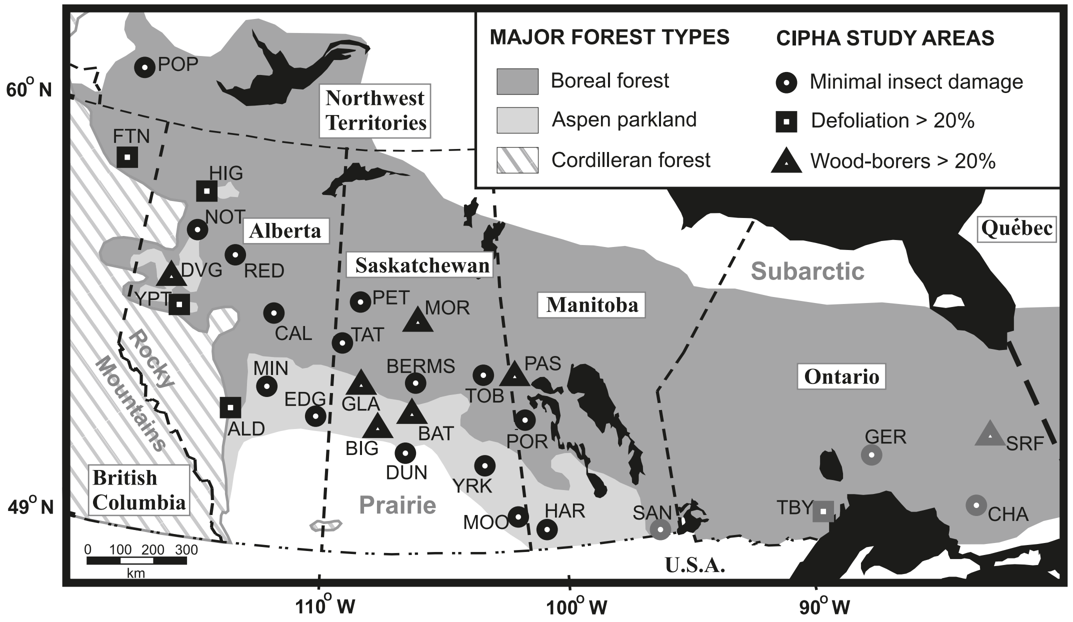
The CIPHA study includes a network of long-term monitoring plots located in 30 study areas across the boreal forest and adjacent aspen parkland of western and central Canada (Fig. 1). The original plot network of study areas was established in 2000 (Hogg et al. 2005), and the remaining plots were established during 2001 (ALD and SRF study areas) and 2004–2005 (CHA, GER, TBY, and SAN study areas, Fig. 1).

The study region has a continental climate, with a large seasonal variation in mean monthly temperatures from about –20 °C in January to 17 °C in July. Mean annual precipitation is typically 350–500 mm in the west and increases to 700–900 mm in Ontario. The present analysis focuses on the 25 study areas (150 plots) situated in the climatically drier portions of the region west of 100°W (Fig. 1). Twelve of these study areas are located in the aspen parkland, a predominantly agricultural zone that represents a transition between forest and prairie (Bird 1961; Hogg and Hurdle 1995). The soils in this region are primarily gray luvisols in the southern boreal forest and black or dark brown chernozemic soils in the parkland zone (Clayton et al. 1977).

In each study area, three pure aspen stands (40–80 years old) were selected within a distance of 30 km. In each stand, two plots were established that were 50–100 m apart and at least 50 m from the stand edge, where possible. Plots were rectangular with a width of 10 m and having a sufficient length (typically 15–35 m) to include at least 25 living aspen trees when plots were established. All living and dead trees with stem diameter >7 cm were labeled with numbered tags. Total height and stem DBH (diameter at breast height, 1.3 m) of each tree was measured during the year of plot establishment and again in 2004. Annual, tree-based health assessments were conducted within each plot during the early part of the growing seasons (late May to July) of 2000–2005. Assessments included tree status (species, dominance, percent crown dieback, and live versus dead) and the incidence of insects, diseases, and other damage agents. The percentage loss of leaf area by defoliating insects was also estimated. In 2002, a sample of the uppermost 15 cm of mineral soil was collected at each plot. Soil analyses were conducted according to the methods of Kalra and Maynard (1991) and included analyses of particle size (sand, silt, and clay), pH, electrical conductivity, extractable NO_3-N, cation exchange capacity, and exchangeable calcium.

Tree-ring analysis was conducted on all plots during the autumn of 2004 or in 2005. Trees were selected for sampling according to the method of Hogg et al. (2005) that enables "scaling up" stem radial growth to provide estimates of stand-level growth. The method involves the selection of one off-plot tree to represent each of three DBH classes (large, medium, and small) within each plot. Tree-ring samples were collected at the 1.3 m height, using either an increment borer or by destructive sampling. Samples were prepared and ring widths were measured (two radii per tree) and cross-dated according to methods described by Hogg et al. (2005). The percent incidence of "white" tree

Fig. 1. CIPHA study areas in the west-central Canadian interior. Symbol shapes show levels of insect damage recorded over 5 years of aspen health assessments (2000–2004), based on mean percent defoliation or the mean percentage of stems with external symptoms of wood-boring insects. Grey symbols denote eastern CIPHA study areas not included in the main analysis of drought impacts. Distribution of major forest types is also shown.



rings, which denote years with severe insect defoliation (Hogg et al. 2002*b*), was also recorded and was used to provide an indicator of defoliation impacts in the years prior to the onset of annual monitoring. Mean stem age for each plot was determined from the earlier sampling (2000 or 2001) that included collections of disks at 1.3 m and at stump height (Hogg et al. 2005). The tree-ring analysis of these samples indicated that aspen had attained a height of 1.3 m within an average of 2 or 3 years (maximum of 9 years).

Estimates of stand biomass, growth increments, and mortality losses

Stand-level, aboveground aspen biomass was determined for each plot using the Canadian national equations of Lambert et al. (2005), as follows. Firstly, the biomass of each living aspen within the plot was estimated from the field measurements in June or July 2004 using the DBH- and height-based equation for this species. Plot-level biomass in 2004 was then estimated as the sum of the biomass of all living aspen in the plot. For simplicity, we assumed that these biomass estimates were applicable to the start of the 2004 growing season (i.e., excluding stem growth in 2004).

Growth in stem biomass was determined using two methods. The first was the mensuration method, in which we applied the biomass equations of Lambert et al. (2005) to the tree-level measurements of DBH and height on two dates (2000–2001 and 2004). However, this method was prone to several sources of error. Notably, it was found that the measurement of aspen tree height (typically 15–22 m) had a low precision (±0.5 m at best) relative to mean height growth (0.49 m) during the period between measurements. Growth in mean stem diameter was also small (0.56 cm) relative to measurement error, and dendrometer measurements have shown that diameters of aspen stems vary up to 0.3 cm seasonally from freezing and changes in moisture content (E.H. Hogg, unpublished data). Finally, it was not feasible to measure all stands at the same time of year because of the wide geographic extent of the plot network.

As an alternative, we used a combination of forest mensuration and tree-ring analysis (method MTR) for the estimation of stand-level biomass increment. This method also enabled the estimation of biomass increment at an annual resolution. A previous tree-ring study of the CIPHA plots showed that interannual variation in aspen radial growth was highly synchronous at different heights along the stem (Hogg et al. 2005), so that annual growth in DBH should provide a good relative indicator of growth variation at the tree level. First, we used tree-ring widths to determine xylem (inside bark) DBH of each (off-plot) sampled aspen tree at the start of each growing season, expressed as a proportion of xylem DBH at the start of the 2004 growing season. These results were then used to reconstruct past changes in DBH for all living aspen in the adjacent plot that were in the same DBH class as the sampled tree. Specifically, DBH was reconstructed for the spring of each year from 1996 to 2003 through back-calculation from the field measurements of DBH in 2004. Similarly, DBH in spring 2005 was estimated by applying the proportional increase in xylem diameter during 2004 (from the tree-ring analysis) to the field-measured DBH in 2004.

