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FOREST TYPE AND WILDFIRE IN THE ALBERTA BOREAL MIXEDWOOD: WHAT DO FIRES BURN?

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Abstract. Two determinants of fire behavior are fire weather and spatial variation in fuels. Their relative importance in boreal forests has been unclear. I evaluated the effect of fuels on a ~74 000-km² landscape in the boreal mixedwood region of western Canada. My data were the compositions, or the proportional areas of different forest types, of 48 mapped lightning fires and of their immediate surroundings. I measured areal compositions from forest inventory maps, using a five-way classification representing deciduous forest, three types of coniferous forest, and wetlands. The fires burned between 1980 and 1993. Fire sizes ranged from 70 ha to 70 000 ha. By multivariate linear regression, fire surroundings explain 57% of the variation in forest types within mapped fires. Fire compositions are not representative of the study area as a whole, or of a fire's surroundings, and are unrelated to fire size and location within the study area. Using the model, I predicted the areas of the five types burned within all other lightning fires >200 ha in the study area during 1961–1996 and estimated type-specific mean annual burn rates. These rates vary by an order of magnitude. Deciduous stands burn at the lowest rate, and black spruce stands burn at the highest rate. Fires exhibit significant preferences between forest types at both local and regional scales. Preference orderings are similar at both scales and are generally consistent with the rank order of estimated burn rates. Preferential burning may result from between-class differences in vertical canopy structure and foliage characteristics. The statistical model and the postulated variations in fire behavior between classes indicate that landscape-scale fuels management may be feasible in this system. The rank ordering of burning frequencies and preferences is the inverse of the planned disturbance rates under forest management.

Key words: Alberta, Canada, boreal forest fires; boreal mixedwood forest; compositional data; crown fire initiation; fire behavior; fire history; forest management; fuels management in forests; multivariate linear regression; natural disturbance regimes; *Picea glauca*; *Populus tremuloides*.

INTRODUCTION

The boreal mixedwood forest in western Canada is thought to be structured by large wildfires (Johnson et al. 1998, Weber and Stocks 1998), which are certainly the most conspicuous of natural disturbances in boreal regions. A much-studied property of wildfire is its frequency or rate of occurrence, measured as the mean proportion of a study area that burns annually. This rate is the most important (often the only) parameter in mathematical models relating fire frequency to landscape age structure (Johnson and Van Wagner 1985). Reliable time series of fire maps produced by direct observation (e.g., post-fire aerial photography) exist only for recent decades. Thus, inferences about fire, and, in particular, about the rates at which various types of forest burn, are usually indirect. In the western boreal forest, rates have been estimated from forest inventory age data (Van Wagner 1978) and from point estimates of "time since fire" (Yarie 1981, Larsen

1997). The latter method requires estimating the ages of selected patches of forest, usually from samples of tree ages.

Very little attention has been paid to what individual fires in these regions actually burn. The mixedwood forest is a complex mosaic of wetland areas, relatively pure stands of coniferous or deciduous species (mostly trembling aspen, *Populus tremuloides* Michx.), and stands that are mixtures of both. The mean size of distinct forested patches is ~10 ha (Cumming et al. 1996), so large fires necessarily burn heterogeneous areas. *Fire compositions*, which I define as the proportional area of various forested and nonforested stand classes that burn in individual fires, are the focus of the present study. The empirical question I address is to what degree stand classes in the mixedwood region differ significantly in their rates of burn. I do this by reconstructing, by direct measurement and by multivariate linear modeling, the compositions of almost all the area burned by wildfire in a large area of boreal mixedwood forest, over the interval 1961–1996.

The question bears on a disagreement in the literature concerning the relative importance of factors controlling fire behavior in western North America, which Agee (1997) has framed as two alternative hypotheses:

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the weather hypothesis and the fuels hypothesis. The *weather hypothesis* is that "large severe fires are driven by extreme weather events and burn intensely through forests regardless of the condition of their fuels" (Agee 1997:153). Severe fires are those that kill all or most of the canopy trees, and replace or reinitiate stands. In boreal forests, high severity is associated with crown fires, where "flames extend into and ignite the tree crowns" (Johnson 1992:47). For the purpose of this study, the *fuel hypothesis* is that spatial variation in fuels influences fire spread or severity. As fuel characteristics are partly determined by stand structure, which varies between forest stand classes, this study tests a special case of the fuels hypothesis.

The weather hypothesis is supported by a recent study of subalpine coniferous forests in the southern Canadian Rockies. Bessie and Johnson (1995) conducted a sensitivity analysis of a model of crown-fire initiation (Van Wagner 1977). They found that the probability of crowning was more sensitive to variation in fire weather (measured by surface fuel moisture and by wind speed) than to variation in fuels. Although they acknowledge that fuels can be significant under marginal weather conditions, they note that the majority of area burned occurs during extreme weather conditions. They conclude (Bessie and Johnson 1995:757) that "fire behavior should not vary strongly with stand age or with species composition types." Johnson et al. (1998) generalize this result to the boreal forest as a whole.

