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Aspen, climate, and sudden decline in western USA

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ABSTRACT

A bioclimate model predicting the presence or absence of aspen, *Populus tremuloides*, in western USA from climate variables was developed by using the Random Forests classification tree on Forest Inventory data from about 118,000 permanent sample plots. A reasonably parsimonious model used eight predictors to describe aspen's climate profile. Classification errors averaged 4.5%, most of which were errors of commission. The model was driven primarily by three variables: an annual dryness index, the ratio of summer to annual precipitation, and an interaction of growing season precipitation with the summer–winter temperature differential. Projecting the contemporary climate profile into the future climate provided by three General Circulation Models and two scenarios (SRES A2 and either B1 or B2) suggested that the area occupied by the profile should diminish rapidly over the course of the century, 6–41% by the decade surrounding 2030, 40–75% for that surrounding 2060, and 46–94% for 2090. The relevance of the climate profile to understanding climate-based responses is illustrated by relating trends in climate to the recent incidence of sudden aspen dieback that has plagued portions of the aspen distribution. Of the eight variables in the profile, four reached extreme values during 2000–2003, the period immediately preceding the appearance of damage in aerial surveys.

1. Introduction

The enormous transcontinental distribution of aspen (*Populus tremuloides*) lies primarily within the Canadian boreal forest but reaches its southern limits in the mountains of western USA (Perala, 1991). Recent infirmity of aspen in this region (see Bartos, 2001; Worrall et al., 2008), the prairie provinces of Canada (Hogg et al., 2002), and eastern Canada (Candau et al., 2002) has focused attention on aspen's ecological relationships (e.g., Frey et al., 2004) with its biotic and abiotic environment.

For the latter half of the 20th century, aspen has been in a period of general decline thought to result from the suppression of wildfire, the absence of which has allowed plant succession to proceed toward a culmination that ordinarily excludes aspen (Di Orio et al., 2005; Bartos, 2001; Frey et al., 2004). Recent episodes of aspen dieback have been superimposed on this general decline. Dieback can be recognized by the suddenness of the impact and by an epidemiology that begins with the death of branch tips, death of mature trees, and expiration of entire clones (Frey et al., 2004; Hogg et al., 2008). The process is reviewed thoroughly by Frey et al. (2004), who discuss primary and secondary causal effects, but these researchers and most others (Candau et al., 2002; Hogg et al., 2005, 2008; Worrall et al., 2008) suspect that drought is the primary stimulus. Because of the suddenness of the impact, the condition generally is referred to as 'sudden aspen decline'.

Other than a general recognition of the extremely broad range of temperatures and precipitation under which aspen exists (see Mueggler, 1988; Perala, 1991), much of what is known about aspen–climate relationships stems from the work of Hogg (1994, 1997) who has related the transition of grasslands to forests containing aspen in the prairie provinces in western Canada to the excess of annual precipitation over potential evaporation. Because global warming scenarios generally couple relatively large increases in temperature with modest increases in precipitation, potential impacts of a changing climate on aspen have become of concern (Hogg and Hurdle, 1995; Hogg et al., 2002).

Our objectives are to (1) define aspen's climate profile (*sensu* Rehfeldt et al., 2006) with a bioclimatic model that predicts presence or absence from climate variables, (2) assess the impacts of global warming on the future distribution of the contemporary profile, and (3) illustrate the utility of bioclimate models for understanding climate-based responses such as sudden aspen decline. Our analyses are concentrated in that portion of the aspen distribution in the conterminous USA west of -102° longitude. Any mapped predictions for southwestern Canada are extrapolations from USA data. For relating climate to dieback, we concentrate on the U.S. Forest Service's Rocky Mountain Region, 37–45° N latitude and -102° to -107° longitude, where the outbreak has been best documented (see Worrall et al., 2008).

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2. Methods

We use data from permanent sample plots of Forest Inventory and Analysis, U.S. Forest Service, for western USA. The plots are systematically located to sample the vegetation on forested and non-forested lands (see Alerich et al., 2004; Bechtold and Patterson, 2005). Plots ordinarily are established with four subplots, but for our analyses, data from subplots were combined. We use presence–absence data for aspen from the *ca.* 118,000 plots. Aspen was recorded as present in 3098 plots, 2.6% of the total number; 874 of the plots with aspen lie within the Rocky Mountain Region. Inventory plots ordinarily are re-measured on 10-year intervals, but we used the original data taken on plot establishment, most of which date to the period of climate normals, 1961–1990.

The thin plate spline surfaces of Rehfeldt (2006), available at URL: http://forest.moscowfsl.wsu.edu/climate/, were used to estimate normalized (1961–1990) monthly means of total precipitation and average, maximum, and minimum temperature of each inventory plot. These surfaces, constructed with the software of Hutchinson (1991, 2000), provide point predictions of climate from geographic input (latitude, longitude, and elevation). An act of the Congress of the United States prevents Forest Inventory from revealing the precise geographic location of their plots. At the outset of a series of analyses (see Rehfeldt et al., 2006), we had been permitted access to inventory databases in order to generate monthly climate normals from actual coordinates. Forest Inventory, however, has made available public locations for their plots using ‘fuzzy’ coordinates, those for which actual geographic coordinates have been altered. Forest Inventory does not divulge the degree of falsification. Point locations in illustrations that follow employ these fuzzy coordinates.

The analyses employ 34 variables derived from monthly climate estimates (see Rehfeldt, 2006), 18 of which are derived directly from the monthly estimates. The derived variables include simple expressions of average temperature and precipitation (e.g., mean annual temperature, mean annual precipitation), temperature sums (e.g., degree-days $>5\,^{\circ}$C, degree-days $<0\,^{\circ}$C), freezing dates (e.g., date of the last freeze of spring), and expressions of the balance between temperature and precipitation (e.g., the ratio of degree-days $>5\,^{\circ}$C to mean annual precipitation). The remaining variables were interactions among these eighteen.

2.1. Bioclimate model

Our statistical models are built on the framework of Iverson and Prasad (1998) and closely parallel to those of Rehfeldt et al. (2006). We use the Random Forests classification tree (Breiman, 2001) to predict the presence–absence of aspen from climate variables. The model thus predicts the realized niche for the contemporary climate, which is referred to as the climate profile (see Rehfeldt et al., 2006). The Random Forests algorithm, available in R (R Development Core Team, 2004; Liaw and Wiener, 2002), constructs a set of regression or classification trees from an input data set. The trees in their aggregate are called a forest. The process begins with the drawing of a bootstrap sample consisting of about 64% of the total number of observations. This sample is used to build a tree while those omitted, collectively termed the out-of-bag sample, are used to compute classification errors. At each node of a tree, a random sample of the predictor variables is selected, ordinarily equaling the square root of the number of predictors. Of these, the variable that minimizes the classification error is selected. Nodes are further split until no more improvement can be achieved.

Out-of-bag errors are composed of errors of omission (a prediction of false when true) or errors of commission (a prediction of true when false) and are calculated as the proportion of the total number of errors to the total number of observations in the forest. In making predictions, each tree of each forest provides a ‘vote’ concerning the classification of an observation. Because the error converges to a limit as the number of trees in the forest becomes large, overfitting is inconsequential.

For classification trees, Breiman (2001) recommends that the number of observations within classes be approximately equal. Because aspen occurs in only 2.6% of the inventory plots, a sampling protocol was required to satisfy Breiman’s recommendation. We use the general approach of Rehfeldt et al. (2006) to draw 14 samples from the inventory database. All observations with aspen were selected for each sample, weighted by a factor of 2, and fixed in the sample at 40% of the total. Weighting by a factor of 2 allowed twice as many observations with no aspen to be included in the sample while maintaining presence at 40% and absence at 60% of the total. Each sample, therefore, contained about 15,500 observations, 6196 observations with aspen, and about 9300 observations without aspen.