Initial estimates of annual biomass growth were made for each year (1995–2005) for each on-plot, living aspen using the alternative, DBH-based equations of Lambert et al. (2005). For 2004, we also had estimates of biomass from equations that use both DBH and height, and these are considered to be more reliable than estimates based on DBH alone (Lambert et al. 2005). Thus, for each living tree we calculated a height-based correction factor (k_h) as

$$[1] \qquad k_{\mathrm{h}} = \frac{B_{\mathrm{dh},2004}}{B_{\mathrm{d},2004}}$$

where $B_{\mathrm{dh},2004}$ is the 2004 biomass from the equations that use both height and DBH, and $B_{\mathrm{d},2004}$ is the 2004 biomass from the equations that use DBH only. Height-corrected estimates of aboveground tree biomass for each year ($B'_{\mathrm{dh,year}}$) were then estimated as $k_{\mathrm{h}} \times B_{\mathrm{d,year}}$.

For aspen that died during the monitoring period (2000–2005), aboveground tree biomass was estimated using the same procedure as described above but with the following modifications: (*i*) we used the DBH and height measurements from 2000 (when these trees were living) rather than 2004; (*ii*) annual growth in DBH of dying trees was assumed to be zero during the year prior to stem death; and (*iii*) live tree biomass of dying trees was set to zero starting in the year of stem death.

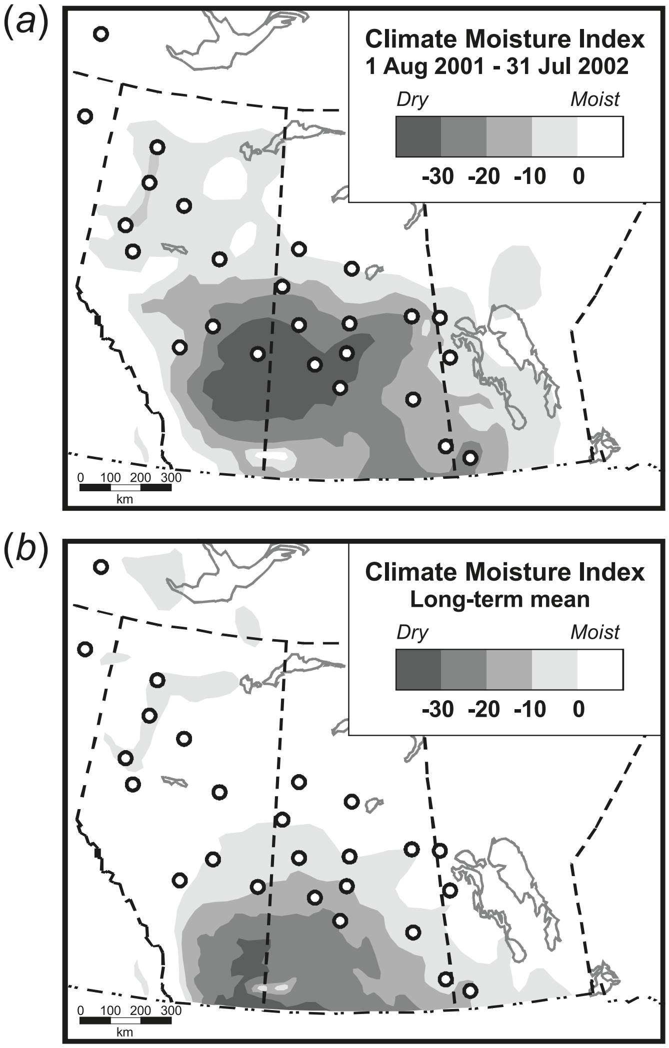
Annual estimates of biomass at the plot level ($\mathrm{t \cdot ha^{-1}}$) were calculated as the sum of $B'_{\mathrm{dh,year}}$ for all living trees in each given plot divided by plot area. Similarly, annual mortality losses of biomass at the plot level ($\mathrm{t \cdot ha^{-1} \cdot year^{-1}}$) were determined as the sum of $B'_{\mathrm{dh,year}}$ for all trees dying in a given plot, divided by plot area. Annual growth at the stand level was calculated as the increase in biomass density between successive years ($\mathrm{t \cdot ha^{-1} \cdot year^{-1}}$); growth estimates were reported separately for aspen that were living in 2005 versus aspen that had died during the period of monitoring (2000–2005).

Analyses of factors affecting aspen growth, mortality and biomass

Monthly climate variables for the period 1902–2004 were determined for each CIPHA stand using a national, spatially interpolated database (McKenney et al. 2006) that includes mean daily maximum temperature ($T_{\max}$), mean daily minimum temperature ($T_{\min}$), and precipitation (PCP). Spatial interpolations were derived using the program ANUSPLIN that provides estimations of climate variables as a function of site latitude, longitude, and elevation (McKenney et al. 2006).

Spatial and temporal variation in moisture regimes and drought severity were determined through monthly calculations of a CMI that has been previously shown to provide a good indicator of moisture effects on interannual variation in aspen growth (Hogg et al. 2002*a*, Hogg et al. 2005). Monthly CMI values were determined as PCP minus PET, where PET is potential evapotranspiration as estimated from $T_{\max}$, $T_{\min}$, and elevation (Hogg 1997). Annual CMI values were determined by summing the monthly CMI over 12 month periods ending on 31 July of each given year, corresponding to the period most relevant to the seasonal pattern of radial growth in aspen (Hogg et al. 2005). Annual CMI values were expressed in units of centimetres per year of water balance, where positive values denote moist conditions that normally occur in boreal and cordilleran forests, and negative values denote dry conditions normally associated with the aspen parkland and prairies of western Canada (Hogg and Bernier 2005). For the present study of regional-scale, spatial variation in aspen responses, CMI values were calculated over several time periods including longer term mean CMI during 1961–2004 ($\mathrm{CMI}_{61\text{–}04}$) and mean CMI during 2000–2004 ($\mathrm{CMI}_{00\text{–}04}$), that is, the period covering the plot-based assessments of aspen growth, health, and mortality. The driest 12 month period was generally that in 2002 (i.e., CMI for 1 August 2001 – 31 July 2002; Fig. 2), but the most northerly study areas were drier in 2000 (FTN) or 2004 (HIG, NOT, and POP). Thus, we estimated drought severity as the minimum annual CMI during 2000–2004 ($\mathrm{CMI}_{00\text{-}04\_\mathrm{MIN}}$).

Fig. 2. Spatial extent and severity of drought in the western Canadian interior, based on the more strongly negative values of the climate moisture index (Hogg 1997) during 2001–2002 (*a*) compared with the long-term mean for 1961–1990 (*b*). Maps are based on interpolations of monthly climate using ANUSPLIN (McKenney et al. 2006). CIPHA study areas used in the analysis of drought impacts are also shown (open circles).



We examined the factors affecting aspen responses through modelling using stepwise multiple regressions (REG procedure of SAS/STAT statistical software, SAS version 9.1, SAS Institute Inc., Cary, North Carolina). Analyses were conducted at the stand level (based on mean values of variables for two plots per stand) and at the level of the study area (mean values for three stands or six plots per study area).

Dependent variables included live aspen stem biomass in

Table 1. Characteristics of aspen stands included in the analysis of factors affecting aspen mortality, dieback, growth, and biomass in the western Canadian interior (total of 25 study areas shown in Fig. 1).

	Mean ± SD (excluding TOB)	Range (excluding TOB)	TOB study area
Stand characteristics (2004)			
Year of stem origin (basal disks)	1939±10	1919–1958	1940
Stem density (>7 cm DBH)	1352±476	626–2342	1124
DBH (cm)	17±3	13–23	22
Height (m)	18±3	10–22	**25**
Live basal area (m^2·ha^{-1})	29±5	21–39	**45**
Aboveground biomass (t·ha^{-1})	131±38	68–197	**273**
Aboveground growth (2000–2004) (t·ha^{-1}·year^{-1})	3.2±1.0	1.8–5.6	**8.7**
Mineral soil (upper 15 cm)			
Sand (%)	44±22	10–84	**8**
Silt (%)	34±15	8–63	58
Clay (%)	22±12	8–56	35
pH	6.0±0.6	5.1–7.0	**7.7**
CEC (cmol [+]·kg^{-1})	16.0±9.4	5.0–48	36
Exchangeable Ca (cmol [+]·kg^{-1})	12.3±8.2	3.5–26	**40**
Extractable NO_3-N (µg·g^{-1})	1.1±1.9	0.0–6.4	**7.6**

Note: Means and ranges are calculated from values for the 6 plots in each of 24 study areas (excluding TOB). Mean characteristics are given separately for the anomalously productive, lowland study area east of Tobin Lake, Saskatchewan (TOB; Fig. 1). Values in boldfaced type are characteristics at the TOB study area that fell outside the range of values recorded in the other 24 CIPHA study areas.