On the other hand, a study of montane coniferous forests in Yellowstone National Park tends to support the fuels hypothesis. From sets of mapped fires, Renkin and Despain (1992) determined the area burned (in hectares) of different types of coniferous forest. By contingency-table methods, they compared the burned areas to the total areas of the forest types available in the park, and detected significant nonrandom associations between forest type and the likelihood of stand-replacing fire. These associations persisted, though with reduced magnitude, even under severe conditions of drought and fire weather. However, their reliance on statistical methods designed for count data is problematic.

There is also support for the fuels hypothesis in boreal forests. Van Wagner (1977:31) discusses various coniferous forest types in which crown fires would be rare, and remarks that "aspen stands do not crown." He further observes (see his Fig. 4) that "aerial photos of [large fires] often suggest how short-term variations in wind speed interact with stand structure and topography to produce intermittent active crowning" (Van Wagner 1977:32). According to Quintilio et al. (1991:1), "during the summer fire season (i.e., following leaf-out), pure healthy aspen stands are virtually impenetrable by fire, except under extreme burning conditions . . .". Viereck (1973) summarized unpublished studies of Alaskan fires, which indicate that fires burn "un-

forested" areas more than expected, and "commercial" forested areas less than expected, given their abundances on the landscape. However, these reports have not been supported by any quantitative analysis at large spatial scales. The main goal of this paper is to offer such an analysis.

The weather hypothesis implies that fires are unselective between classes of forest stands. This has two testable consequences: (1) the mean composition of individual fires should approximate the composition of the entire study area, i.e., burn rates should be similar for all stand classes; and (2) either the composition of an individual fire should be a random sample of the forest in the vicinity of the point of ignition, or, if not, fire composition should be related to fire size. This is because, since large fires are associated with extremes of weather, the importance of fuels, if any, should decrease with size. The larger the fire, the more closely its composition should resemble that of its surroundings.

DATA AND METHODS

Study area

My study area comprises ~73 600 km² of the boreal mixedwood ecological region (Rowe 1972) in northeastern Alberta (Fig. 1). It is, for the most part, the forest tenure area of Alberta Pacific Forest Industries, Inc. (APFI), operators of a large bleached-kraft pulp mill. The ~485 000 km² mixedwood region, is transitional between colder, conifer-dominated forests to the north and warmer, dryer, aspen parklands to the south, which are now mostly farmland. In Alberta, ~270 000 km² of mixedwood is still forested (Strong 1992) and, so far, largely unlogged. The most abundant tree species are trembling aspen (*Populus tremuloides*), black spruce (*Picea mariana* (Mill.) B.S.P.), jack pine (*Pinus banksiana* Lamb), white spruce (*Picea glauca* (Moench) Voss), and balsam poplar (*Populus balsamifera* L.). Paper birch (*Betula papyrifera* Marsh.), tamarack (*Larix laricina* (Du Roi) Koch), and balsam fir (*Abies balsamea* (L.) Mill) are widely distributed, but rarely form pure stands. Mature mixed stands containing both aspen and white spruce are characteristic of the region. Peatlands and sparsely treed muskeg cover about half of the study area. The regional ecology is described by Kabzems et al. (1986) and Strong (1992).

Forest inventory data

The only complete forest inventory for the study area is the Alberta Phase 3 inventory (Alberta Forest Service 1985), which is maintained by Alberta Environmental Protection (AEP). The inventory was interpreted from 1:15 000 scale aerial photography, flown between 1970 and 1982. Most of the study area was flown between 1975 and 1979 (AEP, unpublished map). Phase 3 data are available as 1:15 000 paper maps and as machine-readable extracts from the Alberta Forest

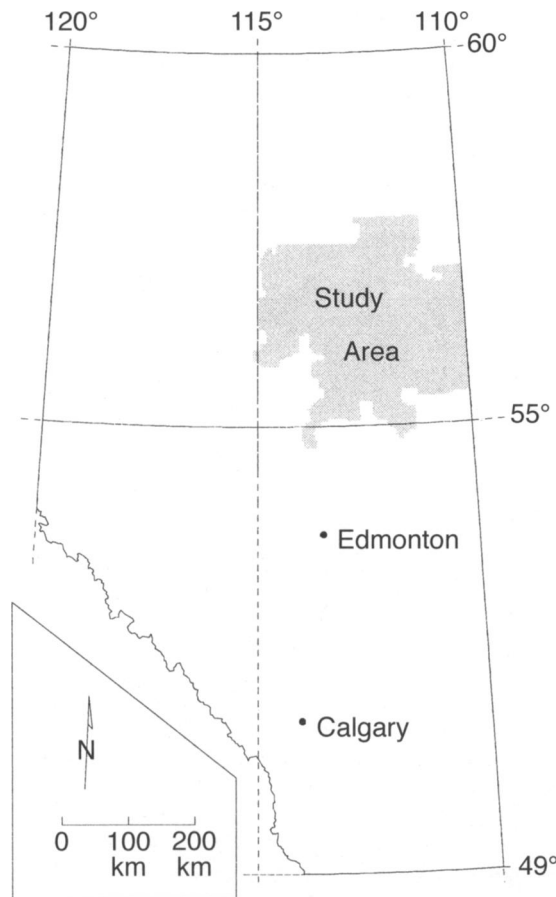


FIG. 1. Location of the 74 000 km² boreal mixedwood study area in the Province of Alberta, Canada.