Observations without aspen were allocated to each sample in two steps. The first step assured that the most of the observations without aspen would be the most difficult to separate from those with aspen. To do this, we defined an 18-variable hypervolume (*sensu* Hutchinson, 1958), each dimension of which consisted of an estimate of aspen’s climatic limits expanded by $\pm$ 0.1 standard deviations. Climatic limits were estimated from the mean of all observations with aspen. The hypervolume contained about 82,000 observations without aspen. From within this hypervolume, 40% of the total sample (about 6200 observations) was selected at random. The remaining observations without aspen (20% of the total, 3100 observations) were selected from outside the hypervolume such that a broad range of climate variation was represented. We did this by drawing a random sample of 155 observations (1% of the total) from each of 10 uniform classes subtending each of the first and second principal components calculated from the 18-variable network for all observations in the inventory database.

This sampling procedure thus used all observations with aspen, concentrated the remainder of the sample in those climates for which separating presence from absence would be the most difficult, but still represented the full range of variation among the plots. Weighting permitted a higher proportion of the total observations to be used in each forest. Fourteen forests were used so that the probability would be high that all observations within the hypervolume would be used in at least one forest.

For classification trees, Random Forests provides two statistics for judging the importance of independent variables, the mean decrease in accuracy and the mean decrease in the Gini index of class purity (Breiman and Cutler, 2004). The first relies on an iterative process of randomly permuting (noising up) a predictor variable to assess the effect of a variable on the classification error. The second, also known in ecological research as the Gini–Simpson index (Sen, 2005), expresses the reduction in node purity attributable to a variable when it is used to split a node. For bioclimate modeling, the mean decrease in accuracy tended to provide Rehfeldt et al. (2006) with superior models and is used exclusively herein to judge variable importance.

Our analyses consisted of 14 forests of 100 trees, with an independent sample drawn for each forest. A stepwise procedure was used to iteratively cull predictors according to an average of importance values for the 14 forests. The program began by using a full complement of the 34 climate variables. Out-of-bag errors were used to select the final model: when errors began increasing consistently, we assumed that the corresponding model was of reasonable parsimony. A visual assessment of the fit of the model was made by comparing predicted distributions of the climate profile with the two-dimensional range maps of Little (1971), available as digitized files from USGS (2005).

2.2. Mapping predictions

Nearly 6 million pixels of ~1 km (0.0083°) resolution comprise the terrestrial portion of our geographic window. Using the digitized elevations of GLOBE (1999), we estimated the climate of each pixel from the surfaces of Rehfeldt (2006). The estimates were then run through the bioclimate model, with each tree of each forest providing a vote as to whether a pixel fell within aspen's climate profile. A pixel was assumed to have a suitable climate when receiving a majority of favorable votes.

Projections of the contemporary climate profile into future climate space were made for three General Circulation Models (GCM) and two scenarios: (1) Canadian Center for Climate Modelling and Analysis (CCCMA), using the CGCM3 (T63 resolution) model, SRES A2 and B1 scenarios; (2) Met Office, Hadley Centre (UKMO), using the HadCM3 model, SRES A2 and B2 scenarios; and (3) Geophysical Fluid Dynamics Laboratory (GFDL), using the CM2.1 model, SRES A2 and B1 scenarios. Data, their descriptions, and explanation of the scenarios are available at the International Panel on Climate Change Data Distribution Center (http://www.ipcc-data.org/). In general, the SRES A2 scenario reflects unrestrained carbon emissions while the B1 and B2 scenarios incorporate social and economic restraints; the scenarios we use should begin diverging by 2030.

GCM output was used to calculate the monthly change in climate between the normalization period and the decades surrounding 2030, 2060, and 2090 for each weather station used in developing the climate surfaces (for details, see Rehfeldt et al., 2006). Calculation of monthly changes in average, minimum and maximum temperature used actual values; those for precipitation used proportions. Downscaling from the relatively coarse grids of the GCMs to the point locations of the weather stations used a weighted average of the monthly change in climate calculated for the GCM cell centers lying within 400 km of a station. The inverse of the square of the distance from the station to the cell center was used for weighting. Monthly climate surfaces for average, minimum, and maximum temperature and precipitation were then fit anew for each GCM and each scenario. These procedures thus resulted in a total of 72 new climate surfaces for each month. The surfaces were then used to project the derived variables for the future climate of each pixel in our geographic window. Climate variables for each pixel were run again down the classification trees of the 14 forests to obtain votes as to the suitability of the future climate to aspen.

Projections of the climate profile were made for three time periods, the decades surrounding 2030 (i.e., 2026–2035), 2060, and 2090. In total, therefore, these procedures produced 18 maps (3 GCMs $\times$ 3 time periods $\times$ 2 scenarios).

2.3. Sudden aspen decline

Projecting the contemporary climate profile into future climate space allows delineation of areas where aspen should be vulnerable to the change in climate. Yet, sudden aspen decline has been observed during specific years and on specific sites, particularly in the U.S. Forest Service's Rocky Mountain Region. We illustrate the utility of the climate profile for assessing sudden aspen decline on two fronts: (1) examining the 1950–2006 trends in those climate variables relevant to the aspen profile, and (2) comparing the recent climate trends for all inventory plots containing aspen in Rocky Mountain Region to those for areas in which dieback has been observed. Because the calculation of negative degree-days uses sums for winter months rather than for the calendar year, the period 1950–2006 contained 56 years of climate records.

On the first front, we assemble for the Rocky Mountain Region climate data from Earthinfo (2006) for 1950–2006. Data were used from only those weather stations with a complete set of valid months (i.e., no more than 10 missing daily observations) for at least 50 years of the 56-year period. Only 51 stations satisfied these criteria. These stations, however, were at an average elevation of 1755 m, approximately 800 m lower than that of the 874 inventory plots containing aspen. To provide assurance that the climate at locations inhabited by aspen were being represented without bias, yearly climate estimates using unpublished spline surfaces for 1950–2006 were made for each of the 874 inventory plots containing aspen in the Rocky Mountain Region. The unpublished spline surfaces were developed from the same procedures used by Rehfeldt (2006), contain approximately the same number of observations, and have comparable fit statistics.

However, for estimating annual climate for inventory plots, actual geographic coordinates were no longer available. Instead, we used the fuzzy coordinates to estimate plot climate. Because actual coordinates had been used to estimate climate normals, a difference between the mean of a derived variable for the period 1961–1990 based on fuzzy locations and the normal for the same data point can be viewed as an adjustment factor suitable for correcting data from fuzzy locations to actual locations. In justifying this approach, it is important to realize that plot elevation has not been falsified by Forest Inventory. In mathematical notation, the process by which yearly climates of falsified locations was adjusted was:

$$X'_{ij} = X_{ij} + (N_i - \bar{x}_i)$$

where X is a derived climate variable for plot i in year j; N is the 1961–1990 climate normal for plot i; $\bar{x}$ is the mean for plot i for years 1961–1990.

For the second front, the yearly spline surfaces were used to estimate the climate at 3431 locations in the Rocky Mountain Region where sudden decline has been observed. Dieback locations were obtained from digitized files produced from aerial surveys of 2006 (URL: http://www.fs.fed.us/r2/resources/fhm/aerialsurvey/). According to this survey, the area encompassed by those polygons in which dieback had occurred ranged in size from a fraction of a hectare to more than 3000 ha, with a total area of about 72,000 ha. The geographic coordinates for the center of each polygon were located and exported from ARCMAP software and the associated elevation of each was estimated from GLOBE (1999), using a 1 km grid.