2005 (BIOMASS$_{05}$, t·ha^{-1}), mean annual stem growth over 5 years (t·ha^{-1}·year^{-1} during 2000–2004) based on estimation method MTR (GROWTH), total percentage of stem biomass lost to mortality during 2000–2005 (%MORT$_{00-05}$), visually estimated percentage of crown dieback in living aspen stems in 2005 (%DIEBACK$_{05}$, %), and the mean annual change in live aspen biomass during 2000–2005 (ΔBIOMASS, t·ha^{-1}·year^{-1}).

Independent variables included climatic, biotic, and site (soil) factors. Slope and aspect were not considered, because all CIPHA stands were situated on level to gently rolling terrain. Climatic factors included variables indicating moisture conditions (CMI and PCP) over the periods described above. Thermal variables included mean temperature calculated annually (T_{annual}), for spring ($T_{\mathrm{Apr.–May}}$), summer ($T_{\mathrm{June–July}}$), or the growing season ($T_{\mathrm{May–Sept.}}$) during 1961–2004 or for 2000–2004. We also included mean temperature of the warmest and coldest months (T_{warm} and T_{cold}) during 2000–2004, mean temperature during the relatively cool spring of April–May 2002 ($T_{\mathrm{Apr.–May\_02}}$), and deviation of this temperature from the long-term normal (d$T_{\mathrm{Apr.–May_02}}$). Biotic factors included mean basal age of aspen stems in 2000 (AGE in years), and 5 year (2000–2004) means of visually estimated percentage foliage loss from insect defoliation (DEFOL, %) and plot-based percentage of living stems with externally visible damage by wood-boring insects (BORERS, %). Soil variables included mineral soil texture (SAND, SILT, and CLAY; %), and four other variables from the soil analyses, as indicated above. To minimize potential problems with multicollinearity in the regression analysis (Zar 1996), we did not include more than one variable representing each major process or factor, that is, drought (CMI or PCP), temperature, age, defoliation, stem damage, and soil characteristics.

Results

Site characteristics

The aspen stands ranged in age from 47 to 86 years old at the end of the period of analysis (2000–2005), based on the mean stem origin dates from basal disks (Table 1). The mean year of stem origin was 1940 (SD 10 years) for the 25 western study areas included in the detailed analysis of factors affecting aspen growth and mortality. Of these 25 study areas, the Tobin Lake, Saskatchewan (TOB), study area was anomalously productive in terms of stand height, basal area, growth, and biomass despite having a mean stem origin date (1939) close to the overall mean. Soil characteristics at TOB were also anomalous, notably the low sand content and high values of silt, pH, calcium, and nitrates in the upper 15 cm of mineral soil. Unlike the other CIPHA study areas, TOB is situated within a former floodplain of the lower Saskatchewan River, with regosolic soils (Sipanok Association) consisting of strongly calcareous and stratified levee deposits (Ayres et al. 1978). The remaining study areas were all situated in upland sites removed from riparian influences. Thus, we treated the TOB study area as a lowland outlier in the analyses of factors affecting spatial variation in aspen responses.

Climatic and biotic stressors during 2000–2004

The most notable climatic event was the severe drought that affected much of the study region during the 12 month period of 1 August 2001 – 31 July 2002 (Fig. 2), when the regional mean PCP for the 25 western CIPHA study areas was 318 mm (Table 2), 27% below the long-term normal. During this period, the regional mean CMI was –16.8, which is indicative of dry, prairie-like conditions (Hogg and Hurdle 1995). The driest areas were in the aspen parklands of east-

Table 2. Mean values of annual climatic variables for 25 CIPHA study areas in the western Canadian interior (Fig. 2) during 1996–2004.

Year	PCP (mm)	PET (mm)	CMI (cm)	T_{annual} (°C)	$T_{\text{Apr.–May}}$ (°C)	T_{warm} (°C)	T_{cold} (°C)
1996	505	420	8.6	–0.5	4.2	16.9	–24.2
1997	508	424	8.3	–0.2	4.5	17.7	–20.7
1998	407	514	–10.8	3.2	9.2	18.5	–19.8
1999	456	471	–1.6	2.0	6.9	18.2	–17.9
2000	414	446	–3.2	2.4	5.4	17.5	–17.6
2001	434	451	–1.7	1.7	6.9	17.8	–19.5
2002	318	486	–16.8	1.3	2.5	18.3	–15.6
2003	428	440	–1.2	1.3	6.6	18.1	–16.2
2004	435	455	–2.0	1.6	5.0	18.0	–20.2
1961–2004	437	454	–1.7	1.0	6.0	17.5	–19.5
2000–2004	406	456	–5.0	1.6	5.3	17.9	–17.8

Note: Variable abbreviations are annual total precipitation (PCP), annual total potential evapotranspiration (PET), the climate moisture index (CMI), and mean temperatures calculated annually (T_{annual}), for 1 April to 31 May ($T_{\text{Apr.–May}}$), for the warmest month (T_{warm}), and for the coldest month (T_{cold}). All annual values are based on 12 month periods ending on 31 July of the listed year.

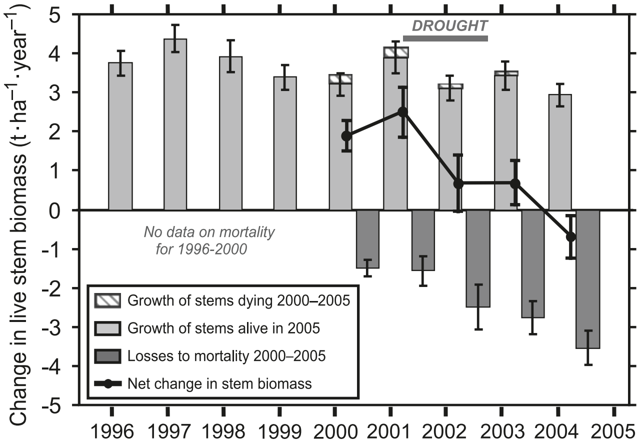
ern Alberta and western Saskatchewan, where the CMI reached values less than –30 across a large area (Fig. 2). At two of the CIPHA study areas (BAT and EDG), PCP was <170 mm (58% below normal) and CMI was less than –40, indicating conditions that were the driest ever recorded during the period of available climate data (1902–2004). For years prior to the drought, 1996 and 1997 were generally wetter and cooler than average, whereas 1998 was much warmer than average (Table 2). During 2000–2004, the period covering the current analysis of aspen responses, temperatures were generally above the long-term normal, except in the spring of 2002 when April–May temperatures were 3.5 °C cooler than normal.

Major biotic stressors included insect defoliation (DEFOL) and stem damage by wood-boring insects (BORERS). Regionally, mean levels of DEFOL were low (16% in 2000 and 7%–13% in each of 2001–2005), but an outbreak of large aspen tortrix (*Choristoneura conflictana* Walker) caused moderate to severe defoliation at the HIG, FTN, and YPT study areas during 2000–2001 (Fig. 1; see also Hall et al. 2003). Forest tent caterpillar had a minimal impact in most areas but caused moderate to severe defoliation at a few sites during 2001–2005 (ALD, SAN, and TBY). The mean incidence of BORERS (2000–2004) exceeded 20% in seven of the CIPHA study areas, including five study areas in Saskatchewan (Fig. 1). The most abundant wood-boring insect was the poplar borer (*Saperda calcarata* Say), but we also recorded *Agrilus liragus* (Barter & Brown), *Trypodendron retusum* (Le Conte), and *Dicerca* spp. Overall, there was a notable and steady increase in BORERS, from 5% of stems affected in 2000 to 23% in 2005, although some of this increase might have been a result of increasing experience and abilities of our field crews to detect external signs of damage by these insects.

Temporal variation in growth, mortality and biomass increment

Interannual variation in stem biomass increment (GROWTH) at the regional scale is shown in Fig. 3 based on mean values for all 25 western CIPHA study areas. The results showed that there was an overall 33% decrease in mean growth, from a maximum of 4.37 t·ha^{-1}·year^{-1} in 1997 to a minimum of 2.94 t·ha^{-1}·year^{-1} in 2004. However, growth estimates prior to 2000 do not include the growth of dying aspen. The most pronounced growth decrease occurred during the major drought period between 2001 and 2002 (Fig. 3).

Fig. 3. Interannual variation in aspen growth, mortality, and net change in aboveground biomass for 150 CIPHA plots in 25 study areas located across the western Canadian interior (Fig. 1). Bars and plotted points are means and error bars are SEs.