Service Inventory Storage and Maintenance System (AFORISM) database. Both versions are spatially organized to survey units called "townships," most of which are square regions exactly six miles (~9.66 km) on a side (~93.2 km²); the study area intersects 825 townships. Mapped forested stands are regions of uniform canopy attributes, where the canopy is defined as the tallest stratum of trees that has at least 6% canopy cover. Canopy attributes include height and proportional canopy cover, species composition, area, and an estimate of stand age. Deciduous species (aspen, balsam poplar, and birch) are not usually distinguished. Canopy species composition is expressed as proportions of estimated merchantable volume for stands >12 m in height, and by proportion of canopy cover otherwise. Various classes of nonforested "stands" such as wetlands, bodies of water, clearings, burned areas, and clearcuts are also mapped. For the latter two categories, the year of disturbance is usually recorded. The minimum mapping unit is 2 ha. AFORISM data are just lists of stand attributes abstracted from the maps, with no representation of map topology. Since 1980, AEP has updated Phase 3 maps with the boundaries of fires >12 ha, using post-fire aerial photography.

AFORISM records are also updated, so that the pre-fire attributes of burned areas mostly cannot be deduced. However, the attributes can be recovered from annotations on the original map sheets. AFORISM data for the study area, as of 1998, were provided by AEP. Phase 3 map sheets were obtained from AEP, as needed. The only stand attributes used in the present study are area (in hectares), the species composition of forested stands, and the class of unforested stands.

A higher resolution digital inventory was available for most of the study area. In 1993, APFI contractors digitized the location of one or two points in the approximate center of each mapped Phase 3 stand in the study area, excluding two large wetland complexes. From these points, they generated a Theissen or Voronoi polygonization (Aurenhammer 1991). This is a method of covering a region with polygons constructed from a set of points in such a way that each point is at the center of one polygon. The result may be regarded as an approximate digitization of the stand boundaries. As the original stand attributes were linked to the derived polygons, the coverage may be used to estimate the set of stands within arbitrary regions, without reference to the paper maps.

Stand classification.—I assigned mapped polygons to one of five classes: Deciduous, White spruce, Black spruce, Other, and Pine. Class "Other" includes all nonforested areas, predominantly wetlands, with the exception of open water. The four forested classes are based on the polygon's dominant species (or species type, in the case of the Deciduous class). The characteristic mixed stands are thus classed as either White spruce or Deciduous. To make the classification exhaustive, I consider balsam fir to be equivalent to white spruce, and larch to be equivalent to black spruce. This reflects the site associations and/or successional relationships of these species (Kabzems et al. 1986).

Fire-history data

Alberta Environmental Protection provides databases of fire records from 1961 through 1997 (AEP 1998). Fire attributes recorded over this interval include location at detection, the final size, and an indication of cause: whether by lightning or human agency. Locations are determined by triangulation from a network of fire towers or by aerial surveillance. I assembled a consistent version of the database up to 1993 that includes all fires. For 1994–1996, I manually extracted records for fires >200 ha from the published databases. AEP has also made available geographic information system (GIS) coverages of the boundaries of all fires >200 ha that burned in Alberta during the interval 1931–1996. For older fires, the boundaries were interpreted from one of several sets of aerial photography covering the province, the earliest flown ca. 1947. Fires since 1980 were mapped as noted above.

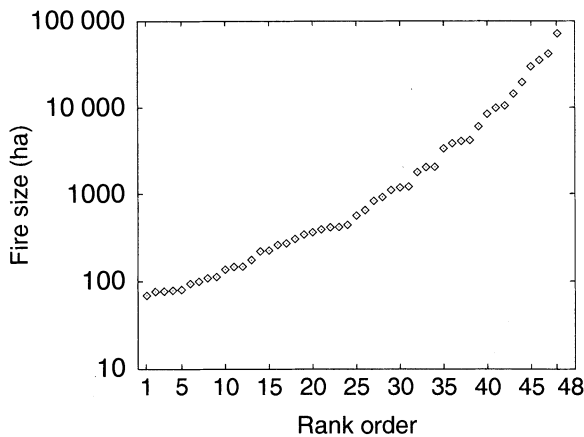


FIG. 2. The 48 sampled lightning fires started in the study area between 1980 and 1993, rank-ordered by fire size. Note the y-axis logarithmic scale.

Measuring the composition of mapped forest fires

I selected 48 lightning fires that started in the study area between 1980 and 1993. I stratified fires by year so that sampling effort was approximately even across years (the annual number of fires is highly variable), and by size on a logarithmic scale (Fig. 2). For each fire, the annotations of all burned stands were recorded from copies of the original Phase 3 map sheets. Where necessary, as when fire boundaries passed through un-forested patches such as muskeg, burned areas were measured with a 0.25-ha-resolution dot planimeter. Areas of open water and any mapped unburned islands within the fire were excluded. The individual burned polygons were then classified under the scheme described above. Finally, I generated five-dimensional vectors whose elements are the proportion of the total area burned in each class, as follows. Let w_{ij} be the area of class j in the i th fire. Then $t_i = \sum_{j=1}^5 w_{ij}$ is the total area of the i th fire, and the vector of proportions \mathbf{x}_i is

$$\mathbf{x}_i = (w_{i1}/t_i, \dots, w_{i5}/t_i)$$

whose elements are the proportional areas of the Deciduous, White spruce, Black spruce, Other, and Pine classes, respectively. Such data are referred to as "compositional data" (Aitchison 1986) and individual vectors are called "compositions" henceforth, and the term "composition" always refers to such a vector.

