

Recent declines of *Populus tremuloides* in North America linked to climate

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ABSTRACT

Populus tremuloides (trembling aspen) recently experienced extensive crown thinning, branch dieback, and mortality across North America. To investigate the role of climate, we developed a range-wide bioclimate model that characterizes climatic factors controlling distribution of aspen. We also examined indices of moisture stress, insect defoliation and other factors as potential causes of the decline. Historic climate records show that most decline regions experienced exceptionally severe drought preceding the recent episodes. The bioclimate model, driven primarily by maximum summer temperatures and April–September precipitation, shows that decline tended to occur in marginally suitable habitat, and that climatic suitability decreased markedly in the period leading up to decline in almost all decline regions. Other factors, notably multi-year defoliation by tent caterpillars (*Malacosoma* spp.) and stem damage by fungi and insects, also play a substantial role in decline episodes, and may amplify or prolong the impacts of moisture stress on aspen over large areas. Many severely affected stands have poor regeneration potential, raising concerns that increasing aridity could ultimately lead to widespread loss of aspen forest cover. The analysis indicates that exceptional droughts were a major cause of the decline episodes, especially in the drier regions, and that aspen is sensitive to drought in much of its range. Coupling the bioclimate model with climate projections suggests that we should expect substantial loss of suitable habitat within the current distribution, especially in the USA and Mexico.

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1. Introduction

Trembling aspen (*Populus tremuloides*; hereafter referred to as aspen) is the most widely distributed tree species in North America and is a unique and important keystone species in many parts of its range. Over the first decade of the 21st century, large areas of overstory aspen with unusually abundant dieback¹ and mortality appeared in several regions of North America (e.g., Candau et al., 2002; Michaelian et al., 2011; Worrall et al., 2008). This has caused special concern because warm, dry climatic conditions are implicated in most cases that have been studied, and the climate is projected to become even warmer and, in some cases, drier through at least this century (Core Writing Team et al., 2008).

We distinguish three patterns of aspen mortality and landscape change, only the third of which is treated in detail here:

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¹ Dieback is a symptom: the death of twigs and branches in a living tree (Boyce, 1961). It often precedes tree mortality, especially in decline diseases (Sinclair and Lyon, 2005). The term is therefore sometimes included in names of decline diseases, but is not a synonym for a decline disease or widespread mortality.

1. *Cohort dynamics*: Stem mortality is a regular part of cohort development in both seral and persistent aspen stands (Fralish, 1972; Shepperd, 1993; Weigle and Frothingham, 1911). Whether suckers appear in profusion following disturbance, or are produced more sparsely in the understory of an aspen stand, most of them die before reaching maturity. As they mature, stems die at a slower rate. Finally, the cohort deteriorates. Cohort dynamics occurs on the scale of a stand and is due primarily to endogenous processes.
2. *Long-term successional loss*: This is a gradual (over several decades or more) decrease in area of aspen cover type on a regional scale. Decreased disturbance leads to reduced aspen regeneration and greater conifer survival and regeneration, while intensive herbivory by ungulates often decimates aspen suckers and seedlings. Rather than increased overstory mortality, this is essentially enhanced succession. The term “decline” has been applied to this type of change (Bartos, 2008; Bartos and Campbell, 1998; Kay, 1997; Rogers, 2002), but refers to a long-term decline in area of the cover type, not to a decline disease.
3. *Large-scale, episodic decline*: This is an episode of unusually high overstory crown thinning, dieback, and mortality that occurs on a landscape or regional scale over several years or more and

may affect a wide range of ages. It typically has a fairly well-defined onset. This has been variously referred to as a decline disease, dieback, or die-off; we refer to it as decline in this paper. This is our focus.

Our objectives are to: (1) characterize the range-wide distribution of aspen's climatic niche, (2) integrate and interpret information on episodic decline of aspen across North America, (3) assess the causes of recent decline episodes, and (4) project the effects of climate change on aspen's climatic niche.

2. Methods

2.1. Bioclimate model

To assess the potential for climate-triggered, episodic decline in contemporary and future climates, we updated previous bioclimate models (Gray et al., 2011; Gray and Hamann, 2012; Rehfeldt et al., 2009) to produce a range-wide statistical model capable of predicting presence or absence of aspen from climate variables. A summary of the approach is presented here; see Supplement 1 for details. We used the Random Forests algorithm in R (R Development Core Team) with 20 forests, each with 100 trees. Presence-absence data were obtained from forest inventory plots, ecology plots, herbarium accessions, and cover-type maps (see Acknowledgments). In sampling from cover-type maps, we maintained intensity of sampling similar to that provided by the ground plots. Data points from non-forested biomes were randomly sampled from a database used by Rehfeldt et al. (2012) in North American vegetation analyses. The procedures amassed ~610,000 data points, of which ~9% contained aspen.

Climate normals (mean of the 1961–1990 reference period) were estimated for each data point with thin-plate spline surfaces (Crookston, 2012; Rehfeldt, 2006; Sáenz-Romero et al., 2010). The normals were used to calculate 34 variables relevant to plant geography (Rehfeldt, 2006; Rehfeldt et al., 2009).

To prepare the data for analysis, we used a sampling protocol (Rehfeldt, 2006; Rehfeldt et al., 2009) to produce 20 datasets, each of which was used for a single forest in the Random Forests model. Breiman (2001) recommended that when producing Random Forests classification trees, the number of observations within classes be approximately equal. Accordingly, we produced datasets with approximately 40% of the observations with aspen and 60% without aspen. Each dataset contained a sample of aspen's occurrence that spanned its climatic niche, with the observations lacking aspen being concentrated in climates for which separating presence from absence would be most difficult. Observations containing aspen were weighted by a factor of two to assure that the model would be most robust for climates in which aspen actually occurs. Each dataset contained about 100,000 observations.

A stepwise procedure was used to determine which of the 34 climate variables should be included in the model. Variables were eliminated according to importance values averaged across the 20 forests, using the mean decrease in accuracy as the measure of importance. Out of bag errors were used to determine the climate variables comprising the final model.

In making predictions, observations are run down all trees in each forest, with each tree casting one of a total of 2000 votes as to whether or not the climate of the observation is suited to aspen. Votes were used to relate aspen viability (Crookston et al., 2010) to aspen decline and to judge habitat suitability of future climates. Predictions from the bioclimate model used elevations (GLOBE Task Team, 1999) and climate grids (Crookston, 2012) at 1 km resolution. Projections for the decades surrounding 2030 and 2060 used climate means based on the A2 scenario (unrestrained emis-

sions of greenhouse gases) in three general circulation models (GCMs); maps are made from the average of the three predictions.

To represent recent climate trends, we used the 1997–2006 decadal average, which can be interpreted as observed climate change over a 27-year period (the mid-point of the 1961–1990 climate baseline period and the mid-point of the recent decadal average). The decadal average was calculated by interpolating anomalies relative to the 1961–1990 normals which then were overlaid onto high-resolution 1961–1990 climate normals (Mbogga et al., 2009).

2.2. Aspen decline

Data from aerial and, in one case, ground surveys from 2000 to 2010 were gathered from federal, state, and provincial sources. In the United States, the starting point was an “aspen decline rollup,” a national compilation of aspen decline from various regions obtained from the US Forest Service, Forest Health Technology Enterprise Team. In regions with substantial damage, we contacted forest health specialists and adjusted the rollup as needed to optimally capture widespread areas of decline, while excluding other forms of damage, such as temporary defoliation caused directly by insects and foliar pathogens (see Supplement 1 for details). In Canada, the data are from special-purpose surveys conducted by the Canadian Forest Service to document large episodes of damage in northeastern Ontario (Candau et al., 2002) and in the aspen parkland of Alberta and Saskatchewan (Michaelian et al., 2011). We were unable to find reports or personal observations of such damage in Mexico. Polygons from multiple years were merged to avoid counting areas more than once.

We refer to ecological regions of North America as designated by the Commission for Environmental Cooperation (Anonymous, 2009a; Wiken et al., 2011).

2.3. Weather history

To assess weather history in a decline region, we selected three weather stations using criteria of proximity, length of record, and elevation as close as possible to that of affected aspen (Supplement 1: Table 7). Monthly precipitation and mean minimum and maximum temperature were obtained for each station for the period 1901–2011. Gaps in a station's record were filled through an altitude corrected, inverse distance-weighted spatial interpolation of the nearest eight weather stations using the program BioSIM (Régnière and Saint-Amant, 2008). From the monthly averages of the three stations, we calculated summary variables and climate indices described below. Annual values were summed from August of the previous year through July of the current year. We call these “aspen-year” values because a moisture index over this period has shown the best correlation with aspen growth (Hogg et al., 2005).

A climate moisture index (CMI), which represents precipitation minus potential evapotranspiration, was estimated using the simplified Penman–Montieth method of Hogg (1997). An annual dryness index (ADI) was calculated as described by Rehfeldt et al. (2009) except: (a) DD5 (annual degree-days > 5 °C) was estimated from the monthly data using Hitchin's formula and $k = 0.6$ (Day, 2006), giving the same result as Rehfeldt's method (2006); and (b) like CMI, ADI was calculated on an aspen-year basis. In addition, a July–August dryness index (JADI) was calculated as $(DD5)^{0.5}/\text{July and August precipitation}$, where DD5 was summed over the calendar year.

We analyzed time series of modeled soil moisture (Anonymous, 2012; Fan and van den Dool, 2004) using grid points in areas of concentrated aspen damage: in Minnesota, 47.75 N 91.25 W; Arizona, 35.25 N 11.75 W; Colorado, 37.25 N 108.25 W. Because of the large area affected in the aspen parkland, we averaged three

grid points corresponding to the weather stations used: 53.25 N, 113.75 W; 53.25 N, 109.25 W; and 53.25 N, 105.75 W.