For the period 2000–2005, the annual measurements enabled stand-level estimation of stem biomass losses to mortality and interannual net changes in stem biomass. The results showed that mean losses to mortality increased from about 1.5 t·ha^{-1}·year^{-1} during the first 2 years but had more than doubled to 3.6 t·ha^{-1}·year^{-1} during 2004–2005. The combined influence of decreasing growth and increasing mortality led to a collapse in the regional mean estimate of net biomass increment (ΔBIOMASS), from a mean of 2.2 t·ha^{-1}·year^{-1} during the first 2 years to –0.6 t·ha^{-1}·year^{-1} in 2004–2005.

Factors affecting spatial variation in aspen responses

The results of regression analysis indicated that drought severity, as reflected by the variable $\text{CMI}_{00\text{–}04\_\text{MIN}}$, was the most important factor governing spatial variation in net

Table 3. Coefficients for regression of factors affecting mean responses of aspen in 24 CIPHA study areas (excluding TOB) in western Canada.

Dependent variable	Level of analysis	Constant	$CMI_{61–04}$	$CMI_{00–04}$	$CMI_{00–04MIN}$	DEFOL	BORERS	AGE	SILT	Adjusted R^2
		Regression coefficients for independent variables								
$\Delta BIOMASS_{00\_05}$	Study area	8.514	—	—	0.078	–0.117	—	–0.081	—	0.542
	Stand	3.896	—	—	0.099	–0.109	—	—	—	0.226
$\%MORT_{00\_05}$	Study area	4.332	—	—	–0.298	—	—	—	—	0.396
	Stand	4.366	—	—	–0.296	—	—	—	—	0.157
$\%DIEBACK_{05}$	Study area	5.378	—	—	–0.211	0.169	—	—	—	0.464
	Stand	4.429	—	—	–0.185	0.207	0.075	—	—	0.295
GROWTH	Study area	3.751	—	0.038	—	–0.071	–0.024	—	0.023	0.607
	Stand	5.969	—	0.055	—	–0.051		–0.031	—	0.289
$BIOMASS_{05}$	Study area	48.002	2.260	—	—	—	–1.300	1.250	0.810	0.686
	Stand	40.890	2.300	—	—	—	–1.030	1.271	0.883	0.484

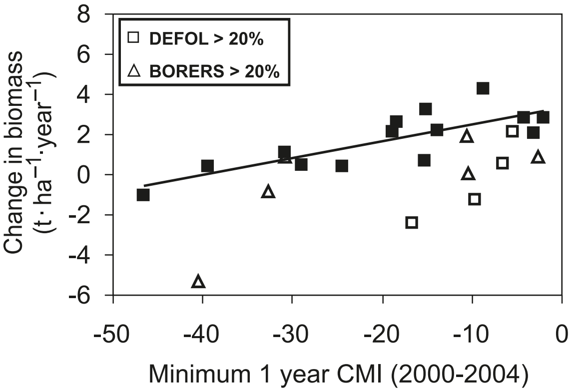
Note: Analyses were conducted at the level of individual stands ($N = 72$) and at the level of the study area ($N = 24$, based on means of three stands per study area). Values are given only for those regression coefficients that are statistically significant at the 5% level. Each regression equation included the most significant CMI variable only. Description of variables and their units of measurement are given in the Materials and methods section.

annual increment of aspen biomass (ΔBIOMASS variable in Table 3, Fig. 4). Similar results were obtained in the analyses conducted at the stand level ($N = 72$) or at the study area level ($N = 24$). Stands and study areas with insect damage showed smaller and often negative increments, although the negative regression coefficients were significant only for DEFOL (Table 3). Spatial variation in net biomass increment was largely governed by the high variation in 5 year mortality (%MORT), which in turn, was most strongly related to drought severity ($CMI_{00–04\_MIN}$; Fig. 5). However, for %MORT, no significant relationships with insect damage (DEFOL and BORERS) were detected (Table 3). Percent crown dieback in 2005 ($\%DIEBACK_{05}$) was also most strongly related to $CMI_{00–04\_MIN}$, and regression coefficients for DEFOL and BORERS were both significant in the stand-level analysis. It should be noted that the variable $\%DIEBACK_{05}$ is based on aspen that were living in 2005, whereas %MORT is based on aspen that died during 2000–2005.

Spatial variation in stand-based stem productivity (GROWTH) during 2000–2004 was significantly related to moisture, but the highest pairwise correlation ($r = 0.56$, $N = 24$ study areas) was with the $CMI_{00–04}$ rather than with the minimum CMI ($r = 0.50$). In the multiple regression analysis, the best-fitting relationship included $CMI_{00–04}$, DEFOL, BORERS, and SILT at the study area level ($r^2 = 0.607$; Table 3). At the stand level, the relationship was much weaker ($r^2 = 0.289$) and included $CMI_{00–04}$, DEFOL, and AGE. At both levels, partial regression coefficients were positive for $CMI_{00–04}$ and SILT and negative for DEFOL, BORERS, and AGE. Figure 6 shows the strongly positive relationship between productivity and moisture, as well as the lower productivity in study areas affected by defoliation and wood-boring insects.

Figure 6 also includes the productivity of the five eastern study areas in Ontario and eastern Manitoba that had similar dates of stand origin (range 1930–1956) to those of the western study areas (Table 1). Considering only study areas with minimal insect damage, there was no indication of enhanced productivity at the two wettest eastern study areas with $CMI_{00–04}$ near 40 (CHA and GER), relative to that of western study areas with $CMI_{00–04}$ close to zero or 10.

Fig. 4. Regional variation in the mean annual net change in living aspen biomass for CIPHA plots in 24 study areas in western Canada (excluding TOB), in relation to the minimum 1 year value of the climate moisture index (CMI) during 2000–2004. Open symbols are study areas with pronounced insect damage (defoliation severity > 20% or incidence of borers > 20%). The linear trend is shown for 14 study areas with minimal insect damage (solid symbols: $\Delta BIOMASS = 3.36 + 0.0843(CMI)$, $r^2 = 0.610$, $P < 0.001$).



Aboveground biomass in 2005 also showed a significant relationship with moisture, but the highest pairwise correlation ($r = 0.68$, $N = 24$) was with mean CMI values over the longer term ($CMI_{61–04}$). At both levels, the best-fitting multiple regressions ($r^2 = 0.686$ for study areas and $r^2 = 0.484$ for stands) included significant positive relationships with $CMI_{61–04}$, AGE, and SILT and significant negative coefficients for BORERS. As for productivity, biomass densities at the climatically wettest study areas in Ontario were similar to that of the most productive study areas in the west (excluding TOB), suggesting that the quasilinear relationship between CMI and biomass does not extend beyond the highest CMI values (up to 14) of western sites (Fig. 7).

For the independent variables included in each multiple regression equation (Table 3), no significant correlations ($P > 0.05$) were found in any of the pairwise comparisons among the variables for CMI, DEFOL, BORERS, or AGE. However, the variable SILT was positively correlated with each of the three CMI variables (r = 0.558, 0.438, and

Fig. 5. Regional variation in mean aspen mortality (*a*) and dieback (*b*) for CIPHA plots in 25 study areas in western Canada in relation to the minimum 1 year value of the CMI during 2000–2004. Mortality is expressed as percent loss of stand-level biomass from trees that died during 2000–2005, whereas dieback is expressed as the mean visually estimated percent crown dieback on trees that were living in 2005. Linear trends are shown for 14 study areas with minimal insect damage (solid symbols: %MORT = 4.79 – 0.180(CMI), r^2 = 0.454, P = 0.002; and %DIEBACK = 6.92 – 0.171(CMI), r^2 = 0.369, P = 0.013).