Yearly climate estimates in the Rocky Mountain Region for (1) inventory plots containing aspen and (2) polygons locating aspen dieback were run through the bioclimate classification tree. Votes were used to assess whether the climate in each year had been favorable or severe for aspen. Because the precise location of inventory plots was not available for these calculations, plots in which dieback had occurred could not be removed from the inventory data. We compare, therefore, votes garnered by locations where dieback had occurred to those of all locations in the inventory database containing aspen, even though some of these locations undoubtedly would have contained aspen trees suffering dieback.

3. Results

3.1. Bioclimate model

Out-of-bag errors for the 34-variable model averaged 4.3% across the 14 forests. This error remained relatively constant throughout the stepwise elimination of variables until 10 variables remained (Fig. 1). Thereafter, the errors increased slowly as variables were removed, reaching 4.5% with eight variables, 7.0% with two, and culminating with 9.7% error with a 1-variable model.

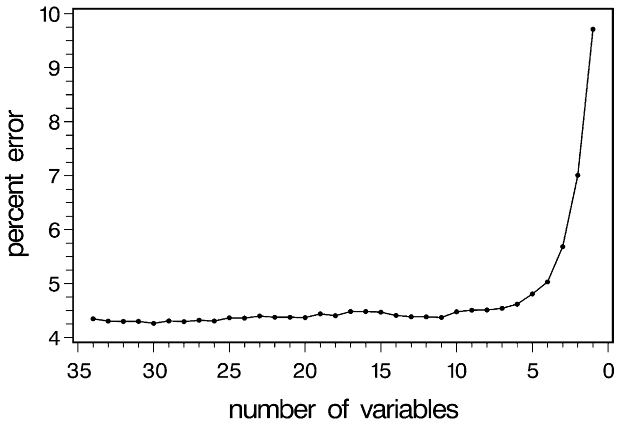

Fig. 1. Out-of-bag errors plotted against the number of independent variables in the model.

We chose the 8-variable model as being reasonably parsimonious while providing buffer against reliance on single variables.

Out-of-bag errors for the 8-variable model were comprised primarily of the errors of commission, the error that arose from predicting aspen to be present when absent. When averaged across the 14 forests, errors of commission averaged 7.5% for the 9300 observations without aspen represented in each forest. Errors of omission, predicting aspen to be absent when present, averaged 0.15%; on average, the model correctly classified all but *ca.* 9 of the 6196 aspen observations in each forest. These errors, therefore, produced out-of bag error of about 4.5% of the 15,500 observations.

We assume that the variable comprising the 1-variable model is the most important in the aspen climate profile. This variable, the annual dryness index, is a ratio that reflects the balance between summer temperatures and annual precipitation (Table 1). This index was joined in the 2-variable model by a variable reflecting the periodicity of precipitation, the ratio of summer precipitation to the annual total. As measured by the mean decrease in accuracy, the importance of these two variables in the 2-variable model was nearly identical.

The variable ranked third in importance to the climate profile was an interaction between summer precipitation and growing degree-days (Table 1), another variable expressing the balance between temperature and precipitation. All of the remaining variables except for the mean maximum temperature in the warmest month (MMAX) involved interactions of precipitation with winter temperatures. The most notable of these were the products of the annual dryness index and summer dryness index with negative degree-days calculated from the minimum temperature.

In the histograms showing the frequency of aspen in each of 100 uniform classes for each of the 8-predictor variables (Fig. 2), the breadth of the *x*-axis is relevant only to the distribution of plots containing aspen. Table 2 provides data that allow these histograms to be viewed in context of either all lands of western USA in the inventory database or from just those lands that are forested. In compiling the statistics for this table, we discarded the largest and smallest 0.05% of the observations, assuming, as suggested in Fig. 2, that most of the outliers were within these percentiles. Table 2 shows, for instance, that the relatively narrow limits of aspen's distribution for ADI (Fig. 2), is about one-half of that for forested lands and one-fifth of that for all lands in western USA as a whole. Likewise, for the other variables in the climate profile except PRATIO, the data in Table 2 show that in comparison to forested and non-forested lands, aspen tends to be absent where either summers or winters are either dry or warm. Values for PRATIO (Fig. 2) show that aspen occurs across a broad range of values but is most frequent where summer and winter precipitation is evenly balanced, that is, PRATIO of 0.4–0.6.

Occurrence of aspen in Fig. 2 is based on frequencies. When these frequencies are expressed as a proportion of the total number of plots containing aspen, none of the classes in the histograms would peak at values higher than 0.15, suggesting that (a) factors other than climate (e.g., soils, disturbance, succession) also may be important, and (b) multivariate models are required to accurately predict occurrence.

3.2. Mapped climate profile

Limitations of using digitized versions of two-dimensional range maps for verifying predictions from bioclimatic models (see Rehfeldt et al., 2006) are centered on (1) the coarse resolution of a range map in comparison to the grids of GLOBE (1999), (2) the inability to represent altitudinal distributions on two-dimensional surfaces, and (3) a lack of alignment between the range map and the digitized elevations used for estimating climate. Nonetheless, colored pixels in the mapped climate profile (Fig. 3), those indicating a voting percentage >50%, tend to be in close agreement with Little's (1971) range map. This is particularly true for pixels colored red, those predicted by the bioclimate model of having a climate suitable for aspen at the highest probabilities.

Inserts within Fig. 3 clearly demonstrate the problems inherent with using range maps for a visual validation of bioclimate models.

Table 1
Acronyms, derivation, and ranking of climate variables of relevance to the climate profile of aspen.

Acronym	Definition	Importance ranking
DD5	Degree-days >5 °C	–
MAP	Mean annual precipitation	–
ADI	Annual dryness index: $(DD5)^{0.5}/MAP$	1
GSP	April–September precipitation	–
PRATIO	GSP/MAP	2
GSPDD5	(GSP × DD5)/1000	3
GSDD5	Degree-days >5° summed between the last freeze of spring and the first freeze of autumn	–
MINDD0	Degree-days <0 °C based on the minimum temperature	–
SDI	Summer dryness index: $(GSDD5)^{0.5}/GSP$	–
SDIMINDD0	SDI × MINDD0	4
MTCM	Mean temperature in coldest month	–
MTWM	Mean temperature in warmest month	–
TDIFF	Summer–winter temperature differential: MTWM-MTCM	–
GSPTD	(GSP × TDIFF)/100	5
ADIMINDD0	ADI × MINDD0	6
MMAX	Mean maximum temperature in warmest month	7
DD5MTCM	(DD5 × MTCM)/1000	8