3. Results and discussion

3.1. Bioclimate model

The bioclimate model was used to assess the distribution of aspen's climate niche, as one approach to assessing the role of climate in recent declines, and as the first step in assessing the future of aspen under climate change. The stepwise elimination process showed that a six-variable model produced low errors of estimate while being reasonably parsimonious. For this model, the out of bag error averaged across the 20 forests was 5.6%, with errors of commission of 9.9% and errors of omission 0.3%. The stepwise process also showed that of the six predictors, two were by far the most important: the mean maximum temperature in the warmest month and precipitation summed from April to September. Other predictors were the summer–winter temperature differential, precipitation summed for winter months (November–February), degree-days > 5 °C, and mean annual precipitation (Supplement 1: Table 1). Like previous assessments (e.g., Hogg, 1994, 1997; Rehfeldt et al., 2009), these variables illustrate that moisture and temperature interact to limit the distribution of aspen.

From the model output, we mapped the percentage of 2000 votes in favor of the climate being suited to aspen (Fig. 1; Supplement 2 is a PDF file containing all the maps presented here). We used a subjective classification to convert votes into probabilities of presence (Fig. 1, legend) based on a histogram showing, for observations where aspen is present, frequencies according to 20 uniform classes of votes (Supplement 1: Fig. 1). We use these subjective classes to refer to the probability of aspen's presence in recent climates and the probability that a future climate would be suited to aspen.

The map (Fig. 1, inset) suggests that an astonishing one-third of the land mass in North America is climatically suited to aspen at probabilities of presence between low and excellent, that is, more than 40% of the votes. The map also allows a comparison between Little's (1971) mapping of the limits of aspen's distribution with our model's projection of suitable climates. Close inspection shows that the relationship is outstanding, particularly in regions where the model indicates a high probability that the climate is suitable. In the material that follows, we use the inset of Fig. 1 to approximate the current species distribution.

As global surface temperatures have warmed since the reference period of 1961–1990 (Hansen et al., 2006), we used the bioclimate model to assess the effect of recent climatic change on aspen's climatic niche within the contemporary distribution. We ran the model with the average climate data for 1997–2006, and subtracted the 1961–1990 proportion of votes from the 1997–2006 proportion. These differences estimate the increases and decreases in climatic suitability in the period that preceded and accompanied the episodes of decline in 2000–2010 (Fig. 2). In eastern North America, latitude dominates change in suitability, with decreases predominantly in the south and increases in the north. In western North America, elevation also plays a large role, with decreases in suitability at low elevations and increases at high elevations.

3.2. Decline episodes of the 20th century

While aspen mortality is certainly not new, early reports suggest that typical cohort dynamics and diseases were generally at play, rather than unusual episodes (Baker, 1925; Meinecke, 1929; Weigle and Frothingham, 1911). However, Baker (1925) noted

the high susceptibility of aspen to late spring frost, which caused extensive twig dieback and mortality in 1919 (see Section 3.4.4). If decline episodes followed major droughts in the early to middle parts of the century, they apparently were not documented.

With perhaps the first use of the term “aspen decline,” Packard (1942) reported heavy mortality of aspen in Rocky Mountain National Park, Colorado, after elk were reintroduced to the Park and quickly exceeded the carrying capacity of the winter range. An epidemic of canker caused by the fungus *Cytospora chrysosperma* affected a large portion of the park, but especially the winter range, where trees were dying in groups of hundreds. Wounding of the stems by elk feeding was ultimately responsible for the epidemic.

In the Mixed Wood Forest ecoregion around Lake Superior, cutting and fire in the early 20th century reduced much of the presettlement forest to scattered patches (Cleland et al., 2001; Fralish, 1975). The aspen that mostly colonized such areas began to decline by the late 1970s (Shields and Bockheim, 1981). Aspen typically begins to deteriorate at 40–60 years of age in this region. It thus appears that a 20-year period of cutting and burning in the early 20th century, followed 40–60 years later by cohort senescence, could largely explain the decline.

However, moisture stress can also affect aspen longevity in this region. Longevity is low where temperatures are high and on xeric sites (Shields and Bockheim, 1981). Decline followed a severe drought of 1976–1977 (Anonymous, 2011b), by some measures the worst drought of the century in northeastern Minnesota. Aspen-year precipitation (not shown), CMI, and ADI set records in 1977 and modeled soil moisture dropped below two standard deviations under the mean for 6 months (Fig. 3A, B, and D). Thus, drought further tightened the regional synchrony of deterioration that resulted from widespread disturbance early in the century.

A similar process was reported in the Wasatch and Uinta Mountains of Utah: deterioration of stands one at a time, beginning with death of individual stems and progressing to loss of most of the overstory (Schier, 1975). In the Western Cordillera, the process was synchronized loosely by the maturation of aspen clones that originated in the latter 19th century, before fire exclusion (Kulawski et al., 2004; Margolis et al., 2007, 2011).

Here also was evidence that xeric sites and drought contributed to short lifespan and deterioration. Deteriorating clones were significantly younger than healthy clones (Schier and Campbell, 1980). Soils under deteriorating stands had lower moisture-holding capacity and were shallower than soils under healthy stands. Utah experienced its longest drought of the 20th century from 1953 to 1965 (Wilkowske et al., 2003), ending several years before concern led to studies into aspen deterioration (Schier, 1975; Schier and Campbell, 1980).

Concern over loss of aspen in the western US grew in the 1970s and continued through the end of the century, but most reports focused on cover-type change through succession and lack of recruitment rather than unusual episodes of overstory mortality (e.g., Bartos, 2001; Bartos and Campbell, 1998; Kay and Bartos, 2000; Rogers, 2002). One focus was an important winter range for elk in the Gros Ventre Mountains, western Wyoming (Krebill, 1972). Elk killed large numbers of small stems, preventing overstory recruitment, but mortality of larger stems was low and due to typical causes.

3.3. Decline episodes of 2000–2010

More recent decline episodes suggest local shifts of the climatic niche. From 2000 to 2010, aspen decline was mapped on about 3.2 million ha in North America, concentrated in what we recognize as six decline regions (Fig. 4). This excludes unquantified dam-

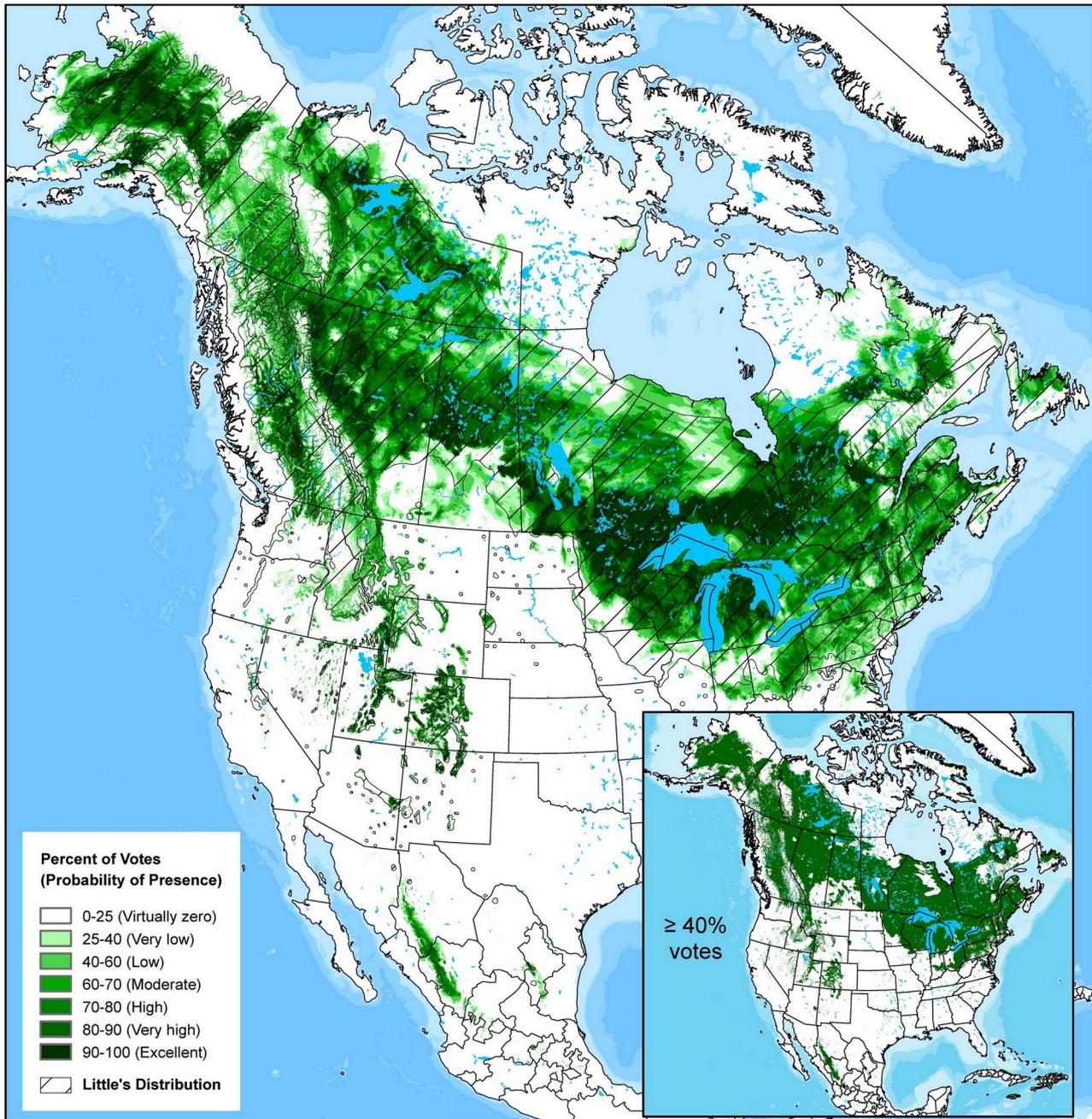


Fig. 1. Distribution of aspen's climatic niche in North America as determined through the bioclimate model, based on the reference period 1961–1990. Percent of votes generated by the model, indicating climatic suitability, is shown together with the corresponding probability of presence of aspen (Supplement 1: Fig. 1). Also shown is Little's (1971) range map.

age in northwestern Quebec, northwestern Ontario and northwestern Alberta.