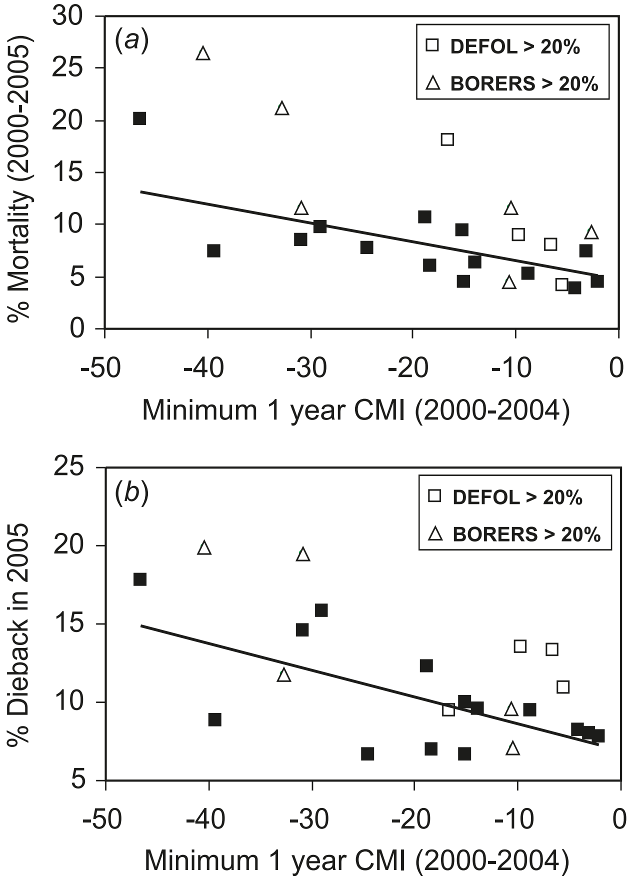


Fig. 6. Regional variation in mean annual growth of aboveground aspen biomass for CIPHA plots in 25 study areas in western Canada in relation to mean CMI during 2000–2004. Growth is also shown for plots in five additional CIPHA study areas in the climatically moister region of central Canada (grey symbols). Linear trend is shown for 14 study areas in western Canada with minimal insect damage (solid black symbols: GROWTH = 4.08 + 0.0767(CMI), r^2 = 0.624, P < 0.001).

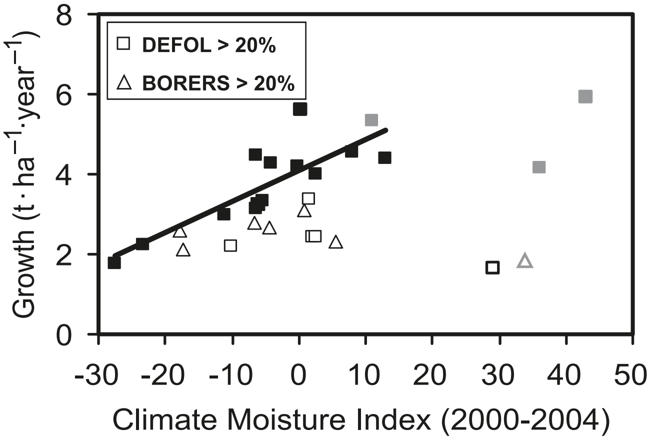
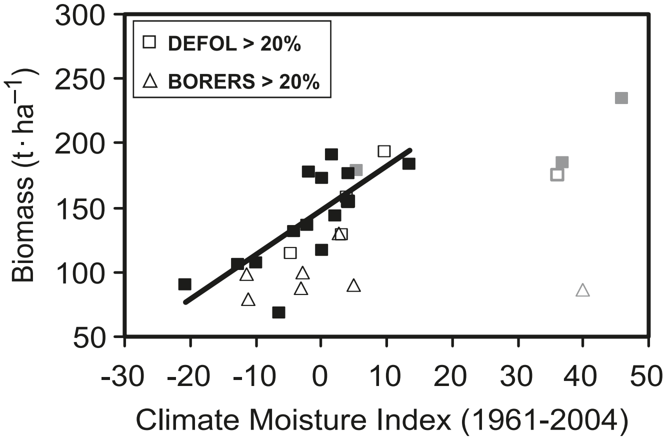


Fig. 7. Regional variation in aboveground aspen biomass in 2005 in relation to mean long-term CMI (1961–2004). Results are shown for CIPHA plots in western Canada (25 study areas) and central Canada (five study areas, grey symbols). Linear trend is shown for 14 study areas with minimal insect damage (solid black symbols: BIOMASS = 147.4 + 3.438(CMI), r^2 = 0.529, P = 0.002).



0.455 and P = 0.005, 0.032, and 0.029, respectively, for $\mathrm{CMI}_{00\text{–}04\_\mathrm{MIN}}$, $\mathrm{CMI}_{00\text{–}04}$, and $\mathrm{CMI}_{61\text{–}04}$), and SILT was also positively correlated with DEFOL (r = 0.446, t = 2.34, P = 0.029). As expected, there was a high degree of intercorrelation among climate variables denoting moisture (CMI or PCP) or temperature over different periods, but none of the multiple regression equations included more than one climate variable.

Regression analyses that included PCP rather than the CMI gave similar results but gave equations with weaker r^2 values (not shown). When temperature variables (indicated in the Materials and methods section) were included in the regression analysis, their coefficients were either not significant or indicated relationships that were opposite to those with the CMI variables. In all cases, multiple regressions involving temperature gave lower values of r^2 than those based on the CMI. The variables describing temperature during the cool spring of April–May 2002 (($T_{\mathrm{Apr.–May\_02}}$ and $\mathrm{d}T_{\mathrm{Apr.–May\_02}}$) showed significantly positive relationships with $\mathrm{DIEBACK}_{05}$, indicating that the dieback was not promoted by the cool conditions.

Discussion

A previous tree-ring study of the CIPHA plot network in western Canada (Hogg et al. 2005) showed that moisture was the main climatic factor affecting short-term, temporal variation in aspen growth during 1951–2000. The results of the present study show that moisture was also the most important climatic factor governing spatial variation in stand-level growth, dieback, and mortality during a more recent 5 year period (2000–2005) that included the severe drought of 2001–2002. Dieback and mortality was most evident in the most severely drought-affected areas of the parkland zone (Figs. 1, 2, and 5). A comprehensive research and monitoring program at the BERMS site in the adjacent boreal forest (Fig. 1) has documented major impacts of this drought on aspen leaf area index, evapotranspiration, stem growth, and carbon uptake (Barr et al. 2004, 2007; Krishnan et al. 2006). Our regional analysis indicates that longer term accrual of aspen biomass is also strongly influenced by moisture, as reflected by the positive relationships between estimated stem biomass (2005) and long-term values of the CMI (1961–2005) (Fig. 7). Furthermore, the results showed that that during the 2–3 years following the 2001–2002 drought, there was a collapse in the net accrual of aspen biomass in the regional CIPHA plot network. Thus, the climatically drier conditions of the parkland can largely account for the smaller biomass of aspen stands in this zone compared with those in the moister (but cooler) boreal forest immediately to the north (Hogg et al. 2005).

Despite the high spatial variation in aspen mortality, we obtained significant relationships between mortality and the minimum annual CMI, which provides a measure of drought severity (Fig. 5*a*). A remarkably similar relationship was observed for the mean percent dieback of crowns on aspen that were still living in 2005 (Fig. 5*b*). The timing of drought conditions varied across the region, but the 12 month period ending on 31 July 2002 was the driest at each of the CIPHA study areas where severe drought (CMI less than –20) was recorded. Thus, there was a generally good correspondence between the spatial extent of severe drought conditions in 2001–2002 (Fig. 2) and the distribution of CIPHA study areas with high levels of mortality and dieback, notably those in the parkland zone of eastern Alberta and west-central Saskatchewan (BAT, BIG, EDG, and GLA; Fig. 1). Extensive mortality of aspen was also recorded across this area during aerial surveys in August 2004 (M. Michaelian and E.H. Hogg, unpublished data). Considerable patchiness was observed in both aspen cover and in the severity of dieback and mortality (M. Michaelian and E.H. Hogg, unpublished data), which has prompted the inclusion of a remote sensing component in the CIPHA project for “scaling up” from the plot to the landscape level (Hall et al. 2003).

Although aspen decline has been a long-term concern in several areas of North America (Packard 1942; Schier 1975; Shields and Bockheim 1981; Kay 1997), more recent episodes of severe aspen dieback and mortality have led to a heightened awareness of the issue in northeastern Ontario (Candau et al. 2002), the western United States (Guyon 2006; Worrall et al. 2008) as well as the Canadian prairie provinces (Hogg and Schwarz 1999; Hogg et al. 2002*a*). Many previous studies have emphasized the role of fungal pathogens, insect defoliation, wildlife damage, and stand age as major factors causing aspen dieback and decline (e.g., Schier 1975; DeByle 1985; Jones et al. 1985; Kay 1997; Pothier et al. 2004). High populations of elk (*Cervus canadensis* Erxleben) have had major impacts on aspen forests throughout the western United States (DeByle 1985) and in the Canadian Rocky Mountains (e.g., Beschta and Ripple 2007). However, in contrast, we have observed relatively little evidence of aspen damage by native ungulates in the Canadian boreal forest, and our CIPHA plots in the predominantly agricultural parkland zone were selected in areas that were relatively free of damage by cattle.