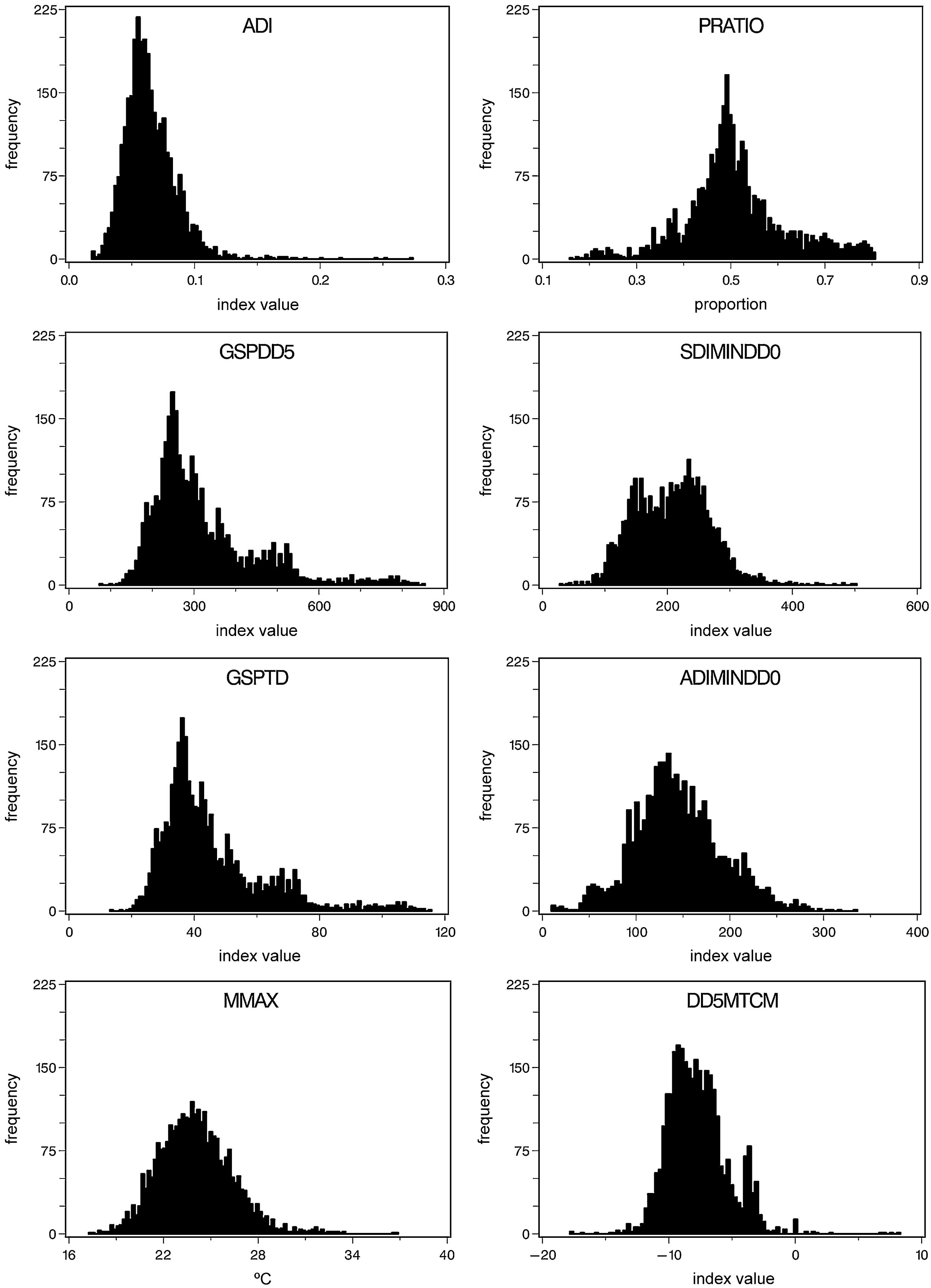

Fig. 2. Histograms for each variable relevant to aspen's climate profile showing the number of inventory plots containing aspen within each of 100 classes. Acronyms are defined in Table 1.

Table 2
Range (minimum and maximum) in values of relevant climate variables (Fig. 2) for all inventory plots, those that are forested, and those containing aspen for western USA after deleting the lowest and highest 0.05%. Acronyms are defined in Table 1.

Variable	All plots (n = 117,581[a])	Forested plots (n = 41,873)	Aspen (n = 3059)
ADI (index)	0.01–0.69	0.01–0.23	0.03–0.16
PRATIO (proportion)	0.11–0.82	0.12–0.76	0.21–0.79
GSPDD5 (index)	121–1196	120–1204	140–793
SDIMINDD0 (index)	13–654	12–498	80–395
GSPTD (index)	6–99	13–99	22–110
ADIMINDD0 (index)	3–455	3–313	32–278
MMAX (°C)	17.3–42.4	17.5–35.8	19.1–32.5
DD5MTCM (index)	−24.2–74.8	−16.3–29.1	−13.3 to −0.8

[a] Number of observations.

Table 3
Percent reduction in area occupied by the contemporary climate profile of aspen according to three general circulation models, two scenarios, and three time periods.

Circulation model and scenario	Period[a]		
	2030	2060	2090
CCCMA_A2	27.3	49.5	77.6
GFDL_A2	41.0	74.1	94.4
UKMO_A2	6.7	54.9	84.3
CCCMA_B1	23.6	39.7	46.2
GFDL_B1	25.5	42.1	49.4
UKMO_B2	12.8	48.1	64.7

CCCMA, Canadian Center for Climate and Modeling; GFDL, Geophysical Fluid Dynamics Laboratory; UKMO, Met Office, Hadley Centre
[a] Decade surrounding the date, e.g., 2026–2035

In these inserts, black dots, despite their fuzzy coordinates, invariably are closely associated with pixels predicted to have climates suitable for aspen. Blue dots are the fuzzy locations of plots having no aspen. Note, however, that a gridded, systematic pattern of blue dots is apparent, suggesting that the degree of falsification of their coordinates was slight. The insert on the lower left shows an area where aspen is rare, a frequency correctly portrayed by the bioclimate model but not necessarily by the range map. This same insert also shows plots outside polygons on the range map that are correctly classified by the model. The other two inserts in this figure show areas within range map polygons where the frequency of aspen grades from abundant to rare; again, correctly portrayed by the model. Because of their accuracy in predicting presence, bioclimate models can infer abundance as well as limits of distribution.

Mapped projections of the contemporary climate profile into the future climate space described by three GCMs for only SRES A2 scenarios (Fig. 4) show that the area occupied by the contemporary climate profile should shrink drastically during the course of the century. The impact portrayed by GFDL projections, however, are the most severe while those of CCCMA are the least. Although concurrence among GCMs for the decade surrounding 2030 is remarkably high, differences afterwards eventually would produce a 77.6% reduction in aspen's climate profile for CCCMA, 84.3% for UKMO, and 94.4% for GFDL (Table 3). Reduction in area of the climate profile for SRES B1 or B2 scenarios would be about 25% less than for the A2 scenarios after 2030.

The disparate impacts projected by these GCMs stem directly from precipitation effects. For the A2 scenarios, the GCMs are remarkably consistent for mean annual temperature, projecting for

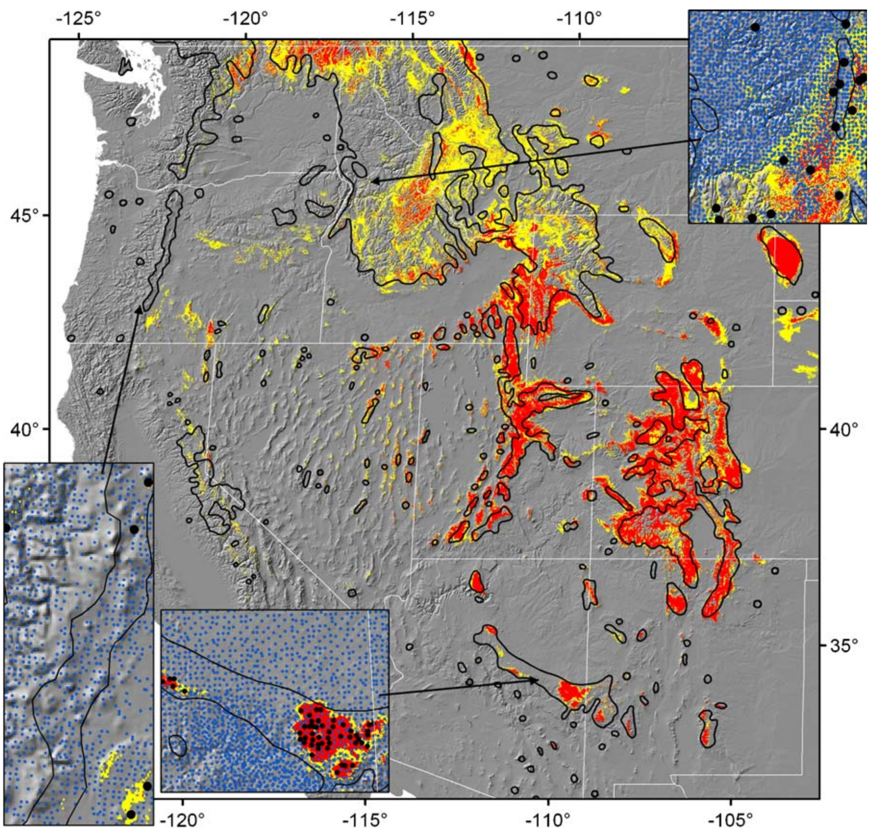

Fig. 3. Aspen's mapped climate profile (yellow and red pixels) in relation to Little's (1971) digitized range map (lines). Yellow, 50–75% of the votes; red, 75–100% of the votes; for inserts, black dots, Forest Inventory plots with aspen; blue, without aspen. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