In the west, declines occurred primarily at the margins of the contemporary geographic distribution and climatic niche (Fig. 4). A comparison of decline to changes in climatic suitability between the reference period and 1997–2006 (Fig. 5) shows that, in all areas except Kapuskasing, decline occurred predominantly in areas of decreased suitability.

3.3.1. Kapuskasing – Softwood Shield

The area of particular interest here is the ecoregion Abitibi Plains and Rivière Rupert Plateau, comprising much of the boreal forests of northern Ontario and Quebec. Although on the Canadian

Shield, its central portion is dominated by the Clay Belt, where clay from postglacial Lake Ojibway was deposited over the bedrock and where the decline has occurred. The climatic suitability of this area is generally excellent (Fig. 4) and the climate has remained favorable recently (Fig. 5A).

The forest tent caterpillar (FTC; *Malacosoma disstria*) can be a voracious consumer of aspen in the northern forests, completely removing all leaves when caterpillars are abundant. In the Kapuskasing area of northeastern Ontario, two outbreaks comprised a reversing wave of defoliation, passing from west to east in 1990–1993 and east to west in 1995–2003 (Candau et al., 2002; Cooke et al., 2009). Extensive decline was first observed in 2000 by aerial survey and by 2005 covered over 518,000 ha. Cumulative mortality

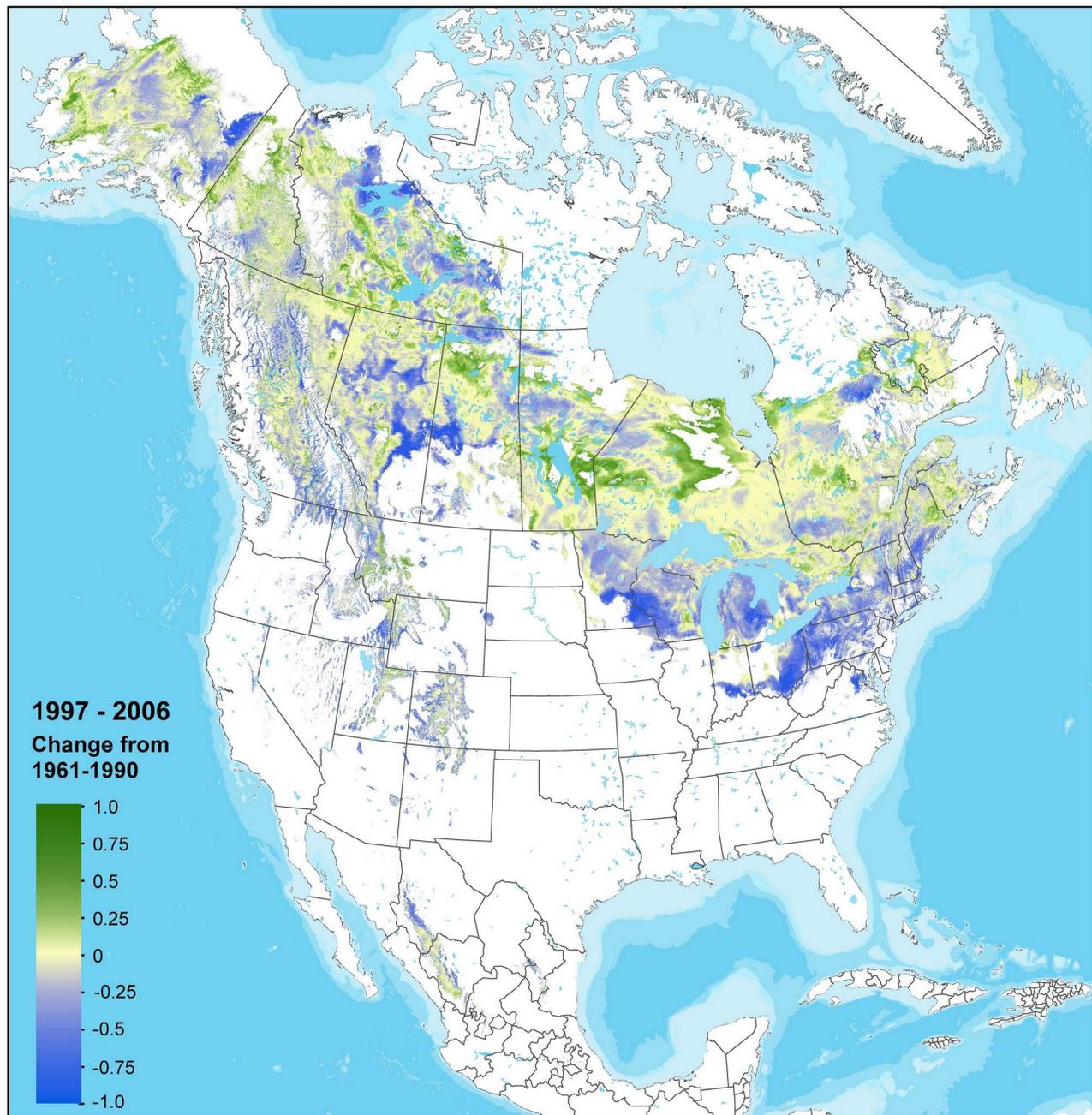


Fig. 2. Distribution of differences between 1961–1990 (normal) and 1997–2006 climate suitability for aspen in North America within the contemporary distribution (see Fig. 1 inset). This represents changes in climatic suitability that preceded and accompanied the episodes of decline mapped during 2000–2010. Positive numbers (green) indicate an increase in suitability and negative numbers (blue) a decrease. The values +1 and –1 represent changes in proportion of votes from 0 to 1 and 1 to 0, respectively.

in late 2005 averaged 52% of stems (41% of basal area) and ranged up to 100% (Man and Rice, 2010).

Mortality was most strongly related to consecutive years of defoliation since 1985 (Man and Rice, 2010) and was unrelated to stand age (Candau et al., 2002). Virtually none of the area was undefoliated; 80% of it had been defoliated at least 3 years between 1989 and 1999. The distributions of frequent defoliation vs. decline coincided remarkably well, further suggesting a cause–effect relationship (Candau et al., 2002).

However, drought and soil conditions may also influence growth and decline of aspen in this region. Candau et al. (2002) found evidence of a significant drought in the Kapuskasing area

throughout the 1998 growing season. Wet, heavy, and thin soils restrict productivity in most of this area (Candau et al., 2002), restricting rooting and increasing vulnerability to short-term, seasonal drought. The data suggested that the primary cause, defoliation, combined with drought stress to exacerbate decline, with soils playing an additional role. Our examination of moisture indices revealed no extraordinary annual or seasonal droughts, although there were 4 years of moderate seasonal drought in the late 1990s (not shown).

The damaging FTC outbreak also extended east into the Abitibi area of western Quebec (Fig. 4), affecting about 1.4 million ha. By 2008, decline there resulted in increased canopy opening from

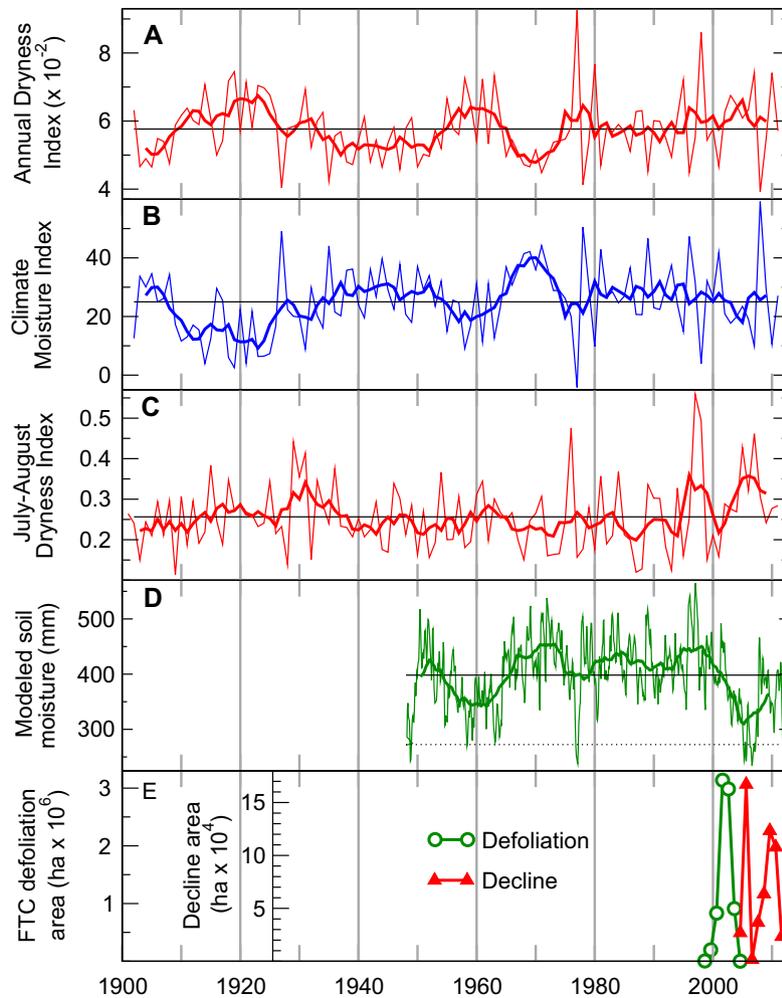


Fig. 3. Time series of climate indices, defoliation by forest tent caterpillar (FTC), and symptoms of decline in northeastern Minnesota. (A–C) Three indices of moisture balance based on data beginning 1901. (D) Monthly modeled soil moisture beginning 1948. The dotted line is two standard deviations below the mean. (E) Defoliation of aspen by FTC and symptoms of decline (thin crowns; small, discolored leaves; branch dieback; mortality) from 1998 to 2011 in northern Minnesota from aerial survey records. In (A–D), the horizontal lines indicate the long-term means and the heavy lines are 5-year running averages.

about 12% in undefoliated stands to nearly 50% in stands defoliated for 3 years (Moulinier et al., 2011).