I also measured the composition of each fire's unburned surroundings, which I define as all unburned stands in the set of townships intersected by the fire (Fig. 3). To classify these stands, I used 1998 AFORISM records, backdated insofar as possible to the year of the particular fire. To ensure that the spatial resolution of these data were consistent with that used in predictive modeling (see below), I excluded any stands that overlapped the mapped fire boundary. I refer to this set of stands as a fire's "locale." The 48 paired

compositions of fires and locales are the basic data set used in this study.

Statistical analysis and modeling

My samples are individual fires, described by $D =$ five-dimensional compositions. The appropriate methods for analyzing such data were developed by Aitchison (1986), and introduced to the ecological literature by Aebischer et al. (1993). I first review some alternative methods and their deficiencies. Renkin and Despain (1992) pooled similar data and analyzed the aggregate component wise. For each of eight forest types "the area of stand replacing fire in [the] type was compared with the availability of that unburned forest type as well as the combined burned and unburned areas of all other forest types in a 2×2 contingency table" (Renkin and Despain 1992:39). From the table entries, apparently from Cole (1949:423), they computed a coefficient of association between fire and forest type and a standard error, using the quotient as a t statistic to test significance. As with all contingency-table methods, Cole's was developed for count data. However, within a fire the individual entities being counted are not well defined—Renkin and Despain (1992) seem to have used hectares. The values of Cole's coefficients are independent of the total count, n , but the standard errors are proportional to $1/\sqrt{n}$. Had Renkin and Despain (1992) used square kilometers as their units, their reported t statistics would have been divided by 10, and fewer significant associations would have been reported. Valid statistical inference must depend on the sample size and the underlying population, not on an arbitrary choice of unit. As a test for nonrandom patterns of burning, Renkin and Despain (1992) used 2×8 contingency tables to compare area burned with the area available. When using hectares as their counts, they report χ^2 statistics of several thousands. Had they used 1000-ha units, as in their Table 2, two of three such tests they reported would have become nonsig-

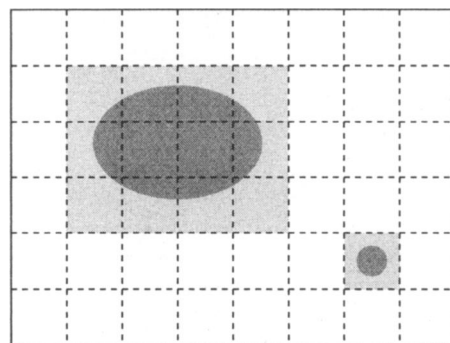


FIG. 3. Schematic representation of two fires and their locales, as estimated at township resolution. A fire locale is defined as the unburned area in the set of townships intersected by the fire. Fires are shown in dark grey, and the set of townships comprising the locales are shown in light grey. Township boundaries are shown as dashed lines.

TABLE 1. Estimated size of areas burned in the study area during 1961–1996 and derived mean annual burn rates, by stand class. “Burn rates” are the quotients of burn and areal totals divided by 36 yr, the length of the sample interval.

Stand class	Burned area (km ²)				Total area¶	Burn rate
	Measured†	Predicted‡	Mean§	Total		
Deciduous	219	95	14	328	17 360	0.0005
White spruce	191	97	12	300	4 847	0.0017
Black spruce	648	929	37	1614	9 004	0.0050
Other	1130	893	54	2077	33 190	0.0017
Pine	624	317	16	957	6 294	0.0042
Total	2812	2331	133	5276	70 695	0.0021

† Areas obtained directly from 48 mapped lightning fires.
 ‡ Areas predicted from the locales of 54 large fires, by multivariate linear modeling.
 § Totals for all fires <200 ha, estimated from sample mean composition of Eq. 3.
 || The sum of the measured, predicted, and mean areas.
 ¶ The total amount of each stand class in the entire study area ca. 1980.

nificant. There is no a priori reason that one unit is more natural than the other to the problem at hand. One might consider translating the data to proportions expressed as percentages, and then treating the data as a fixed-margin comparative trial; however this procedure is invalid (Zar 1996:500). Fixed-margin trials assume a multinomial distribution of the counts, which is not the case for percentages. In addition, percentages are just proportions, scaled by an arbitrary factor of 100. For these reasons, multivariate contingency-table methods cannot be used to model my data.