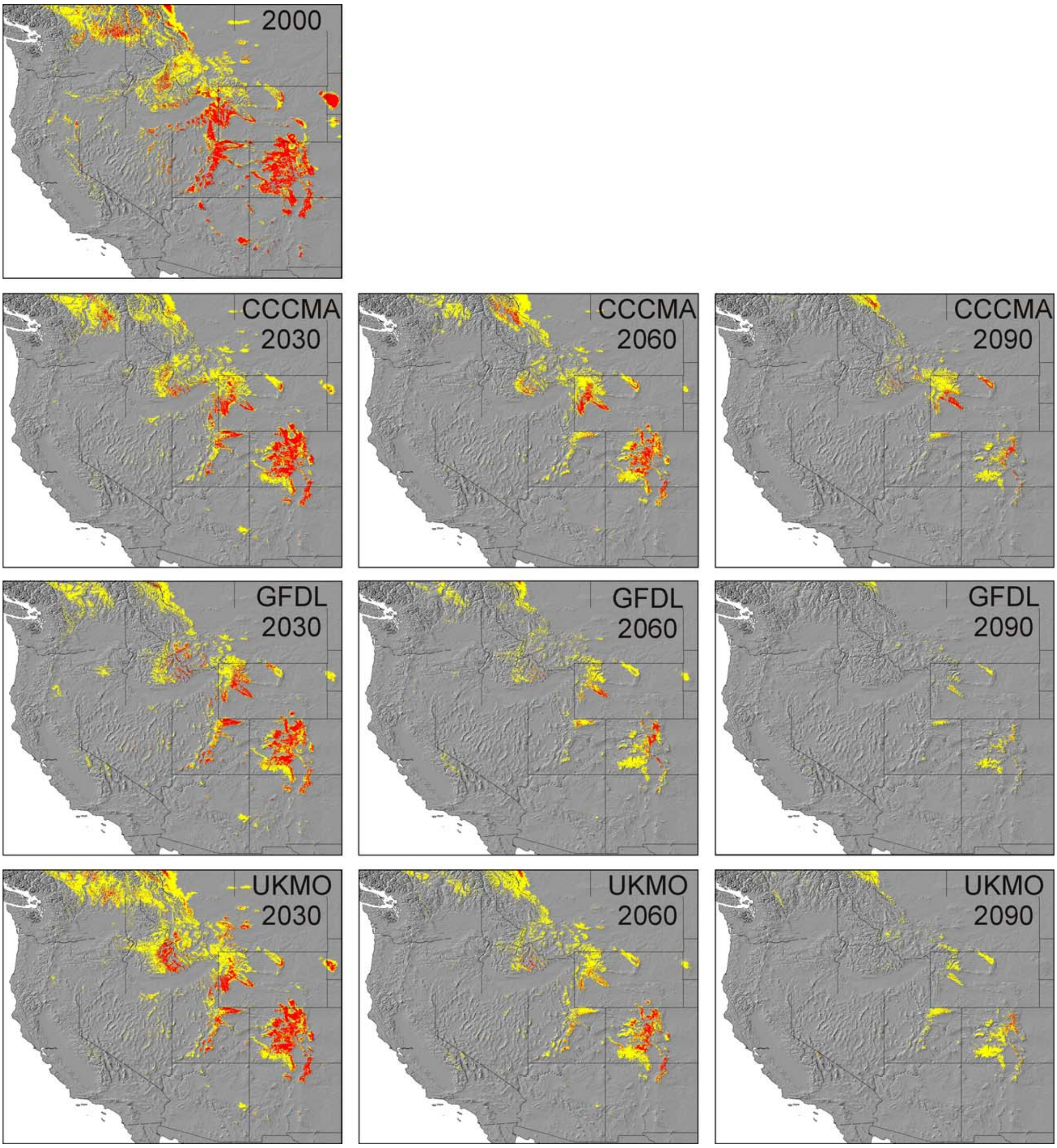

Fig. 4. Aspen's mapped climate profile for the contemporary climate (upper left) and for future climates as depicted for the SRES A2 scenarios and three GCMs in decades centered on 2030, 2060, and 2090. CCCMA, Canadian Center for Climate Modeling; GFDL, Geophysical Fluid Dynamics Laboratory; UKMO, Met Office, Hadley Centre. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

our geographic window an increase of 1.4–1.8 °C for the decade surrounding 2030, 3.0–3.4 °C for 2060, and 5.0–5.1 °C by 2090. For precipitation, however, GFDL projects a change of −10% for the end of the century while UKMO projects a change of +2% and CCCMA +6%. Because the balance between temperature and precipitation is fundamental to aspen's climate profile, projected impacts are greatest by far for GFDL (Fig. 4, Table 3).

Despite the obvious differences (Fig. 4), the degree of concurrence among GCM projections is high, particularly early in the century (Fig. 5). The projections for all six of the scenarios are superimposed in Fig. 5, and pixels have been colored according to the number of scenarios for which the 2030 climate has been predicted to be within aspen's climate profile. Illustrating GCM projections in this manner emphasizes their similarities rather than differences (Czucz et al., 2009). Of the total number pixels predicted to have a 2030 climate suitable for aspen, the six scenarios concurred on 29.1% of them, five concurred on 14.5%, four on 13.9%, three on 13.7%, and two on 11.2%; 17.1% received favorable votes from only one scenario.

Not obvious in Fig. 4 are the projected changes in altitude that accompany the decrease in area of the climate profile. In U.S. Forest Service's Rocky Mountain Region, for instance, the aspen profile would move upwards by about 250 m by 2030, 400 m by 2060, and 750 m by 2090 according to CCCMA, scenario SRES A2. Altitudinal displacement for the profile would be somewhat less for UKMO (650 m by 2090) and somewhat more for GFDL (about 1000 m by 2090); the B scenarios would result in an altitudinal displacement of about one-half that of the A2 scenarios after 2030.

3.3. Climate and sudden aspen decline

Examination of the annual climate between 1950 and 2006 for variables relevant to aspen's climate profile revealed patterns in six variables that correspond with the sudden decline evident in the Rocky Mountain Region. In Fig. 6, trends for four of these variables are presented for (1) 51 weather stations from the region and (2) spline estimates for the 874 inventory plots containing aspen within the same region. The two variables not considered in the figure, SDIMINDD0 and ADIMINDD0, exhibited annual trends that closely paralleled that of ADI.

Fig. 6 shows that weather stations, located about 800 m lower in elevation than the aspen forests, are, as expected, much warmer and drier than the sites inhabited by aspen. More importantly, the annual trends for actual data and spline estimates are remarkably similar. Linear regressions of weather station means on the spline estimates for these variables and several additional variables produced values of R^2 that ranged from 0.67 (MMAX) to 0.75 (ADI). With 55 degrees of freedom, all were statistically significant ($P < .0001$). However, the regression coefficients varied from 0.68 for MAP to 1.78 for ADI, suggesting biasness when data from the closest weather station are used to characterize the climate of a forested site.