3.3.2. Great Lakes – Mixed Wood Shield

In the Mixed Wood Shield ecoregion south and west of Lake Superior, climatic suitability for aspen mostly ranges from moderate to excellent (Fig. 4), although suitability decreased over much of the area recently (Fig. 5B). FTC dynamics here are similar to those in Ontario and Quebec. Tree mortality generally increases sharply with severity of defoliation history, and is higher on poor sites than good sites (Churchill et al., 1964).

Recently, a series of events triggered decline of aspen (Anonymous, 2009b, 2011a; Mike Albers, pers. comm.). An exceptional drought in 1997 and 1998 had near-record ADI and CMI levels and record JADI (Fig. 3A–C), indicating extremely dry growing seasons. From 2000 to 2003 was the largest outbreak of FTC on record in northern Minnesota (Fig. 3E). Beginning in 2004 and peaking in 2005, a small area showed primarily foliar symptoms, including small, sparse, and/or chlorotic foliage. Meanwhile, another drought focused primarily in the growing season steadily worsened, reaching maximum severity in 2005–2007. This drought was reflected in: (a) the 5-year average of JADI, which reached record highs, suggesting a cumulative effect of stressful growing seasons; and (b) the lowest modeled soil moisture and the lowest 5-year average

on record occurred during this drought (Fig. 3C and D). Soil moisture dipped under two standard deviations below the mean for 18 months in 2005–2007 (Fig. 3D).

In 2007, as the drought culminated, a second wave of decline began, this time including mortality that was scattered or in clusters of up to 30–40 trees. Area of damage increased steadily to 121,000 ha in 2009 before dropping.

Decline was also noted in northern Wisconsin and Michigan. Aerial mapping is not feasible there because aspen is scattered in small patches in diverse forests. In Wisconsin, some areas were surveyed on the ground (Brian Schwingle, unpublished) and are reflected in Figs. 4 and 5. Declining aspen would likely be more prevalent there, but such stands are often promptly harvested.

The soils on the Canadian Shield in this ecoregion are largely derived from thin glacial till over bedrock (Prettyman, 2002). Most are low in nutrients and moisture-holding capacity, and forest productivity is generally correspondingly low. Moisture-related soil factors affect productivity and longevity of aspen in this ecoregion, especially in areas with high mean annual temperature (Shields and Bockheim, 1981).

In northwestern Ontario, 3.8 million ha of moderate to severe aspen decline was mapped by aerial survey in 2009 (Scarr et al., 2012). This is more than was mapped on the rest of the continent during the entire decade (Fig. 4). Visible symptoms included sparse

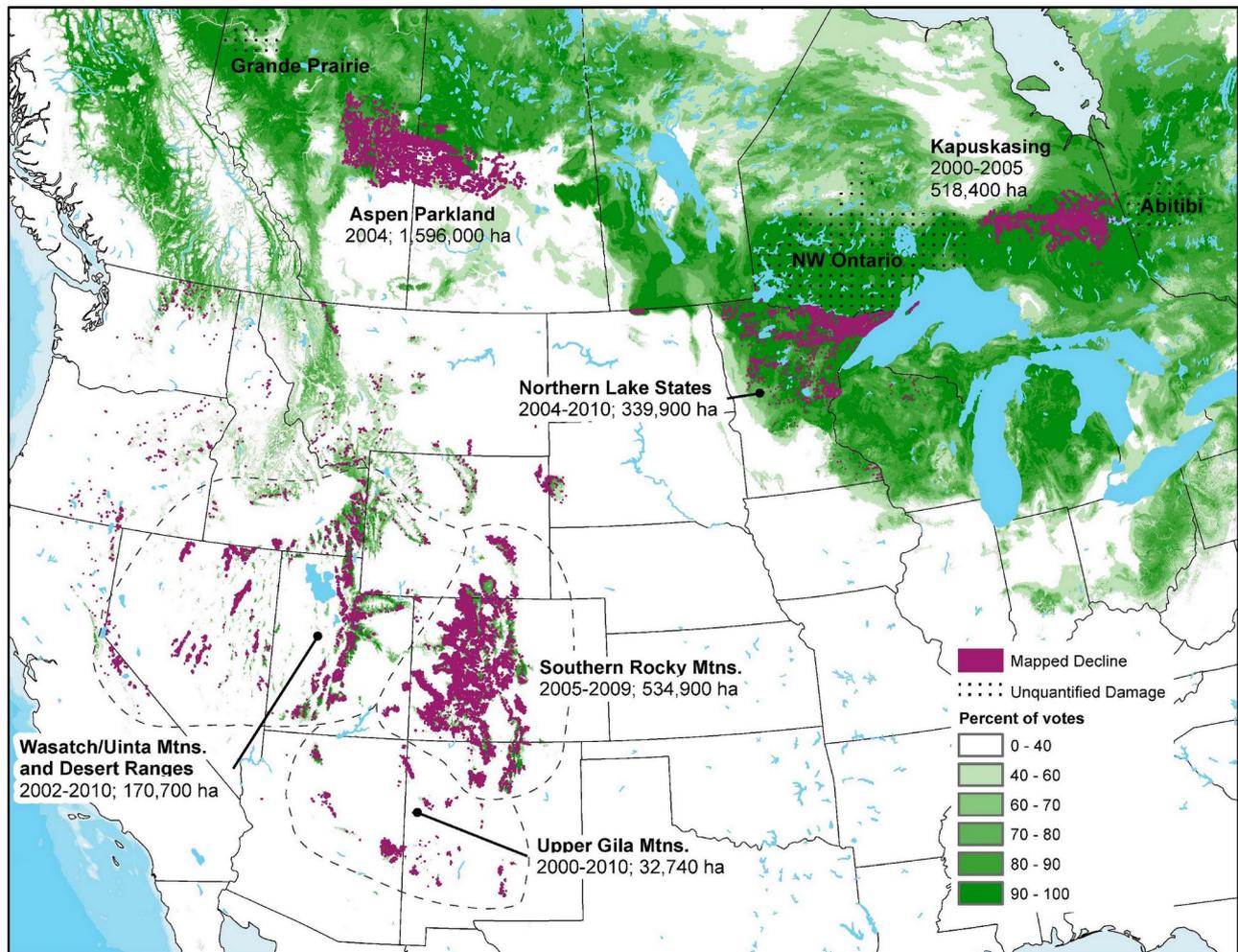


Fig. 4. Distribution of aspen decline mapped during 2000–2010. Aspen's climatic niche during 1961–1990 is shown in green (see Fig. 1). The dashed lines demarcate regions of decline where demarcation is unclear. Many areas were not surveyed, so additional symptomatic areas exist that were not mapped. In decline polygons, severity varies and rarely are all trees dead or symptomatic. Other types of damage may be included in some polygons and additional decline in other areas may have been misidentified and not included. Because most polygons are small relative to the scale of this map, an outline has been added to make them visible.

foliage and branch dieback as well as whole-tree mortality. In 2010, the reported total area increased to 15.9 million ha, of which 3.2 million ha was moderate to severe. We chose not to include any of this damage in our total because the affected aspen were often sparsely distributed within large polygons, and because the decline was much less evident in 2011 (Scarr et al., 2012).

3.3.3. Aspen parkland of western Canada

The aspen parkland is a transition between boreal forest and prairie in Alberta and Saskatchewan (Hogg and Hurdle, 1995). It varies in climatic suitability for aspen (Fig. 4), but suitability in nearly all of the area decreased greatly in recent times (Fig. 5C).

In the early 1990s, localized episodes of aspen dieback were reported from the St. Walburg area in western Saskatchewan and the Grande Prairie area of northwestern Alberta (Fig. 4), raising public and industry concern. Growth collapses had occurred following periods of drought in the 1980s which coincided with outbreaks of FTC (Hogg et al., 2002; Hogg and Schwarz, 1999). However, the precise causes of dieback were difficult to determine from these retrospective studies. Both areas were affected by an extreme thaw–freeze event in March–April 1992 that may have incited branch dieback in trees previously stressed by drought and defoliation. Subsequent 1997 forest health assessments in the Grande

Prairie area showed that declining aspen stands also had greater damage by wood-boring insects and fungal pathogens than healthy stands (Hogg et al., 2002). Thus, it appeared that these dieback episodes were driven by the combined impact of several climatic and biotic factors.

During 2001–2002, an exceptional drought affected large areas of western North America, including the Canadian prairie provinces (Bonsal and Regier, 2007). Aerial surveys in 2004 revealed massive dieback and mortality of aspen across a large area of the aspen parkland and adjacent boreal forest between Edmonton, Alberta and Prince Albert, Saskatchewan (Fig. 4). Within this survey area, the 2001–2002 drought was the most severe in more than a century based on values of CMI and ADI (Fig. 6). A spatial interpolation of plot-based measurements indicated that the 11.5-Mha survey area had 45 Mt of dead aspen, representing about 20% of the total above-ground biomass (Michaelian et al., 2011). In some stands, nearly 100% of the aboveground aspen stems were killed so that from the air, the drought's impact resembled the aftermath of stand-replacing fire. In the adjacent boreal forest, the drought's impacts were less severe but led to multi-year decreases in aspen leaf area, stem growth and forest carbon uptake (Krishnan et al., 2006).