Aitchison (1986) outlines several difficulties presented by compositional data. The unit sum constraint $\sum_{i=1}^D x_i = 1$ implies that elements of \mathbf{x} are not independent. In consequence, correlation matrices must contain at least D negative entries. The data are distributed on a D -dimensional simplex, for which no convenient distributional theory exists to support statistical inference or parametric modeling. To circumvent these difficulties, Aitchison (1986) introduced the log-ratio transformation $\mathbf{y} = \text{lrt } \mathbf{x}$, defined by

$$y_i = \log(x_i/x_D) \quad i = 0, 1, \dots, d = D - 1. \quad (1)$$

This is a one-to-one mapping from vectors of proportions \mathbf{x} to vectors \mathbf{y} distributed in d -dimensional Euclidean space. The elements of \mathbf{y} are independent. In many cases, the transformation induces multivariate normality. Compositional analysis is “the application, to these log-ratios, of the range of statistical methods such as MANOVA based on multivariate normality” (Aebischer et al. 1993:1315). These methods are instances of multivariate linear models,

$$\mathbf{Y} = \mathbf{A}\Theta + \mathbf{E} \quad (2)$$

where \mathbf{Y} is an $n \times d$ log-ratio data matrix, \mathbf{A} an $n \times m$ regressor matrix of row vectors \mathbf{a} , Θ an $m \times d$ matrix of parameters to be estimated, and \mathbf{E} an $n \times d$ error matrix of independent row vectors. \mathbf{E} is multivariate normal, with mean $\mathbf{0}$ and covariance matrix Σ . Components of the vectors \mathbf{a} may also be log-ratio data. Aitchison (1986) refers to this as “log-ratio linear modeling.”

Most properties of compositional analysis are invariant under the choice of divisor used in the log-ratio transformation. However, the multivariate normality of log-ratio data and residual matrices is not invariant

TABLE 2. Regional-scale fire preference analysis, by stand class. (a) Matrix of mean preferences of 48 fires for class i over class j , relative to the availability of the classes in the entire study area, as given by Eq. 4. (b) Significance level of a t test on the hypothesis that these means are zero.

Stand class	Stand class				
	Deciduous	White spruce	Black spruce	Other	Pine
a) \bar{p}_{ij} †					
Deciduous		-0.99	-1.6	-1.3	-0.44
White spruce	0.99		-0.59	-0.31	0.54
Black spruce	1.6	0.59		0.28	1.1
Other	1.3	0.31	-0.28		0.85
Pine	0.44	-0.54	-1.1	-0.85	
b) P values					
Deciduous		0.001	0.000	0.000	0.30
White spruce	0.001		0.13	0.32	0.24
Black spruce	0.000	0.13		0.43	0.015
Other	0.000	0.33	0.43		0.056
Pine	0.30	0.24	0.015	0.056	

† \bar{p}_{ij} = the mean of 48 \bar{p}_{ij} 's each of which represents the preference of a fire for type i over type j relative to the availability of these types in the study area.

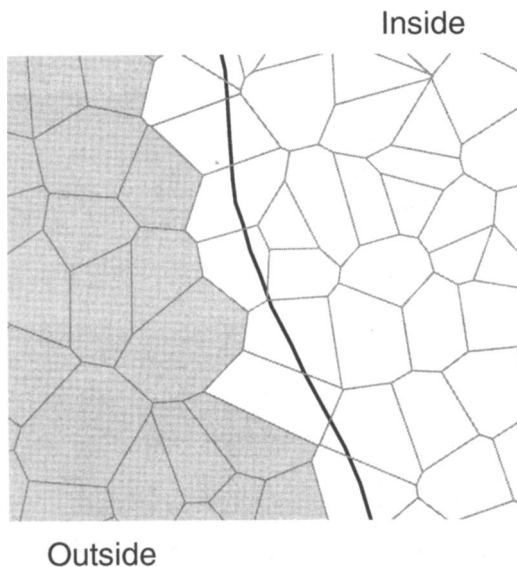


FIG. 4. Schematic diagram of the intersection between a digitized fire boundary and a Voronoi polygonalization of Phase 3 stand centroids, for one township. The fire locale (shaded grey) contains those stands neither within nor falling across the fire boundary.

(Rayens and Srinivasan 1991). Thus, hypotheses tests are sensitive to permutations of the design matrix. I found that the Pine component when used as divisor, consistently produced the best approximations of multivariate normality in model residuals, so it is used throughout. I tested for normality using the battery of $3d$ univariate tests, $3/2d(d-1)$ bivariate tests, and three d -dimensional radius tests prescribed by Aitchison (1986). When residual matrices pass the majority of these tests, I assume that the conditions for multivariate linear regression modeling are satisfied and that standard hypothesis tests are valid.

In the study area the within-township abundances of different stand types are spatially autocorrelated at ranges exceeding 20 km (Cumming et al. 1996). Thus, the compositions of fires and their locales should be related in some way, whether fires burn selectively or not. I used the 48 pairs of measured compositions to develop a multivariate linear-regression model of this relationship, using the locale compositions as independent variables. I tested the weather hypothesis by checking (1) if the sample mean of fire compositions and the composition of the study area were equal; (2) if fire and locale compositions were equal; and (3) if adding fire-size covariates (t , $1/t$, $\log t$, or $1/\log t$) significantly improved the model. I also tested for geographic variability in fire composition, by evaluating the northing and easting of fire centroids as covariates. These were measured as the distance in kilometers from the southeast corner of the regions' bounding box.