Yearly trends (Fig. 6) show that 2002 had the highest summer temperatures, moderately warm winters, the lowest precipitation, and the most extreme temperature:precipitation indices for the 56-year period. Because these variables are relevant to aspen's climate profile, their trends alone would suggest that the climate in 2002 was more severe for aspen than in any other year. Sudden aspen decline became apparent to land managers in the Rocky Mountain Region in 2004 and became obvious in aerial surveys in 2005 (Worrall et al., 2008). Symptoms of sudden decline, therefore, were not obvious until two years following the severe weather of 2002.

Votes cast by the bioclimate classification tree are presented in Fig. 7 as 4-year running means. These means show general trends by eliminating much of the year-to-year variation. In this figure, mean values are plotted according to the first year in the 4-year interval. The figure shows that the suitability of the climate for aspen followed similar patterns for (1) inventory plots containing aspen and (2) locations in which dieback was observed in the aerial survey of 2006. Trends for all inventory plots containing aspen show two periods when the climate was particularly severe: 1953–1956 and 2000–2003. Trends for those locations exhibiting dieback in 2006, however, suggest that there were four severe periods, with that of the mid to late 1950s being the most severe and the most prolonged. Both trends, but particularly that for all aspen plots, are consistent with the extreme climates of Fig. 6. Also obvious in Fig. 7 is that whenever the percentage of favorable votes was low, locations where dieback recently has occurred received the fewest votes. This suggests that the sites where sudden decline is occurring are on the fringe of aspen's realized climate niche and, consequently, are and have been the most vulnerable.

This vulnerability was addressed further by updating the climate at locations now exhibiting sudden decline for future climates expected by the three GCMs and both scenarios. Despite using a 1 km grid to estimate elevations of sites exhibiting dieback today, the classification tree predicted that only 6.3% of these sites should lie outside the contemporary climate profile (Fig. 8). However, when the 2030 climates of these sites were run through the classification tree, on average, 58% of the sites now exhibiting

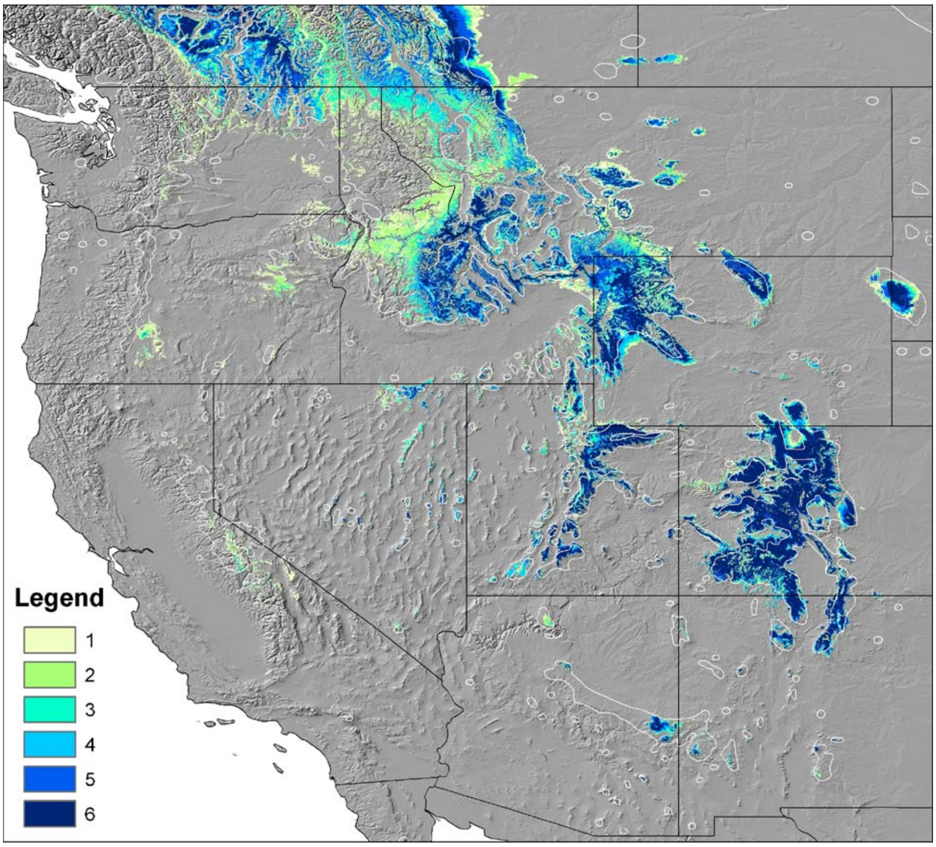

Fig. 5. Aspen's mapped climate profiles for the decade surrounding 2030 superimposed for three GCMs and two scenarios. Coloring indicates the number of scenarios that concur. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

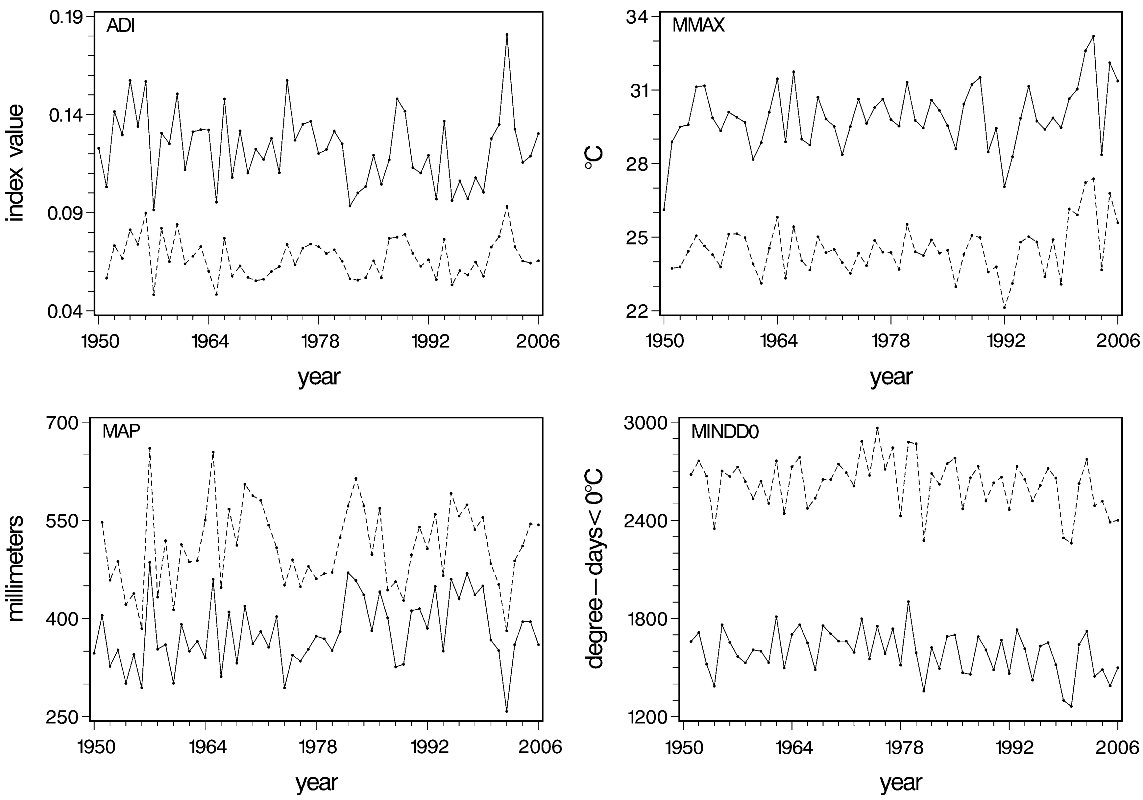

Fig. 6. Trends in annual climate for four variables relevant to aspen's climate profile. Solid lines are the average of data from 51 weather stations located within U.S. Forest Service's Rocky Mountain Region; hash lines are means of spline estimates for 874 inventory plots containing aspen from the same region. Acronyms are keyed to Table 1.

dieback in the Rocky Mountain Region were projected to lie outside aspen's climate profile. Although this percentage varied from 41% to 75% depending on GCM and scenario, the reduction is far greater than that expected for aspen throughout its USA distribution (Table 3). By 2060, 76% of the sites now exhibiting sudden decline are projected to lie outside aspen's climate profile. These statistics along with the maps of Fig. 8 imply that dieback may be a primary agent responsible for adjusting aspen's distribution for the change in climate; indeed, most of the dieback locations are within the portion of the aspen distribution expected to be vacated by 2060.