Even in the absence of significant impacts from ungulates, there are challenges in determining the causes of forest decline, because such events are often caused by several factors acting either sequentially or in combination (Manion 1991). In a conceptual model, Frey et al. (2004) showed how drought can either operate directly to cause rapid aspen dieback through xylem cavitation or indirectly in combination with pathogens and other factors to cause long-term aspen decline through decreased photosynthesis and a gradual exhaustion of carbohydrate reserves.

While recognizing the importance of multiple interacting factors, it is apparent from the results of the present study that both aspen dieback and mortality were strongly influenced by the severity of the 2001–2002 drought. A meteorological analysis (Bonsal and Wheaton 2005) indicated that the 2001–2002 drought in western Canada was associated with a northward extension of the chronic drought conditions that affected large areas of the United States. Indeed, this severe drought has emerged as a major cause of recent, rapid mortality of aspen and other forest types in the southwestern United States (Gitlin et al. 2006; Worrall et al. 2008), notably the drought-induced die-off of pinyon pine (*Pinus edulis* Engelm.) that was recorded in this region during 2002–2003 (Breshears et al. 2005). Thus, the elevated mortality that we have recorded for western Canadian aspen forests may be part of a larger issue of drought-induced forest mortality at the subcontinental scale. There is evidence from studies across North America that the productivity, health, longevity, and regeneration of aspen forests are highly sensitive to moisture deficits (e.g., Shields and Bockheim 1981; Brandt et al. 2003; Hogg and Wein 2005). This poses concerns for the future of aspen forests in drought-sensitive regions, given the model projections of increasing aridity under a changing climate (Hogg and Bernier 2005; Seager et al. 2007).

Insect outbreaks are another major stressor on aspen forests, notably those of the forest tent caterpillar, which caused moderate to severe defoliation across large areas (up to 1000 km × 400 km) of the western Canadian interior during the early 1960s and 1980s (Hogg et al. 2005). However, during the period covered by the present study (2000–2005) insect defoliation was relatively localized and was minimal in the most severely drought-affected areas of Saskatchewan and eastern Alberta (Figs. 1 and 2). Nevertheless, the impact of defoliation was apparent in the regional-scale analysis (Table 3), especially for aspen stem growth (Fig. 6). This result is consistent with previous tree-ring studies showing that defoliation has a strongly negative influence on radial growth (Hogg et al. 2002*a*), even at the regional scale (Hogg et al. 2005). Multiyear defoliation has also been implicated as a major factor causing aspen decline (Candau et al. 2002; Brandt et al. 2003), especially when it occurs in combination with drought (Hogg 2001). Given the history of quasiperiodic, large-scale insect outbreaks, defoliation poses an additional risk for the future, especially for aspen stands already stressed by the recent drought.

Wood-boring insects, notably *Saperda calcarata*, increased during the period of monitoring (2000–2005), and their mean percent incidence showed negative relationships with aspen biomass and productivity and a positive relationship to dieback at the stand level (Table 3). However, for biomass, the relationship may largely reflect the greater susceptibility of more open-grown aspen to attacks by these insects (Ives and Wong 1988). Previous studies indicate that severe heat and drought can trigger outbreaks of wood-boring insects (e.g., Haack 1996; Rouault et al. 2006), which is consistent with the increase we observed in the present study. Stems affected by wood-boring insects are also prone to longer term damage by fungal pathogens and woodpeckers and are at increased risk for breakage by strong winds (Peterson and Peterson 1992; Frey et al. 2004). We observed an increase in regional-scale aspen mortality even in the years following the end of the drought (Fig. 3), which may partly reflect the combined influences of these mechanisms involving wood-boring insects.

Previous studies have demonstrated the importance of site and soil characteristics as factors affecting landscape- to regional-scale variation in aspen longevity (Shields and Bockheim 1981) and productivity (e.g., Stoeckeler 1948; Chen et al. 2002; Gustafson et al. 2003). The influence of topographic factors (slope, slope position, and aspect) was minimal in the present study, because the CIPHA stands were all situated on relatively flat terrain. However, the stands had a wide range of soil conditions, including large differences in soil texture among sites (Table 1). Although we did not detect any significant relationships between soil characteristics and the level of aspen dieback or mortality, silt content showed significant, positive relationships with 5 year stem growth and biomass (Table 3). The importance of site and soil conditions was also demonstrated by the anomalously high productivity and biomass of aspen at the TOB study area (Fig. 1, Table 1), situated on silty, alluvial soils of the Saskatchewan River lowlands. Thus, our results support previous studies showing that aspen productivity is governed by climatic factors in combination with site and soil characteristics. This concept forms the basis of emerging, climate-based models of forest growth and yield that include site-based variables such as soil water-holding capacity (Ung et al. 2001; Gustafson et al. 2003). Based on the method of Saxton and Rawls (2006), the amount of plant-available water (per volume of soil) is strongly correlated with silt content, which might explain the significance of this variable in our regression models of aspen growth and biomass that also included the CMI and other factors (Table 3).

However, knowledge gaps remain as to how soil characteristics affect aspen responses to drought. Aspen is more deeply rooted in sandy soils than in fine-textured soils (Gifford 1966; Strong and La Roi 1983), and aspen occurs on sandy soils even in the climatically driest areas of its range in the Canadian prairie provinces (Hogg 1994). Although it is well-established that aspen productivity is strongly affected by soil properties, there is little information on how soils may affect the vulnerability of western Canadian aspen stands to drought-induced impacts on growth, health, dieback, and mortality (cf. Hogg et al. 2002*a*).

Stand age has been recognized as a factor that predisposes aspen stands to a greater risk of dieback and decline (e.g., Brandt et al. 2003; Frey et al. 2004; Pothier et al. 2004). Our results showed that stand-level stem growth was negatively related to stand age, but we detected no effect of age on levels of dieback or mortality (Table 3). Furthermore, the observed, regional-scale collapse in net stem biomass increment (Fig. 3) occurred much too rapidly to have been driven by stand aging. Under ideal conditions, aspen can achieve a longevity of at least 276 years, suggesting that it may not be age per se that causes dieback and decline but, rather, the age-related accumulation of climatic and biotic stressors throughout the tree's life span (Frey et al. 2004).

Because the present analysis was based on monthly climate data, we did not specifically address the potential impacts of extreme climatic events that operate over hourly to daily time scales. Damage by hail and wind storms tends to be localized, but thaw–freeze events during winter and spring may affect larger areas and have been implicated as a major cause of hardwood forest dieback in eastern North America (e.g., Auclair et al. 1996; Bourque et al. 2005). Thaw–freeze damage to aspen and other trees was documented in Manitoba during the spring of 1958 (Cayford et al. 1959), and severe thaw–freeze events in the springs of 1990 and 1992 may have contributed to dieback of aspen forests in northwestern Alberta (Hogg et al. 2002*a*). However, a preliminary examination of the daily climate record for stations across the CIPHA study region revealed no comparable weather events during 2000–2005. Although the spring of the drought year of 2002 was unusually cool, our analysis indicated that this event was not a significant cause of dieback.

Conclusions

The results indicated that the 2001–2002 drought had a major impact on the aspen forests of west-central Canada, especially in the parkland where the high severity of the drought led to massive aspen dieback and mortality. The analysis also showed the importance of other stressors, especially insects (defoliation and stem damage) that may interact with drought to amplify and prolong its impacts. This could account for the continued increase in stem mortality that was observed during 2004–2005, following the return to generally moist conditions across the region. Thus, it appears that the period covered by this analysis (2000–2005) is not sufficient to fully determine the longer term impacts of this drought. In the areas of high stem mortality, there is also the question of whether aspen stands will regenerate naturally (primarily through vegetative suckering from roots) or whether they will deteriorate further, leading to death of aspen clones (Frey et al. 2004) and potential losses of forest cover on the landscape.

One of the concerns for the future is that climate change is expected to result in an increase in the frequency and severity of drought events in western North America. In this context, an emerging challenge is the detection, mapping, and quantification of the extent of drought impacts that typically occur across large, heterogeneous landscapes. Such knowledge is necessary, for example, in the assessment of drought impacts on wood fiber supply, wildlife habitat, and the global carbon cycle. Given the patchy nature of both aspen cover and mortality patterns in the present study, the ability to "scale up" drought impacts will likely depend on the development of remote sensing methods and systems that are integrated with plot-based monitoring networks.