Regionally, the 2001–2002 drought led to more than a two-fold increase in aspen mortality based on annual, plot-based monitor-

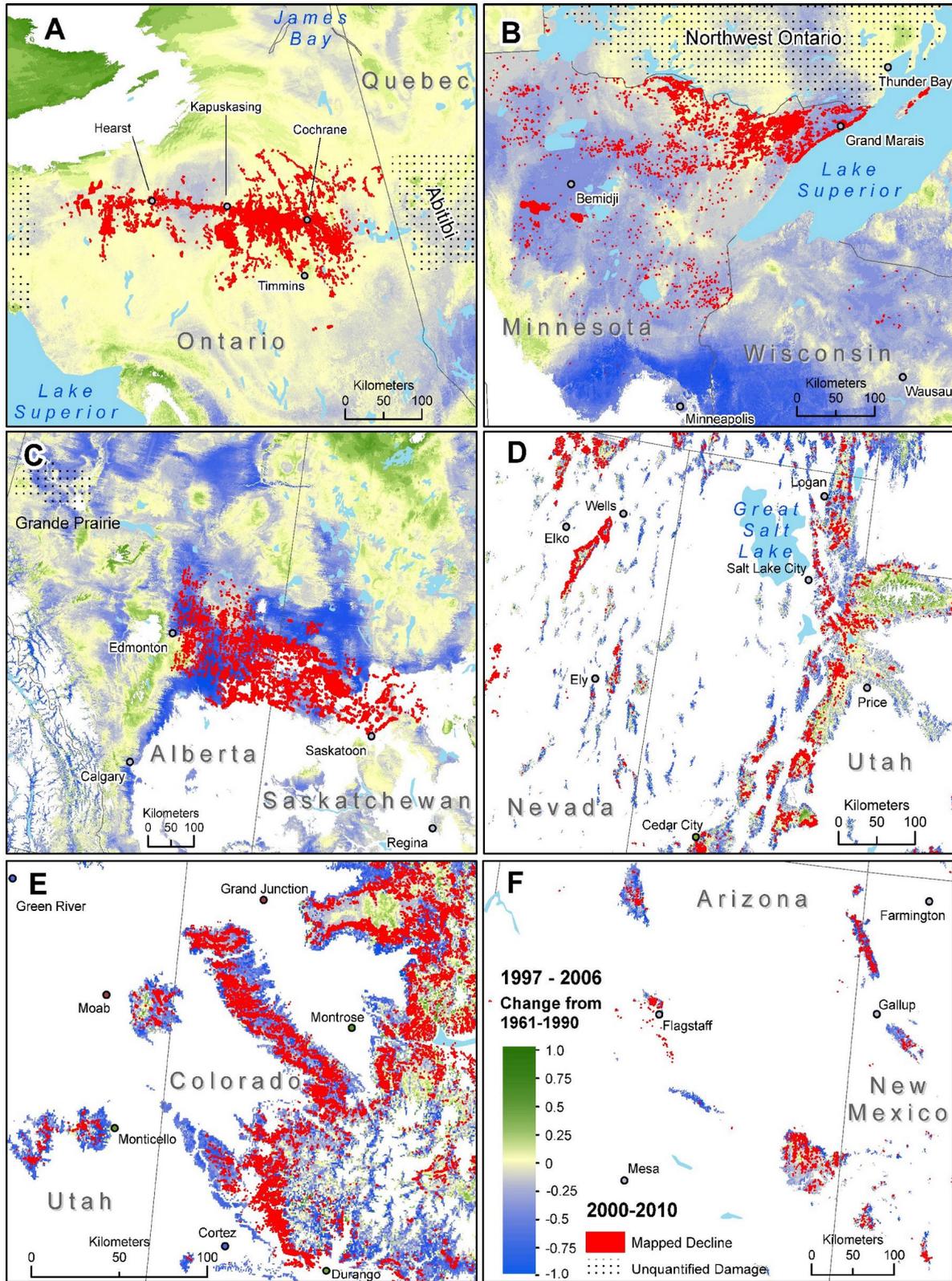


Fig. 5. Close views of areas of decline in North America. The background is the change in climate suitability for aspen between the reference period (1961–1990) and 1997–2006, as shown in Fig. 2. Green and blue indicate increase and decrease in suitability, respectively.

ing in 72 stands distributed across the western Canadian interior (Hogg et al., 2008). Mortality remained high for several years after this drought, and variation in dead aspen biomass in 2005–2006

was significantly correlated with drought severity based on CMI (Michaelian et al., 2011). The drought also led to an overall decrease of about 30% in aspen radial growth across the regional net-

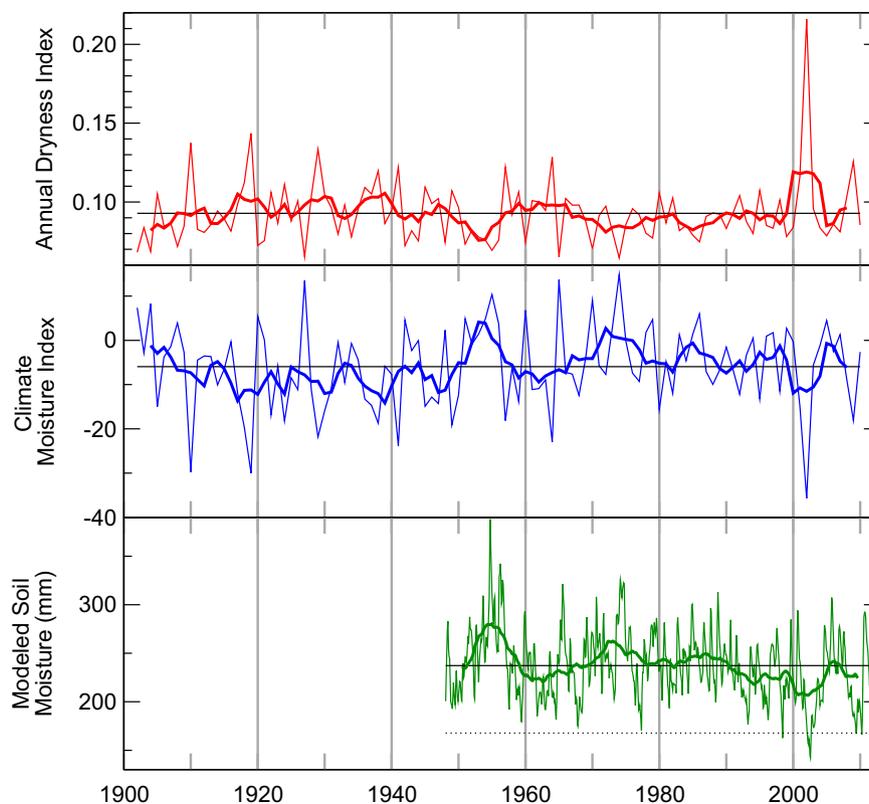


Fig. 6. Time series of indices of moisture balance for the aspen parkland in Alberta and Saskatchewan. Horizontal lines indicate long-term means and heavy lines are 5-year running averages. For modeled soil moisture, the dotted line is two standard deviations below the mean.

work of plots (Hogg et al., 2008). In more recent years (2004–2011), conditions have been generally wetter than normal in Saskatchewan whereas severe droughts have continued to affect northern and central Alberta, leading to renewed concerns about decline of aspen and other forest types in this area.

3.3.4. Western Cordillera

The Western Cordillera includes the Southern Rockies ecoregion, stretching from southern Wyoming to northern New Mexico, and the Wasatch and Uinta Mountains ecoregion, extending from southeastern Idaho through Utah. Climatic suitability varies greatly with elevation (Fig. 4), but suitability has decreased substantially, especially at low to intermediate elevations (Fig. 5D and E). We include here decline in the mountain ranges of Nevada and southern Idaho, where conditions are similar to the Western Cordillera.

3.3.4.1. Wasatch and Uinta mountains and desert ranges. Aspen decline was fairly minor in Utah until about 4100 ha were mapped in 2005 with additional areas in Nevada and southern Idaho (Anonymous, 2005, 2010). A ground survey was conducted in 2006–2007 to gather data on areas mapped as aspen dieback (Guyon and Hoffman, 2011). The proportion of standing trees that were dead ranged from about 25–40% among small trees to 10–28% in larger trees. Regeneration <5.1 cm DBH averaged 6294 stems ha⁻¹, substantially higher than in damaged stands in Arizona and Colorado (Dudley, 2011; Fairweather et al., 2008; Worrall et al., 2010; Zegler et al., 2012).

In 2007, aerial surveyors in Utah recorded 51,000 ha of aspen dieback/decline, the largest area since they began to map it in 2002 (Anonymous, 2010) and about 9% of the aspen forest type in Utah. This number is close to the 49,543 ha over which a decrease in vegetative reflectivity was detected by remote sensing

in Utah that summer (Currit and St. Clair, 2010). Currit and St. Clair hypothesized that this reflectivity loss was due to extreme drought, which had occurred in 2000–2004 and again in 2007.

Spring frost may have added to decline symptoms in 2007 (Currit and St. Clair, 2010; St. Clair et al., 2009). A warm, early spring caused aspen trees in many areas to foliate nearly a month early. Temperatures reached -10°C on the night of May 23, killing aspen foliage across Utah, especially at middle elevations. Refoliation was patchy and branches were killed in severely affected trees. Also in 2006–2007, defoliation by insects was substantial in portions of the region, which may have added to the area of damage and ultimate decline (Guyon and Hoffman, 2011).