To measure the proportion of sample variance explained by the regression, I used the statistic r_i^2 (Mardia

et al. 1979), a multivariate analogue of the R^2 in multiple linear regression. Hypotheses on the means of data or residual matrices were evaluated by an F test based on Hotelling's one-sample T^2 statistic (Mardia et al. 1979: section 5.2). The significance of additional covariates were estimated from standard likelihood ratio tests. The general linear hypothesis (GLH) on the $d \times m$ parameter matrix Θ (Eq. 2) may be written $\mathbf{C}\Theta = \mathbf{D}$, where \mathbf{C} is a $p \times d$ matrix, \mathbf{M} is a $m \times r$ matrix and \mathbf{D} is a $p \times r$ matrix. \mathbf{C} and \mathbf{M} specify tests on the columns and rows of Θ , respectively. Instances of the GLH are tested within the model using a likelihood ratio test, evaluated for significance by Bartlett's approximation of Wilks' lambda distribution. The methods are given in sections 6.3 and 3.7 of Mardia et al. (1979). All computations used a custom interface to the numerical libraries of Press et al. (1992) and a matrix algebra package (Stewart and Leyk 1994). I validated the software against worked examples in Aitchison (1986) and Aebischer et al. (1993).

Prediction and rate estimation

From the AEP data base, for the interval 1961 through 1996, I selected all lightning fires >200 ha that started in or burned into the study area, excepting the 48 fires whose compositions had been measured. The digital fire boundaries were then intersected with the Voronoi polygon coverage (Fig. 4), and the locale compositions computed as in *Measuring the composition of forest fires*, above. Finally, the compositions of the burned areas were predicted from the multivariate linear-regression model. In this application, the model essentially fills in the hole in the inventory data left by the fire.

Multiplying predicted and measured fire compositions by the corresponding fire sizes yielded estimates of the total area burned and of the mean annual rate of disturbance for each of the five stand classes. Mean rates were computed relative to the composition of the entire study area as of 1980. This was estimated from the 1998 inventory by correcting for areas burned or harvested from 1980 through 1998. To correct for burning, I simply used my estimated class-specific totals over the interval. To correct for harvesting, I assumed that all areas logged between 1980 and 1993 had belonged to class White spruce. This is a reasonable approximation, as the rate of deciduous harvest was very low in the study area until the APFI mill was completed in 1993. Areas disturbed between 1993 and 1998 were reconstructed from 1993 attributes maintained by the Voronoi coverage. I chose 1980 as the benchmark year because the inventory had mostly been completed by then, fires during 1980–1982 accounted for most of the area burned during the study interval, and 1980 is close to the middle of the study interval. Thus, bias in the rate estimates due to successional changes in the forest should be low.

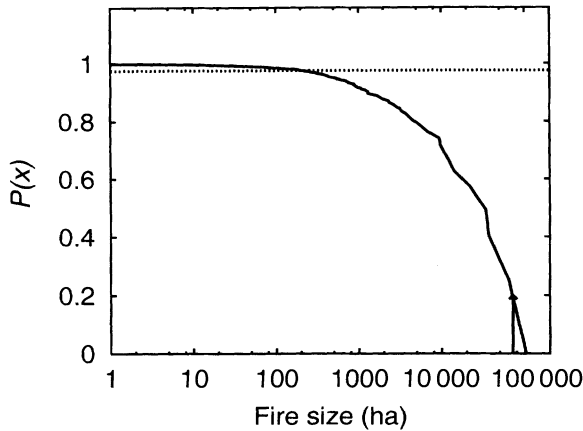


FIG. 5. A view of the size distribution of lightning fires in the study area, 1961–1993. $P(x)$ is the proportion of total fire area due to fires larger than x ha. The value of $P(200)$ is 0.975, indicated by the broken horizontal line. $P(x)$ is nearly flat for $x < 200$ ha. The arrow originating at the x -axis marks the largest of 48 sampled fires, with $P(71\,700) \approx 0.2$. Note the x -axis logarithmic scale.

Fire preferences

Here, I describe an additional test of independence between the components of fire and locale compositions, which I use to rank-order stand classes by their relative susceptibility to fire, at different spatial scales. Aebischer et al. (1993) used compositional analysis to study habitat selection of radio-collared animals at two spatial scales. For each sample animal, the minimum convex polygon (MCP) encompassing all recorded radio locations is interpreted as a home range. The composition of samples of home ranges can be compared to the composition of a reference area containing them. Similarly, the numbers of radio detections at different habitat types within MCPs may be treated as compositional data, and compared with the composition of the MCP. Habitat preferences may be studied at either scale, by comparing observed use with availability. I apply their method to fire composition, where the analogue of observed habitat preferences is the proportion of each forest cover class that burned within a fire, relative to the local and regional abundance of the class. As most evocative words such as “hazard” or “danger” have technical meanings in the fire-behavior literature, I retain the term “preference.”