Acknowledgements

This work was conducted through funding support from the Canadian Forest Service of Natural Resources Canada, the Government of Canada's Climate Change Action Fund, the Program of Energy Research and Development, and Mistik Management Ltd. We acknowledge T. Hook for conducting the tree-ring analyses and a major component of the CIPHA field program. We also thank R. Brett, J. Hammond, B. Tomm, J. Weber, M. Salomons, and the many summer students and term staff who provided field support and technical assistance to this study. The CIPHA field program in Ontario was supported by A. Hopkin and A. Keizer, in collaboration with staff from the Ontario Forest Research Institute. Soil analyses were conducted with the support of Y. Kalra and J. Crumbaugh. D. McKenney, P. Papadopol, D.T. Price, and M. Siltanen provided assistance with the interpolations and mapping of climate indices that originate from the climate monitoring program of Environment Canada. Helpful comments on the manuscript were provided by V.J. Lieffers, J.D. Stewart, and two anonymous reviewers. Finally, we thank the staff at numerous land management agencies for providing assistance with site selection and permission to conduct this work.

References

Auclair, A.N.D., Lill, J.T., and Revenga, C. 1996. The role of climate variability and global warming in the dieback of northern hardwoods. Water Air Soil Pollut. **91**: 163–186. doi:10.1007/BF00666255.

Ayres, K.W., Anderson, D.W., and Ellis, J.G. 1978. The soils of the Northern Provincial Forest in the Pasquia Hills and Saskatchewan portion of The Pas map areas 63E and 63F. Saskatchewan Institute of Pedology, University of Saskatchewan, Saskatoon Sask. Ext. Publ. 260.

Barr, A.G., Black, T.A., Hogg, E.H., Kljun, N., Morgenstern, K., and Nesic, Z. 2004. Inter-annual variability in the leaf area index of a boreal aspen–hazelnut forest in relation to net ecosystem production. Agric. For. Meteorol. **126**: 237–255. doi:10.1016/j.agrformet.2004.06.011.

Barr, A.G., Black, T.A., Hogg, E.H., Griffis, T.J., Morgenstern, K., Kljun, N., Theede, A., and Nesic, Z. 2007. Climatic controls on the carbon and water balances of a boreal aspen forest, 1994–2003. Glob. Change Biol. **13**: 561–576. doi:10.1111/j.1365-2486.2006.01220.x.

Bartos, D.L. 2001. Landscape dynamics of aspen and conifer forests. *In* Sustaining Aspen in Western Landscapes: Symposium Proceedings, 13–15 June 2000, Grand Junction, Colo. *Edited by* W.D. Shepperd, D. Binkley, D.L. Bartos, T.J. Stohlgren, and L.G. Eskew. USDA For. Serv. Rocky Mountain Res. Stn. Proc. RMRS-P-18. pp. 5–14.

Beschta, R.L., and Ripple, W.J. 2007. Wolves, elk, and aspen in the winter range of Jasper National Park, Canada. Can. J. For. Res. **37**: 1873–1885. doi:10.1139/x07-017.

Bird, R.D. 1961. Ecology of the aspen parkland of western Canada in relation to land use. Research Branch, Canada Department of Agriculture, Ottawa, Ont. Contrib. 27.

Bonsal, B., and Wheaton, E. 2005. Atmospheric circulation comparisons between the 2001 and 2002 and the 1961 and 1988 Canadian prairie droughts. Atmos. Ocean, **43**: 163–172. doi:10.3137/ao.430204.

Bourque, C.-P.A., Cox, R.M., Allen, D.J., Arp, P.A., and Meng, F.-R. 2005. Spatial extent of winter thaw events in eastern North America: historical weather records in relation to yellow birch decline. Glob. Change Biol. **11**: 1477–1492. doi:10.1111/j.1365-2486.2005.00956.x.

Brandt, J.P., Cerezke, H.F., Mallet, K.I., Volney, W.J.A., and Weber, J.D. 2003. Factors affecting trembling aspen (*Populus tremuloides* Michx.) health in Alberta, Saskatchewan, and Manitoba, Canada. For. Ecol. Manage. **178**: 287–300.

Breshears, D.D., Cobb, N.S., Rich, P.M., Price, K.P., Allen, C.D., Balice, R.G., Romme, W.H., Kastens, J.H., Floyd, M.L., Belnap, J., Anderson, J.J., Myers, O.B., and Meyer, C.W. 2005. Regional vegetation die-off in response to global-change-type drought. Proc. Natl. Acad. Sci. U.S.A. **102**: 15144–15148. doi:10.1073/pnas.0505734102. PMID:16217022.

Candau, J.-N., Abt, V., and Keatley, L. 2002. Bioclimatic analysis of declining aspen stands in northeastern Ontario. Ontario Ministry of Natural Resources, Ontario Forest Research Institute, Toronto, Ont. For. Res. Rep. 154.

Cayford, J.H., Hildahl, V., Nairn, L.D., and Wheaton, M.P.H. 1959. Injury to trees from winter drying and frost in Manitoba and Saskatchewan in 1958. For. Chron. **35**: 282–290.

Chen, H.Y.H., Krestov, P.V., and Klinka, K. 2002. Trembling aspen site index in relation to environmental measures of site quality at two spatial scales. Can. J. For. Res. **32**: 112–119. doi:10.1139/x01-179.

Clayton, J.S., Ehrlich, W.A., Cann, D.B., Day, J.H., and Marshall, I.B. 1977. Soils of Canada. Agricullture Canada, Ottawa, Ont. Publ. 1544.

DeByle, N.V. 1985. Animal impacts. *In* Aspen: ecology and management in the western United States. *Edited by* N.V. DeByle and R.P. Winokur. USDA For. Serv. Gen. Tech. Rep. RM-119. pp. 115–123.

Di Orio, A.P., Callas, R., and Schaefer, R.J. 2005. Forty-eight year decline and fragmentation of aspen (*Populus tremuloides*) in the South Warner Mountains of California. For. Ecol. Manage. **206**: 307–313. doi:10.1016/j.foreco.2004.11.011.

Frey, B.R., Lieffers, V.J., Hogg, E.H., and Landhäusser, S.M. 2004. Predicting landscape patterns of aspen dieback: mechanisms and knowledge gaps. Can. J. For. Res. **34**: 1379–1390. doi:10.1139/x04-062.

Gifford, G.F. 1966. Aspen root studies on three sites in northern Utah. Am. Midl. Nat. **75**: 132–141. doi:10.2307/2423485.

Gitlin, A.R., Sthultz, C.M., Bowker, M.A., Stumpf, S., Paxton, K.L., Kennedy, K., Muños, A., Bailey, J.K., and Whitham, T.G. 2006. Mortality gradients within and among dominant plant populations as barometers of ecosystem change during extreme drought. Conserv. Biol. **20**: 1477–1486. doi:10.1111/j.1523-1739.2006.00424.x. PMID:17002765.

Gustafson, E.J., Lietz, S.M., and Wright, J.L. 2003. Predicting the spatial distribution of aspen growth potential in the upper Great Lakes region. For. Sci. **49**: 499–508.

Guyon, J.C. 2006. Are the changes in aspen forests in North America a forest decline? *In* Proceedings of the 53rd Western International Forest Disease Work Conference, 26–30 September 2005, Jackson, Wyo. *Compiled by* J.C. Guyon. USDA Forest Service, Intermountain Region, Ogden, Utah. pp. 95–101.

Haack, R.A. 1996. Will global warming alter paper birch susceptibility to bronze birch borer attack? *In* Dynamics of forest herbivory: quest for pattern and principle. *Edited by* W.J. Mattson, P. Niemela, and M. Rousi. USDA For. Serv. Gen. Tech. Rep. NC-183. pp. 234–247.

Hall, R.J., Fernandes, R.A., Hogg, E.H., Brandt, J.P., Butson, C., Case, B.S., and Leblanc, S.G. 2003. Relating aspen defoliation to changes in leaf area derived from field and satellite remote sensing data. Can. J. Remote Sens. **29**: 299–313.

Hogg, E.H. 1994. Climate and the southern limit of the western Canadian boreal forest. Can. J. For. Res. **24**: 1835–1845. doi:10.1139/x94-237.

Hogg, E.H. 1997. Temporal scaling of moisture and the forest–

grassland boundary in western Canada. Agric. For. Meteorol. **84**: 115–122. doi:10.1016/S0168-1923(96)02380-5.