Cedar Mountain in southwestern Utah has received particular attention. Already by 2002 there were many dead stands, some without regeneration (Ohms, 2003). Between 1985 and 2008, live aspen cover decreased 24% over a 272-km² study area (Evans, 2010). Most of the decline occurred between 2001 and 2008 (Oukrop et al., 2011). Decreases in cover were strongly related to precipitation deficits, and dry landscape positions had the highest frequencies of dead aspen (Evans, 2010). Decreases were strongly correlated with summer drought 1–3 years earlier and dry winters 5 years earlier. Because of the length of observations and very limited regeneration (Ohms, 2003; Rogers et al., 2010), it was apparent that much of the loss of aspen was permanent.

A cutting experiment at Cedar Mountain showed that regeneration was highly dependent on the amount of mortality in the stand before cutting (Ohms, 2003). There was a steep decrease in regeneration response as mortality increased from 20% to 40% and by 50% the response was negligible. However, browsing pressure was high in unfenced portions of plots and it was apparent that browsing could prevent clones from replacing themselves with or without cutting.

3.3.4.2. *Southern Rockies*. First reported in southwestern Colorado in 2004, decline increased in area through 2008, when over 220,000 ha were mapped, an estimated 17% of the cover type in the state (Worrall et al., 2010). The damage extended north and south into Wyoming and New Mexico.

In 2008, 45% of the decline area mapped in Colorado was rated as “severe,” with estimated mortality >50% (Worrall et al., 2010). During 2009–2011, it was estimated that over 30% of the total aboveground aspen biomass was dead in southwestern Colorado (Huang and Anderegg, 2012). Damaged areas in southwestern Colorado had on average 54% crown loss and 45% mortality. Damaged plots had fewer healthy roots and more dead roots than nearby healthy plots and, throughout Colorado, showed no evidence of increasing regeneration in response to the overstory mortality (Dudley, 2011; Worrall et al., 2010), raising concern that the hard-hit stands may fail to replace themselves.

Moisture stress appeared to be a key factor. Damage was highest at low elevations, where temperatures are high and precipitation low (Dudley, 2011; Worrall et al., 2008). Damage tended to be high on south- and west-facing slopes and on the shoulders and summits of slopes, (Huang and Anderegg, 2012; Worrall et al., 2010). Declining stands had significantly lower basal area than healthy stands.

A record drought in much of Colorado (Pielke et al., 2005) peaked 2 years before the first reports of damage. The most unfavorable climate in the record occurred in 2002, and even under normal conditions, decline sites lay at the fringe of aspen’s climate niche (Rehfeldt et al., 2009). In southwestern Colorado, areas with aspen damage had lower CMI values during 2002 than did areas that remained healthy (Worrall et al., 2010). In the current analysis (Fig. 7), stations on the San Juan National Forest (where damage was first reported) had a drying trend from the mid-1980s to 2002, which had the lowest aspen-year precipitation on record

(not shown). Summer temperatures reached record highs in 2002. ADI exceeded all previous values in 2002 and the 5-year average remained above the previous record for seven consecutive years (Fig. 7). CMI reached a record low in 2002 and the 5-year average remained below the previous record for 4 years. Similarly, modeled soil moisture and its 5-year running average reached record lows, indicating sustained, extreme moisture conditions.

3.3.5. Upper Gila Mountains

Although the area affected in the Upper Gila Mountains was relatively small, it represents a substantial portion of the aspen cover type in this ecoregion, and the damage was unusually severe. As in the Western Cordillera, climatic suitability varies with elevation (Fig. 4), but has decreased in most of the distribution (Fig. 5F).

A severe frost in June 1999 killed foliage, twigs, and stems (Anonymous, 2000; Fairweather et al., 2008). Beginning in 2002 and 2003, with the culmination of a severe drought, decline increased. Next, in 2004–2007, western tent caterpillar (*Malacosoma californicum*) defoliated aspen over large areas, including areas previously impacted by frost and/or drought (Fairweather et al., 2008). By 2007, plots in damaged stands had cumulative overstory mortality averaging 95% below 2286 m elevation, 61% at middle elevations, and 16% above 2591 m. Low elevations are typically warmest and receive the least precipitation.

Density of suckers was initially moderate to low, but browsing by wild ungulates was heavy and numbers dropped rapidly after 2004 (Fairweather et al., 2008). With aspen regeneration unable to survive, overstory mortality is leading to virtually complete loss of aspen in many stands.

To the west on the southern section of the Kaibab NF, 50% average overstory mortality was found (range 5–100%) in a random sample of representative aspen stands in 2010 (Zegler et al., 2012). Decline was most severe at low elevations. The majority

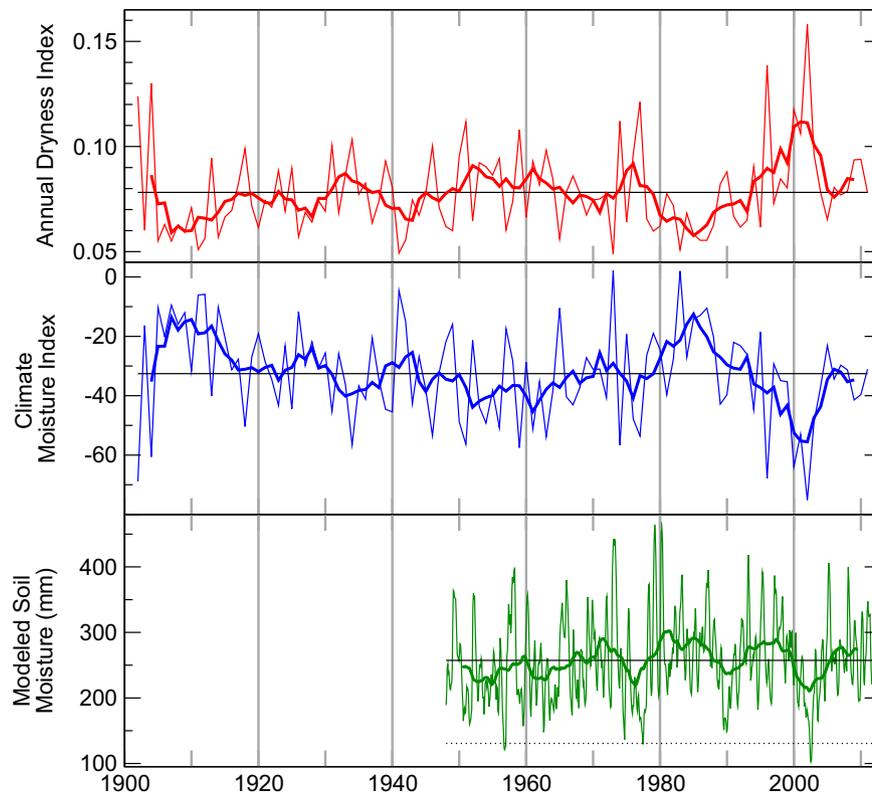


Fig. 7. Time series of indices of moisture balance for the area of the western San Juan Mountains, San Juan National Forest, southwestern Colorado. Horizontal lines indicate long-term means and heavy lines are 5-year running averages. For modeled soil moisture, the dotted line is two standard deviations below the mean.

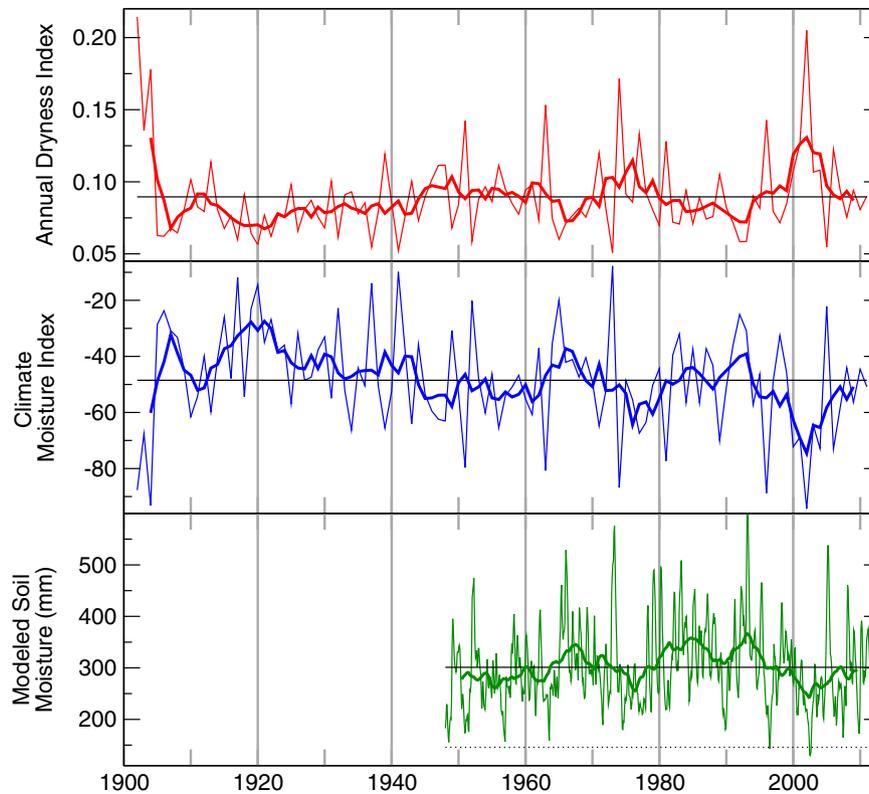


Fig. 8. Time series of indices of moisture balance for the area around the San Francisco Peaks, Coconino National Forest, northern Arizona. Horizontal lines indicate long-term means and heavy lines are 5-year running averages. For modeled soil moisture, the dotted line is two standard deviations below the mean.

of plots had no live stems 1.37 m tall to 10 cm DBH. It was suggested that if mortality and lack of overstory recruitment continue, many of these aspen stands could be lost.