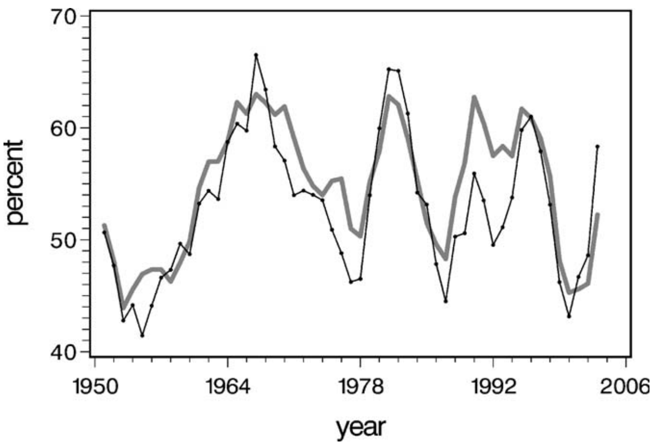

Fig. 7. Annual votes (percent of the total) in favor of the climate being suitable for aspen in U.S. Forest Service's Rocky Mountain Region. Thick gray line, average votes of 874 inventory plots containing aspen; black line with dots, average for 3431 polygons identified on the 2006 aerial survey as having sudden aspen decline.

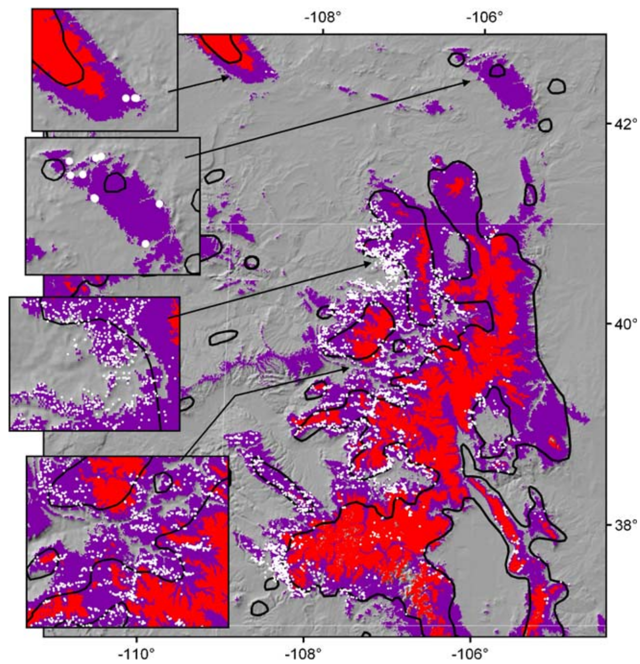

Fig. 8. Aspen's mapped climate profile for the Rocky Mountain Region, USFS for the contemporary climate (purple), the predicted according to output from the A2 scenario of the Geophysical Fluid Dynamics Laboratory for the decade surrounding 2060 (red), and locations identified with sudden aspen dieback (white dots) on 2006 aerial surveys in relation to Little's (1971) range map (polygons outlined in black). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

Table 4
Overall 56-year means and 4-year running means for two periods for climate variables relevant to aspen's climate profile. Means are for the 874 plots containing aspen within the Forest Inventory database for the U.S. Forest Service's Rocky Mountain Region. Acronyms are defined in Table 1.

Variable	Years		
	1953–1956	2000–2003	1951–2006
DD5 (°C)	1116	**1247**	1122
MAP (mm)	**432**	451	509
GSP (mm)	**248**	252	295
MINDD0 (°C)	2597	2537	2626
ADI (index)	0.077	**0.079**	0.067
PRATIO (proportion)	0.57	0.56	0.58
GSPDD5 (index)	**277**	315	329
SDIMINDD0 (index)	256	**270**	228
GSPTD (index)	**54.8**	62.1	69.6
ADIMINDD0 (index)	**202**	**202**	176
MMAX (°C)	24.4	**26.5**	24.5
DD5MTCM (index)	−8.0	−10.0	−9.3

Bold face type indicates an extreme value for the 56-year period.

In examining trends in climate variables relevant to aspen's climate profile, 4-year running means showed that for six of the eight variables, the climate was extreme either during 1953–1956 or 2000–2003, the two periods in which the climate was the most severe for aspen in general. These two periods, moreover, had much similar climates, although the summers of 1953–1956 were somewhat cooler than those of 2000–2003 (Table 4). However, outbreaks of aspen dieback during the decade of 1950 are not of general knowledge within the forest health lore (J.A. Worrall, U.S. Forest Service, Gunnison, Colorado; personal communication, D.L. Bartos, Rocky Mountain Experiment Station, U.S. Forest Service, Logan, Utah, personal communication), although archived reports of individual forests and districts have not been systematically searched.

4. Discussion

4.1. Climate profile

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The classification tree produced out-of-bag errors that averaged less than 5% of the 15,000 observations comprising each forest. Most of this error consisted of the errors of commission that accrue from predicting that the climate would be suitable when aspen was not present. A concomitant lack of errors of omission resulted largely from the composition of the sample. By weighting in our sample observations containing aspen by a factor of 2, we forced the errors of omission to be minimized while doubling the number of observations in the sample with no aspen. While many ecologically sound reasons exist to explain errors of commission (e.g., substrate, disturbance history, succession), predicting the absence of a species when it is present most likely reflects modeling errors. Consequently, structuring the out-of-bag errors to reflect primarily the errors of commission is intuitively appealing.

In drawing a sample of observations for which aspen was absent, we used a multivariate hypervolume, expanded somewhat beyond the limit of aspen's climatic distribution, to concentrate observations into the range of climates for which separating presence from absence would be the most difficult. Observations within this hypervolume were then re-sampled intensively by running 14 independent forests. We also assured that a small number of observations in the sample would represent the full range of climatic variation encompassed by the observations without aspen. The result was a model with little error.

Mapped predictions of the contemporary climate profile show that our predictions generally lie within the polygons of Little's (1971) range map (Fig. 3). In comparing the predicted distribution with the range map, it is worthwhile to note that about 75% of the aspen in western USA occurs in Colorado and Utah (Bartos, 2001), the area receiving the high proportion of red-colored pixels (>75% votes) in Fig. 3. The bioclimate model, therefore, was particularly effective where aspen is prevalent.

With errors of omission approaching zero, the bioclimate model was essentially perfect in correctly predicting the occurrence of aspen when it was present. Fig. 3, moreover, shows unequivocally that species are neither uniformly distributed within nor equally abundant among polygons delineated on a range map. Unlike the two-dimensional range map, abundance indeed is reflected in predictions from the bioclimate model. In addition, dieback locations taken from aerial surveys are a collection of data points containing aspen that are completely independent of the inventory data. Fig. 8, therefore, provides outstanding verification of the bioclimatic model: 93.7% of the locations exhibiting dieback fall on pixels colored purple, that is, those predicted to have a climate suitable for aspen. Discrepancies between data points, the predicted profile, and the range map typically result from inaccuracies in the range map. While the two-dimensional range maps have satisfactorily served the forestry profession for many decades, inventory databases and bioclimate models are ideal resources for their modernization.