Following Aebischer et al. (1993), let p_i be the preference index, a_i the availability, and u_i the proportion burned of class i . Then,

$$u_i = p_i a_i / \sum_{j=1}^{j=D} p_j a_j.$$

Scaling, let $\sum_{j=1}^{j=D} p_j = 1$. Then $p_i = u_i / (t a_i)$ where $t = \sum_{j=1}^{j=D} (u_j / a_j)$. Let \mathbf{x} be the composition of a fire, and \mathbf{z} be the composition of a reference area that determines

class availability. Define the $D \times D$ matrix \mathbf{p} as follows:

$$p_{i,j} = \log(x_i/x_j) - \log(z_i/z_j) = \log(p_i/p_j).$$

When $p_{i,j} > 0$, class i burns more than expected, relative to class j . The number of positive elements in the rows of \mathbf{p} ranges from 0 to $D - 1$, ranking the classes by relative preference. To extend this individual analysis to a sample of fires, one computes the matrix \mathbf{p} for each fire in the sample, and, from these, a matrix of means $\bar{p}_{i,j}$, applying a t test to determine which elements differ from 0. From the number of significantly positive values ($P < 0.05$) in the rows of the matrix $\bar{\mathbf{p}}$, I rank-order the five stand classes by decreasing preference. Because significance depends on both the magnitude of the t statistic and the sample size, it is possible for two or more classes to be equivalent under the ordering, that is, to be equally preferred by fire.

I performed preference analysis at both the regional and local scale. Regionally, the measured compositions of individual fires were compared to the composition of the entire study area. Locally, I compared fire composition with the aggregate composition of the fire and its locale. If individual fires are locally insensitive to forest class, none of the t tests associated with the $\bar{p}_{i,j}$'s should be significant.

Forest management and fire composition

In Alberta, the predominant harvest treatment applied to the Deciduous and White spruce classes is a two-pass, clear-cut system (Anonymous 1994). Although various silvicultural treatments are applied postharvest, intended to hasten the reestablishment of white spruce, regenerating cut blocks will often be dominated by deciduous species for many decades, and so would belong to class Deciduous for the purpose of this study. Similarly, deciduous stands usually regenerate as deciduous after harvest. No significant volumes of pine or black spruce are harvested in the study area at present, but if they were, site conditions would likely ensure regeneration by the dominant preharvest species. No current practices substantially alter the local abundance of wetland areas. Thus, the main affect of forest management in the study area is to transform part of the White spruce class to the Deciduous class. I quantify the effect of this transformation on the expected composition of fires by application of elementary differential calculus to the multivariate linear-regression model.

RESULTS

Basic fire-history statistics

During 1961–1993, fires starting in the study area burned ~614 520 ha. Lightning fires burned 67.6% of this area. A further 22% is attributed to aviation exercises at the Cold Lake Air Weapons Range, at the southeast border of the study area (M. E. Alexander,

personal communication). Disregarding this special case, a total of 477 220 ha burned, of which 87% was due to lightning fires. Fires caused by recreational activities contributed 8.4%, of which a single 1968 burn, ignited at the southern edge of the study area, was responsible for almost all. As access remains poorly developed, I argue that the restriction of the present study to lightning fires is justified.

Fires >200 ha account for 97.5% of the sum of fire areas in the period from 1961 through 1993 (Fig. 5). During the interval 1961–1996, fires exceeding this size burned 514 180 ha of the study area. This figure includes fires that burned into the study area from outside. Dividing by 0.975 to include the total area of all fires <200 ha, I estimate the total area burned to have been ~527 360 ha. Excluding permanent water bodies, the study area is ~70 700 km². Over the 36-yr interval, an area equivalent to 7.5% of the study area was burned, and the mean annual rate of burn was 0.21%. This rate corresponds to a 482-yr fire cycle, which is the amount of time required to burn an area equal in size to the study area (Johnson 1992).

Statistical analysis

The 48 measured lightning fires ranged from 69.4 ha to 71 680 ha in size (Fig. 2), with a mean of 5857 ha and a mode of 502 ha. Their total area was 281 160 ha, equivalent to 53.3% of the estimated total area burned during the study interval. The sample mean composition was

$$\bar{\mathbf{x}} = (0.11, 0.09, 0.28, 0.41, 0.12)$$

where the vector components are the proportional areas in classes Deciduous, White spruce, Black spruce, Other, and Pine, respectively. The sample mean of the log-ratio transformed compositions was

$$\bar{\mathbf{y}} = (0.59, 0.29, 1.52, 2.52). \tag{3}$$

The transformation is nonlinear, so $\bar{\mathbf{y}} \neq \text{lrt } \bar{\mathbf{x}}$. The composition of the total area burned in the 48 fires was

$$\mathbf{x}_1 = (0.078, 0.068, 0.23, 0.22, 0.40)$$

and the composition of the entire study area, ca. 1980, was

$$\mathbf{x}_s = (0.25, 0.069, 0.13, 0.47, 0.089) \tag{4}$$

or, in log-ratio form,

$$\mathbf{y}_s = \left(\log \frac{0.25}{0.089}, \log \frac{0.069}{0.089}, \log \frac{0.13}{0.089}, \log \frac{0.47}{0.089} \right) \tag{5}$$

$$= (1.03, -0.254, 0.379, 1.66). \tag{6}$$

Let \mathbf{Y} and \mathbf{Z} be the 48×4 log-ratio data matrices of fire and locale compositions, respectively. If fire and locale compositions are equal then $\mathbf{Y} - \mathbf{Z}$ should have mean $\mathbf{0}$. This hypothesis is rejected ($F_{4,44} = 7.96, P \sim 6.4 \times 10^{-5}$). If fires sample randomly from the study area then $\bar{\mathbf{y}} = \mathbf{y}_s$. This hypothesis is also rejected ($F_{4,44}$

$= 6.093, P = 0.00054$). I conclude that fires and their locales differ in composition, and that fires are not random samples from the study area.