The year that substantial decline began, 2002, was by many criteria the worst year of the worst drought on record. After a decade of increasing drought, 2002 had the hottest summer temperatures and lowest aspen-year precipitation on record. ADI indicated the driest conditions in 100 years and CMI reached a record low (Fig. 8). Its 5-year average remained below the previous record for four consecutive years. Modeled soil moisture had also been trending downward since the early 1990s. It reached a record low in 1996, but that record was broken in 2002.

3.4. Causes of damage

3.4.1. Predisposing factors

Site factors associated with moisture stress often predisposed aspen to decline. In the semiarid, montane, western US, this includes low elevations, upper slope positions, south-west aspects, and marginal climatic suitability during the reference period. Poor soils and low basal area were sometimes associated with decline.

Age of aspen at the landscape scale is sometimes suggested to predispose aspen to climatic stress or to drive episodes of decline. However, healthy aspen may exceed 200 years of age in western USA, and stems as old as 321 years have been found (Binkley, 2008). In the Colorado episode, among overstories older than 40 years, there was no relationship of decline to age. In fact, we have found no report of decline showing evidence that damage increased with stand age. On the contrary, in studies where ages of healthy and symptomatic stands were systematically studied, there was either no effect of stand age (Candau et al., 2002; Hogg et al., 2008; Shields and Bockheim, 1981; Worrall et al., 2010) or damaged stands were younger than healthy stands (Schier and

Campbell, 1980). Indeed, these recent episodes occurred much too rapidly to have been driven by stand aging (Hogg et al., 2008).

3.4.2. Drought

The wide distribution of aspen across a diverse range of habitats attests to its high tolerance to climatic and biotic stressors (Liefers et al., 2001). Nevertheless, aspen has a fragile existence where moisture is concerned. The southern and lower-elevation edges of its distribution are defined largely by moisture availability (Hogg and Hurdle, 1995; Jones and DeByle, 1985; Rehfeldt et al., 2009; Shields and Bockheim, 1981) and recent decline episodes were largely caused by drought. Our comparisons of decline occurrence with model results (Figs. 4 and 5) indicate that decline occurred where climatic suitability, particularly moisture balance, is marginal and where suitability decreased recently. Tree-ring studies of aspen in western Canada (Hogg et al., 2005, 2008) and in Colorado (Hanna and Kulakowski, 2012) show that drought is also a major cause of multi-year growth reductions that often precede mortality.

There is a significant genetic component in drought tolerance of aspen. In a common garden experiment that was subjected to natural drought, survival varied significantly among clones (St. Clair et al., 2010b). Similarly, under precisely controlled conditions, clones varied in tolerance of diurnal drought (Griffin et al., 1991). Intraspecific genetic variation in drought resistance appears to be driven by vessel diameters (smaller vessel diameters providing higher resistance to cavitation), at least in boreal environments (Schreiber et al., 2011).

3.4.3. Defoliating insects

Clearly, FTC played a dominant role in inciting the Kapuskasing decline episode; drought may have played a lesser role. In northern Minnesota, FTC caused the first wave of decline symptoms. The

droughts may have predisposed stands to the early damage, but apparently precipitated the more severe second wave of damage. Defoliators were also part of the sequence of insults preceding branch dieback and mortality recently in the Upper Gila Mountains and in the early 1990s in the aspen parkland. It appears that drought was the more consequential agent of damage in both of these episodes.

It is tempting to lump all proximate damage agents as part of the cause. However, several cases show that drought alone is often sufficient to cause severe damage. In southwestern Colorado, no significant defoliation by insects occurred for at least 10 years before decline began (Marchetti et al., 2011). No such outbreaks had been reported in the state near the scale of sudden aspen decline. Similarly, in the aspen parkland of western Canada, stands where massive mortality occurred after the 2001–2002 drought (Michaëlian et al., 2011) had been free of significant defoliation since the mid-1990s and the most recent regional-scale outbreak of forest tent caterpillar occurred in 1987–1990. On the other hand, mortality levels were substantially higher in northern Arizona than in Colorado, so the defoliation and/or frost may well have increased the severity of damage.

3.4.4. Frost

Spring frost may have been a factor in two major episodes of damage discussed above, the Upper Gila Mountains and the Wasatch–Uinta Mountains. Both frost events were severe enough to kill branches (and in Arizona, entire ramets) as well as foliage. In other episodes, we found no evidence suggesting that spring frost was involved.

Late spring frost can be unusually damaging to aspen. Well before any anthropogenic climate change, Baker (1925) noted “When late spring frosts occur, not only the leaves but also the twigs of last year’s growth may be frozen, and the second crop from older dormant buds may not become well developed until well into July. These frosts, or more properly freezes, may occasionally be so severe that entire full-grown trees are killed outright. This occurred in many parts of Utah and southern Idaho, especially within the Engelmann spruce zone, during the freeze of May 31, 1919.” Killing of buds, apparent branch mortality, and reduction in radial growth was attributed to a severe frost following an extended warm period in late April, 1958 in southern Saskatchewan and Manitoba (Cayford et al., 1959).

Because early, warm springs can advance phenology, climate change is expected to increase the exposure of trees to damage by spring frost (Hanninen, 2006). Indeed, aspen phenology in Alberta has advanced 2 weeks over the last 70 years, and exposure to spring frost has consequently increased (Beaubien and Hamann, 2011). Thus, the large and damaging events in Arizona in 1999 and Utah in 2007 may become more common.

3.4.5. Winter injury

Cycles of thawing and freezing during winter dormancy can injure plants in a variety of ways, generally referred to as winter injury. Warm periods dehardens buds, twigs, cambium, sapwood, or roots, leaving them vulnerable to freezing temperatures that follow (Hennon et al., 2012). Thaw–freeze cycles also cause winter cavitation of xylem vessels, to which aspen is relatively susceptible (Sperry et al., 1994). Winter injury may have been involved in damage to aspen reported by Cayford et al. (1959), mentioned above under spring frost, but as the authors noted, it can be difficult to distinguish the effects of such events when both occur.

It has been suggested that winter injury may contribute to declines, especially when inadequate snow cover exposes roots to such damage (Hogg et al., 2002; St. Clair et al., 2010a). These are plausible mechanisms of damage, but research is needed to deter-

mine their importance. Like spring frost, incidence of thaw–freeze events will likely increase with climate warming (Hennon et al., 2012).

3.4.6. Contributing factors

In the conceptual model of a decline disease, contributing factors are the final part of a causal chain. These pathogens and insects, also known as secondary agents, generally thrive on stressed trees with reduced resources for defense (Marchetti et al., 2011). Many of these agents kill the phloem and cambium in expanding patches, leading to crown dieback and reducing the resources available for recovery. After populations increase on stressed trees, some species become capable of attacking more vigorous trees (Marchetti et al., 2011). In this way, these agents can increase the severity, extent, and the duration of a decline episode initially incited by extreme climatic events or defoliation.

Secondary agents appear to be involved in every episode of aspen decline that has been studied, and are strongly correlated with tree mortality (Anonymous, 2009c, 2011b; Dudley, 2011; Fairweather et al., 2008; Guyon and Hoffman, 2011; Hogg et al., 2008; Marchetti et al., 2011; Packard, 1942; Zegler et al., 2012). The most common are the bronze poplar borer and poplar borer, *Agrilus liragus* and *Saperda calcarata*, with the flatheaded poplar borer, *Dicerca tenebrica*, in some areas. Cytospora canker is frequently an important contributor, and aspen bark beetles, *Trypophloeus populi* and *Procryphalus mucronatus*, have been particularly important in Colorado and Arizona. Armillaria root disease, caused by *Armillaria* spp., is important in the aspen parkland, Michigan, and Wisconsin, and is suspected to play a role elsewhere. Additional diseases that are not secondary agents, especially sooty-bark canker, caused by *Encoelia pruinosa*, are common in some damaged areas. This may represent a high background rate of such agents, and/or the ability of *E. pruinosa* to become established in wounds created by the wood-boring insects (Guyon and Hoffman, 2011).

3.5. Past distributions of aspen

The paleo-distribution of aspen, and its change with climate, could help us anticipate future changes. Unfortunately, aspen pollen is poorly preserved, so past distributions are poorly understood. The isolated populations of aspen characterizing much of its southern distribution may be relict populations that were more continuous near the time of the Pleistocene glaciations (Baker, 1925; Peterson and Elliot-Fisk, 1987). Boreal forest existed in the Great Plains of central North America as far south as Kansas and Missouri during the last (Wisconsin) glaciation, and there is evidence that its retreat was still underway less than 1000 years ago (Wells, 1970). There was likely a mixed woodland and aspen parkland at its southern extent, as there is today farther north. Thus, the recent episodes of decline at the southern fringes of aspen’s range could be viewed as renewed pulses of change that began with the recession of the Wisconsin glaciation.

3.6. Climatic suitability vs. distribution

Although climatic suitability is most important, it is not the sole determinant of aspen distribution. Within climatically suitable areas, soils, competition, and diseases and insects may limit aspen occurrence. However, where aspen is in the locale, the most important factor influencing distribution and abundance is disturbance regime. Without disturbance, seral aspen will eventually yield to competitors by succession. It has been suggested that climate change may lead to increased frequency of stand-replacing disturbance, such as fire, that would favor aspen over its competitors

(Kulakowski et al., 2012; Rogers et al., 2007). This would tend to skew the population structure toward younger ages, in some cases reflective of conditions before European settlement (Margolis et al., 2011). Because aspen under about 40 year old appears to tolerate drought much better than older stands (Worrall et al., 2010), more frequent disturbance could potentially increase the resilience and survival of aspen in a marginal climate. This could delay and/or moderate the negative effects of climatic warming and drying on distribution.