4.2. Relevant variables

We chose an 8-variable model to describe aspen's climate profile. Although the model is correlative, the Random Forests algorithm nonetheless is useful for sorting through a large number of independent variables to select those most important in predicting responses (Breiman, 2001; Rehfeldt et al., 2008). Our results show that the most important climate variable for predicting the presence of aspen in western USA was an annual dryness index, calculated as a simple ratio of growing-degree-days (5° base) to annual precipitation. Of the remaining variables, two also reflected an interaction between temperature and precipitation (Table 1). These results mesh closely with those of Hogg (1994, 1997) who demonstrated that the difference between annual precipitation and potential evaporation was closely associated with the limits of distribution of aspen in the prairie provinces of Canada. Consequently, Hogg's conclusions seem applicable to the species in general: limits of distribution at the xeric fringe are controlled primarily by the balance between temperature and precipitation. The same conclusions, in fact, are applicable to twelve co-occurring species of Rocky Mountain conifers (Rehfeldt et al., 2008).

The aspen climate profile also contained four interactions involving winter temperatures and either dryness indices or summer temperatures. Obviously, winter temperatures would be primary factors controlling distributions on the cold front where, in western USA, the aspen is supplanted by alpine and tundra vegetation. Our models suggest, however, that even here, moisture stress may have a role, according perhaps to the well known adage that winters are most severe when trees enter winter with moisture deficits (Levit, 1972). In fact, the role of the second-ranked variable in the aspen profile, PRATIO (Table 1, Fig. 2) may also be related to regulation of moisture stress: evenly distributed precipitation may act to ameliorate unfavorable balances between temperature and precipitation.

4.3. Potential impacts of global warming

As illustrated for the montane and subalpine forests of western USA and for several of their constituent species (Rehfeldt et al., 2006), the area occupied by aspen's contemporary climate profile is expected to decline greatly by the end of the century (Table 3) while moving upwards in altitude by as much as 1000 m. The amount of decline projected, however, depends on the GCM and scenario (Table 3; Fig. 4). While these results are remarkably consistent with bioclimate models of aspen for northeastern USA (Iverson et al., 2008), this variation frequently is used to question the advisability of invoking management strategies that would anticipate the change in climate (e.g., Rice and Emery, 2003).

Despite variation among GCM projections, Fig. 4 nonetheless illustrates some remarkable consistencies for the A2 projections. All GCMs, for instance, describe the aspen profile eventually shifting toward the high elevations, especially those of the Rocky Mountain Region. More importantly, all tend to agree on the geographic location of the profile early in the century, with the divergence occurring later. When projections from the six scenarios considered herein are superimposed (Fig. 5) for the decade surrounding 2030, there is unanimous agreement that the future climate will be suited to aspen for 29% of the cumulative area from all scenarios. Indeed, a majority (three or more) of the scenarios are in agreement for all but 18% of cumulative area. This concurrence among the GCMs can be used to design management strategies to target future climates with the proper species and seed sources (see, for instance, Tchebakova et al., 2005; Rehfeldt, 2004) for those areas projected by consensus to lie within the climate profile. For such areas, management of aspen can be undertaken with a relatively high probability of success.

In considering management options, one must be aware that regression models like ours project the contemporary climate profile. To the extent that these projections reflect future distributions (for discussion, see Pearson and Dawson, 2003) depends, first, on rates of migration as aspen attempts to track the climate for which it is physiologically attuned. Migration rates in aspen, however, are problematic. Most aspen reproduction is clonal, with reproduction from seeds generally considered to be rare (Mueggler, 1988; Bartos, 2001). The contemporary profile, moreover, is determined in part by competitive interactions among species. In novel climates (see Williams et al., 2007), competitive interactions are expected to change (see Ackerly, 2003; Jackson and Overpeck, 2000). In addition, as a seral species, aspen's occurrence depends on the frequency of disturbance. Consequently, the future distribution of aspen not only will depend on the future distribution of the contemporary profile, migration rates, and disturbance regimes, but also on the distribution of those novel climates embracing aspen's fundamental niche. Fig. 4 suggests that the rate at which aspen's climate profile would shift across the landscape would be relatively rapid. This rapid shift coupled with the contingencies of disturbance, migration, and competition, implies that a prolonged period would be required for aspen's distribution to regain a semblance of equilibrium with the climate.

4.4. Toward an understanding of climate–dieback relationships

The climate model that we use is not yet capable of adjusting predictions for microtopographic effects (e.g., aspect, soil depth, slope position). This means that making predictions at a resolution finer than the 1 km grid that we used would lend a false precision to the estimates. Nonetheless, aspen dieback is related to both slope and aspect (Worrall et al., 2008). Our results, therefore, can reflect only coarse–scale relationships between climate and dieback rather than the precise site-specific treatment a thorough analysis would require.

Despite these limitations, we used the 8-variable climate profile to assess the relationship between climate during a 56-year period (1951–2006) and the occurrence of sudden aspen decline, first observed in 2004 and becoming prominent in aerial surveys in 2005. Weather data show that in 2002, four of the eight variables in the profile reached extreme values for the 56-year period. Using votes generated from the bioclimate model to judge the suitability of the climate for aspen, we identify two 4-year periods in which the climate was particularly adverse. Although the first, 1953–1956, is not generally remembered as a period of widespread dieback, the second, 2000–2003, immediately preceded the recent infirmity. Indeed, Hogg et al. (2005) also document a major collapse in aspen productivity from the droughts of 2001–2003 in western Canada.

Aspen dieback became noticeable two years following the adverse climate of 2002 and one year after the adverse period of 2000–2003. A lag of two years also corresponds to the 2000–2001 sudden dieback in eastern Canada (Candau et al., 2002). We show, moreover, despite the inability to perform site-specific climate analyses, when the general climate was adverse for aspen, it tended to be slightly more adverse at locations where dieback had occurred recently than for a sample of all sites containing aspen (Fig. 7). Nonetheless, the area afflicted with aspen dieback continued to increase through 2006 (Worrall et al., 2008) and even in 2007 (J.A. Worrall, U.S. Forest Service, Gunnison, Colorado, personal communication), several years after the adverse climate of 2000–2003 ameliorated (Figs. 6 and 7). If the adverse climate of 2000–2003 provided the stimulus, the period of decline lasted at least four years following the stimulus. This lag between cause and effect is ripe for physiological research.

Although not conclusive, we believe our results to be compelling: the incidence of aspen dieback probably stemmed from adverse climates of 2000–2003, a period centering on 2002 during which several variables relevant to aspen's climate profile were at extreme values. Because our results support those of Hogg (1994, 1997) to implicate moisture stresses as limiting aspen's distribution on the xeric fringe, and because grasslands-shrub and woodland communities are expected to expand at the expense of the montane and subalpine conifer communities of western USA as a result of global warming (see Rehfeldt et al., 2006), our results further support the concerns already voiced (Hogg and Hurdle, 1995; Hogg et al., 2002) on the ability of aspen to adjust to climates of the future. We calculate that for western USA, aspen's contemporary climate profile should shrink by 10–40% by 2030, depending on the GCM and scenario. Even though high resolution (e.g., 30 m) analyses are not yet feasible, we nonetheless estimate that aspen's climate profile should vacate about 58% of area in which dieback is now apparent. Aspen, in fact, may be a prime indicator of the impacts of a changing climate on forest growth and productivity as the balance between temperature and precipitation becomes less and less favorable.

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