Hogg, E.H. 2001. Modelling aspen responses to climatic warming and insect defoliation in western Canada. *In* Sustaining Aspen in Western Landscapes: Symposium Proceedings, 13–15 June 2001, Grand Junction, Colo. *Edited by* W.D. Shepperd, D.L. Binkley, D. Bartos, T.J. Stohlgren, and L.G. Eskew. USDA For. Serv. Rocky Mountain Res. Stn. Proc. RMRS-P-18. pp. 325–338.

Hogg, E.H., and Bernier, P.Y. 2005. Climate change impacts on drought-prone forests in western Canada. For. Chron. **81**: 675–682.

Hogg, E.H., and Hurdle, P.A. 1995. The aspen parkland in western Canada: a dry-climate analogue for the future boreal forest? Water Air Soil Pollut. **82**: 391–400. doi:10.1007/BF01182849.

Hogg, E.H., and Schwarz, A.G. 1999. Tree-ring analysis of declining aspen stands in west-central Saskatchewan. Can. For. Serv. North. For. Cent. Inf. Rep. NOR-X-359.

Hogg, E.H., and Wein, R.W. 2005. Impacts of drought on forest growth and regeneration following fire in southwestern Yukon, Canada. Can. J. For. Res. **35**: 2141–2150. doi:10.1139/x05-120.

Hogg, E.H., Brandt, J.P., and Kochtubajda, B. 2002*a*. Growth and dieback of aspen forests in northwestern Alberta, Canada, in relation to climate and insects. Can. J. For. Res. **32**: 823–832. doi:10.1139/x01-152.

Hogg, E.H., Hart, M., and Lieffers, V.J. 2002*b*. White tree rings formed in trembling aspen saplings following experimental defoliation. Can. J. For. Res. **32**: 1929–1934. doi:10.1139/x02-114.

Hogg, E.H., Brandt, J.P., and Kochtubajda, B. 2005. Factors affecting interannual variation in growth of western Canadian aspen forests during 1951–2000. Can. J. For. Res. **35**: 610–622. doi:10.1139/x04-211.

Hogg, E.H., Brandt, J.P., Kochtubajda, B., Michaelian, M., and Frey, B.R. 2006. Impact of the 2001–2003 drought on productivity and health of western Canadian aspen forests. *In* Proceedings of the 53rd Western International Forest Disease Work Conference, 26–30 September 2005, Jackson, Wyo. *Compiled by* J.C. Guyon. USDA Forest Service, Intermountain Region, Ogden, Utah. pp. 89–94.

Ives, W.G.H., and Wong, H.R. 1988. Tree and shrub insects of the prairie provinces. Can. For. Serv. North. For. Cent. Inf. Rep. NOR-X-292.

Jones, J.R., DeByle, N.V., and Bowers, D.M. 1985. Insects and other invertebrates. *In* Aspen: ecology and management in the western United States. *Edited by* N.V. DeByle and R.P. Winokur. USDA For. Serv. Gen. Tech. Rep. RM-119. pp. 107–114.

Kalra, Y.P., and Maynard, D.G. 1991. Methods manual for forest soil and plant analysis. Can. For. Serv. North. For. Cent. Inf. Rep. NOR-X-319

Kay, C.E. 1997. Is aspen doomed? J. For. **95**: 4–11.

Krishnan, P., Black, T.A., Grant, N.J., Barr, A.G., Hogg, E.H., Jassal, R.S., and Morgenstern, K. 2006. Impact of changing soil moisture distribution on net ecosystem productivity of a boreal aspen forest during and following drought. Agric. For. Meteorol. **139**: 208–223. doi:10.1016/j.agrformet.2006.07.002.

Lambert, M.-C., Ung, C.-H., and Raulier, F. 2005. Canadian national tree aboveground biomass equations. Can. J. For. Res. **35**: 1996–2018. doi:10.1139/x05-112.

Lieffers, V.J., Landhäusser, S.M., and Hogg, E.H. 2001. Is the wide distribution of aspen a result of its stress tolerance? *In* Sustaining Aspen in Western Landscapes: Symposium Proceedings, 13–15 June 2001, Grand Junction, Colo. *Edited by* W.D. Shepperd, D.L. Binkley, D. Bartos, T.J. Stohlgren, and L.G. Eskew. USDA For. Serv. Rocky Mountain Res. Stn. Proc. RMRS-P-18. pp. 325–338.

Manion, P.D. 1991. Tree disease concepts. 2nd ed. Prentice-Hall, Englewood Cliffs, N.J.

McKenney, D.W., Pedlar, J.H., Papadopol, P., and Hutchinson, M.F. 2006. The development of 1901–2000 historical monthly climate models for Canada and the United States. Agric. For. Meteorol. **138**: 69–81. doi:10.1016/j.agrformet.2006.03.012.

Packard, F.M. 1942. Wildlife and aspen in Rocky Mountain National Park, Colorado. Ecology, **23**: 478–482. doi:10.2307/1930134.

Perala, D.A. 1990. *Populus tremuloides* Michx.: quaking aspen. *In* Silvics of North America. Vol. 2. Hardwoods. *Edited by* R.M. Burns and B.H. Honkala. USDA For. Serv. Agric. Handb. 654. pp. 555–569.

Peterson, E.B., and Peterson, N.M. 1992. Ecology, management, and use of aspen and balsam poplar in the Prairie Provinces, Canada. For. Can. North. For. Cent. Spec. Rep. 1.

Pothier, D., Raulier, F., and Riopel, M. 2004. Ageing and decline of trembling aspen stands in Quebec. Can. J. For. Res. **34**: 1251–1258. doi:10.1139/x04-017.

Rouault, G., Candau, J.-N., Lieutier, F., Nageleisen, L.-M., Martin, J.-C., and Warzee, N. 2006. Effects of drought and heat on forest insect populations in relation to the 2003 drought in western Europe. Ann. For. Sci. **63**: 613–624. doi:10.1051/forest:200 6044.

Saxton, K.E., and Rawls, W.J. 2006. Soil water characteristic estimates by texture and organic matter for hydrologic solutions. Soil. Sci. Soc. Am. J. **70**: 1569–1578. doi:10.2136/sssaj2005.0117.

Schier, G.A. 1975. Deterioration of aspen clones in the middle Rocky Mountains. USDA For. Serv. Intermountain For. Range Exp. Stn. Res. Pap. INT-170.

Schindler, D.W., and Donahue, W.F. 2006. An impending water crisis in Canada's western prairie provinces. Proc. Natl. Acad. Sci. U.S.A. **103**: 7210–7216. doi:10.1073/pnas.0601568103. PMID:16606829.

Seager, R., Ting, M., Held, I., Kushnir, Y., Lu, J., Vecchi, G., Huang, H.-P., Harnik, N., Leetmaa, A., Lau, N.-C., Li, C., Velez, J., and Naik, N. 2007. Model projections of an imminent transition to a more arid climate in southwestern North. Science (Washington, D.C.) **316**(5828: 1181–1184. doi:10.1126/science.1139601.

Shields, W.J., Jr., and Bockheim, J.G. 1981. Deterioration of trembling aspen clones in the Great Lakes region. Can. J. For. Res. **11**: 530–537. doi:10.1139/x81-073.

Stoeckeler, J.H. 1948. The growth of quaking aspen as affected by soil properties and fire. J. For. **46**: 727–737.

Strong, W.L., and La Roi, G.H. 1983. Root-system morphology of common boreal forest trees in Alberta, Canada. Can. J. For. Res. **13**: 1164–1173. doi:10.1139/x83-155.

Ung, C.-H., Bernier, P.Y., Raulier, F., Fournier, R.A., Lambert, M.-C., and Régnière, J. 2001. Biophysical site indices for shade tolerant and intolerant boreal species. For. Sci. **47**: 83–95.

Volney, W.J.A., Alfaro, R.I., Bothwell, P., Hogg, E.H., Hopkin, A., Laflamme, G., Hurley, J.E., Warren, G., Metsaranta, J., and Mallett, K.I. 2005. A framework for poplar plantation risk assessments. Unasylva, **221**: 20–25.

Worrall, J.J., Egeland, L., Eager, T., Mask, R.A., Johnson, E.W., Kemp, P.A., and Shepperd, W.D. 2008. Rapid mortality of *Populus tremuloides* in southwestern Colorado, USA. For. Ecol. Manage. **255**(3–4): 686–696.

Zar, J.H. 1996. Biostatistical analysis. 3rd ed. Prentice-Hall, Upper Saddle River, N.J.