Aspen distribution may lag behind changes in climatic niche for additional reasons. Where climatic suitability decreases, aspen may persist for decades as overstories die, younger stems survive for a time, and eventually the genet is unable to survive. Where suitability increases, barriers to dispersal and establishment may delay or even prevent the expansion of distribution. However, there is already evidence of rapid upslope expansion of aspen in the Rocky Mountains of western Alberta, facilitated by increased temperatures and disturbance by forest harvesting (Landhäusser et al., 2010).

3.7. Projected effects of climate change on aspen

In geographically disparate regions, we found a strong relationship between recent aspen declines and climate, particularly between decline and the recent decrease in climatic suitability (Fig. 5). Decline in Minnesota and especially Ontario has a weaker climatic signal, partly because the relationship is influenced by other factors such as insect defoliation and suboptimal soil conditions, which cannot yet be treated with precision in climate profile modeling.

To explore further the relationship between recent decline episodes and climate, we ran the centroids of the decline polygons (Fig. 4) through the bioclimate model and calculated for each of the decline regions the average votes in favor of decline sites being climatically suited to aspen. The process was repeated for 1997–2006 and for future climates projected for the centroid points according to output for the A2 scenario of three GCMs. These means were then compared to those of all aspen presence points from the same regions, delimited by latitude and longitude (Sup-

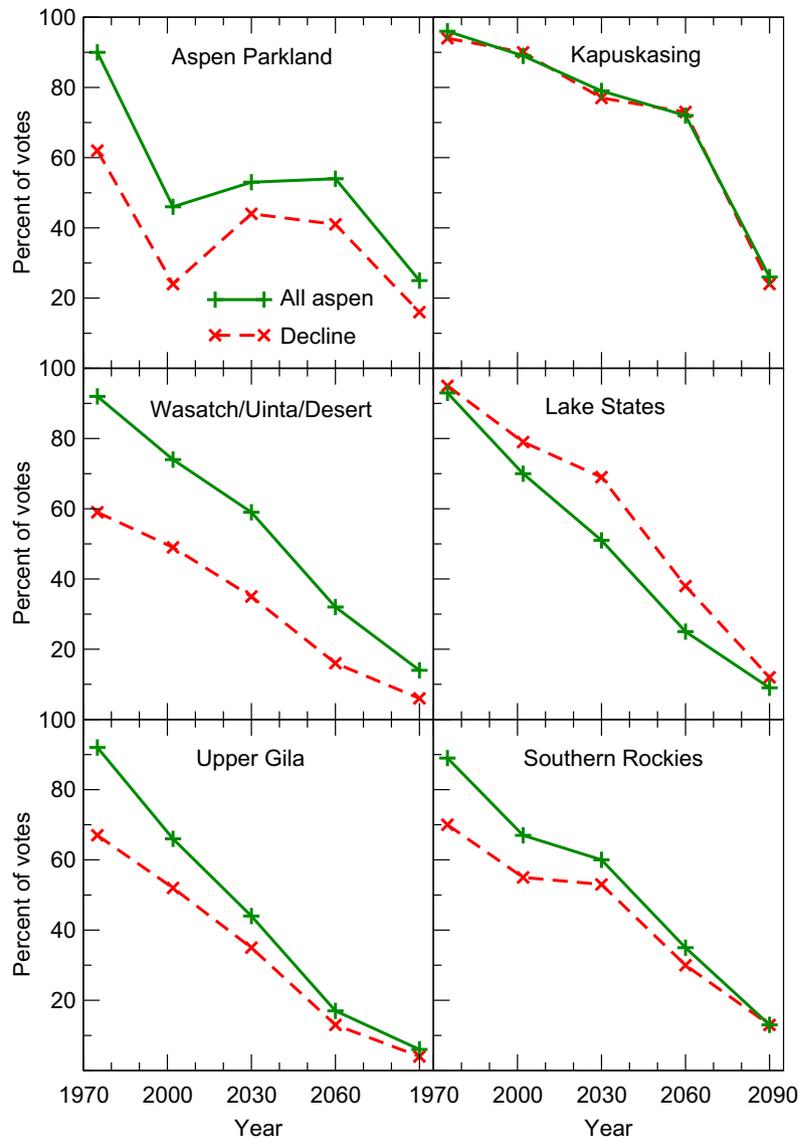


Fig. 9. Comparison of mean proportion of votes (indicating relative climate suitability for aspen) between the centroids of decline polygons vs. all points in the region where aspen is known to be present (serving as control aspen) for the six major decline regions (Fig. 4). In each line, the first two points are based on actual climate data from 1961 to 1990 and 1997 to 2006, respectively. Future projections are average proportions of votes based on climates modeled by three GCMs using the A2 scenario for greenhouse-gas emissions.

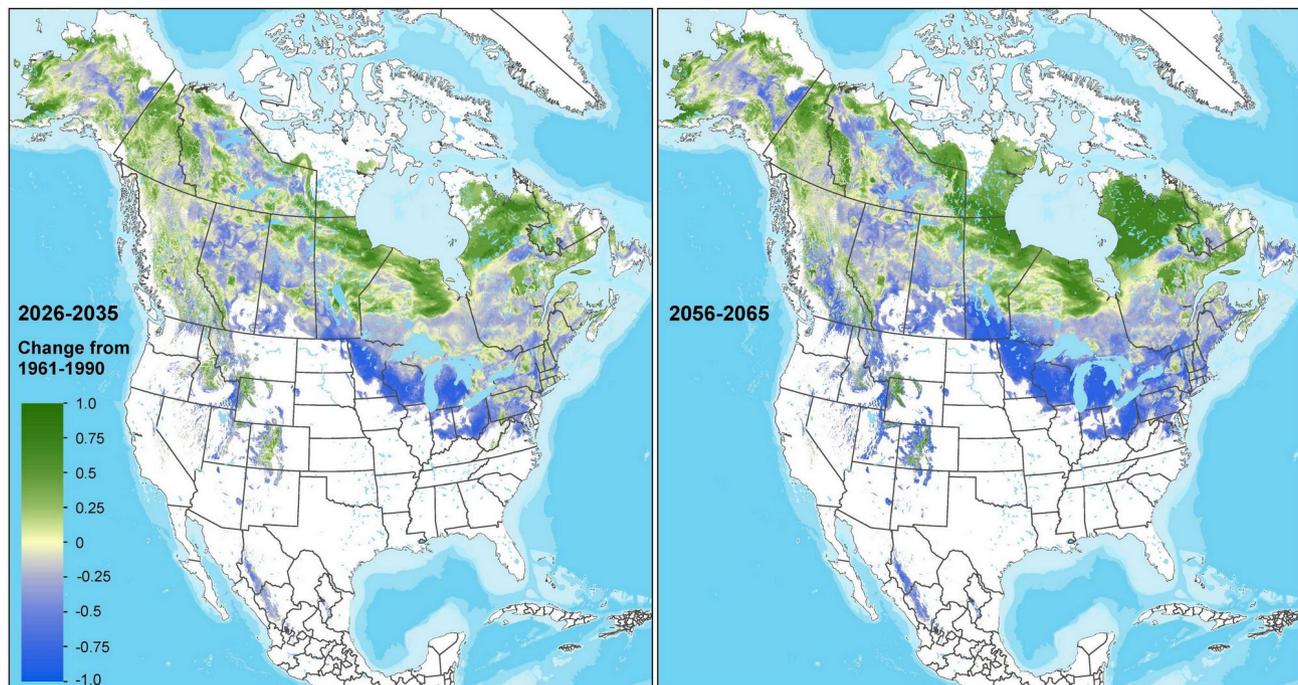


Fig. 10. Distribution of differences between 1961 and 1990 (reference period) vs. projected future climate suitability for aspen in North America, depicted as in Fig. 2. Cells in which both recent and future votes were <0.25 (i.e., neither suitable now nor in the future) are not shown. Projections are average proportion of votes based on three GCMs using the A2 scenario for greenhouse-gas emissions.

Table 1

Area remaining climatically suitable, lost, or gained compared to the 1961–1990 climate to comprise the 2030 and 2060 total suitable area. For this analysis, 40% of votes from the bioclimate model was the minimum threshold for suitability (i.e., low or better probability).

Time period	Total suitable area (Mha)	Future suitability compared to 1961–1990 (Mha)		
		Remain	Lost	Gained
1961–1990	704			
2026–2035	736	598	106	138
2056–2065	716	522	182	194

plement 1: Table 2). The proportion of votes for decline points is considerably less than for aspen presence points, on which the model was built, for all western regions, but not for Kapuskasing nor the Lake States (Fig. 9). Both decline points and known aspen points decreased sharply in suitability recently in all regions except Kapuskasing. This trend is projected to continue through most of the century. In the west, decline sites were affected preferentially by the recent decrease because they had marginally suitable climate to begin with. Fig. 9 reinforces conclusions from the decline narrative, model images, and weather history, that there is a clear association of climate with decline in the west, but that damage in the East, especially Kapuskasing, is less clearly or exclusively climate-driven.

Potential impacts of the changing climate on habitats climatically suited to aspen are illustrated for the decades surrounding 2030 and 2060 as the difference between projections for the future and reference periods (Fig. 10). Losses of habitat predominate in the south (especially US and Mexico) while gains are projected in the north and, to a lesser extent, at high elevations. Projected area of suitable climates remains relatively constant throughout the century because gains tend to balance losses (Table 1). However, by 2060 about 26% of the current distribution would no longer

be suited to aspen. These results are consistent with regional studies and projections for eastern USA (Iverson and Prasad, 1998; Iverson et al., 2008), British Columbia (Hamann and Wang, 2006), western USA (Rehfeldt et al., 2009), and western North America (Gray and Hamann, 2012).

The model suggests that the loss of aspen along the southern edge of its current distribution will result from decline initiated by an unfavorable balance between temperature and precipitation and that the recent decline will substantially increase in the future.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2012.12.033>.

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