I fit the multivariate linear model $\mathbf{Y} = \mathbf{A}\Theta + \mathbf{E}$, where the independent variables $\mathbf{a}_i = [1, z_i]$ are just the rows of \mathbf{Z} , with the addition of a column of 1's to model the mean effect. The maximum likelihood estimate for the parameter matrix is

$$\hat{\Theta} = \begin{bmatrix} 0.80 & 1.68 & 2.75 & 1.63 \\ 0.87 & -0.16 & -0.08 & -0.07 \\ 0.28 & 1.48 & 0.42 & 0.70 \\ 0.34 & 0.25 & 1.42 & 0.59 \\ -0.36 & -0.48 & -0.65 & 0.33 \end{bmatrix} \tag{7}$$

with $r_i^2 = 0.57$. I denote elements of $\hat{\Theta}$ by θ_{ij} , $0 \leq i \leq 4$ and $1 \leq j \leq 4$, so row 0 is the vector of constant coefficients. The residual matrix $\hat{\mathbf{E}}$ failed 1 of 33 tests for multivariate normality with $0.025 \geq P > 0.01$. Two other tests had significance levels $0.1 \geq P > 0.05$. This is about what would be expected by chance, so I conclude that the assumption of multivariate normality need not be rejected, and that my use of inferential statistics based on this assumption is valid.

To test for the significance of additional covariates describing fire size (t , $\log t$, and their inverses) and geographic location (northing and easting), I evaluated $\hat{\Theta}$ against six augmented models, each using one of the additional variables. None of these variables were significant ($P > 0.50$ in all cases). Fire size and location do not explain any additional variance in fire composition.

The general linear hypothesis (GLH)

$$[1 \ 0 \ 0 \ 0 \ 0]\hat{\Theta} = [0 \ 0 \ 0 \ 0]$$

that asserts that the constant coefficients of Θ are 0 is rejected ($P = 0.0024$), which implies a significant mean effect. The analogous hypotheses on the other four rows of Θ were all rejected, at significance levels $P < 0.0001$ for all but row 4 (the log ratio of the areas of class Other and class Pine), which was rejected at $P = 0.013$. These tests are similar to backwards stepwise regression, in which individual independent variables are dropped one at a time. I conclude that all components of a locale's composition significantly affect the composition of a fire.

Negative values of $\theta_{1,2}$, $\theta_{1,3}$, and $\theta_{1,4}$ in the estimated parameter matrix $\hat{\Theta}$ imply that the Deciduous class has a small negative effect on the relative proportions of White spruce, Black spruce, and Other classes that are burned. Because the magnitude of these coefficients is small, I tested the following GLH:

$$[0 \ 1 \ 0 \ 0 \ 0]\hat{\Theta} \begin{bmatrix} 0 & 0 & 0 \\ 1 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 1 \end{bmatrix} = [0 \ 0 \ 0]$$

TABLE 3. Local-scale fire preference analysis, by stand class. (a) Matrix of mean preferences of 48 fires for class i over class j ($\bar{p}_{i,j}$), relative to the availability of these classes in the fire's locale. (b) Significance level of a t test on the hypothesis that these means are zero.

Stand class	Stand class				
	Deciduous	White spruce	Black spruce	Other	Pine
a) $\bar{p}_{i,j}$					
Deciduous		-0.46	-1.0	-0.40	-0.017
White spruce	0.46		-0.55	0.064	0.45
Black spruce	1.0	0.55		0.61	1.0
Other	0.40	-0.064	-0.61		0.38
Pine	0.017	-0.45	-1.0	-0.38	
b) P values					
Deciduous		0.033	0.000	0.12	0.95
White spruce	0.033		0.053	0.78	0.12
Black spruce	0.000	0.053		0.038	0.005
Other	0.12	0.78	0.038		0.15
Pine	0.95	0.12	0.005	0.15	

which asserts that all three coefficients are 0. The hypothesis was not rejected ($P = 0.77$). The analogous hypotheses on the "off-lower-diagonal" elements of rows 2, 3, and 4 could not be rejected, either. Apparently, there are no significant interactions between classes, so a more parsimonious model would satisfy the constraints $\theta_{i,j} = 0, i > 0$ and $j \neq i$. These constraints cannot be formulated as an instance of the GLH, and I have not attempted to solve the constrained estimation problem. In what follows, I will therefore use the estimated parameters of Eq. 7.

Prediction and rate estimation

In addition to the 48 fires whose compositions were directly measured, 54 fires >200 ha started within or burned into the study area between 1961 and 1996. The total area of these fires was 851 296 ha, of which only 233 020 ha intersected the study area. Much of the difference between these two figures is due to a single enormous fire (428 000 ha) that just crossed the northern boundary. Applying the regression model to the locales of these fires, I obtained predicted log ratios of the fire compositions. Applying the inverse transformation to find the compositions and then multiplying by the size of the fire/study-area intersection led to the results summarized in row "Predicted" of Table 1. The table also contains class-specific totals of area burned and mean annual burn rates, estimated as described in *Prediction and rate estimation*, above.

Relative fire preferences

According to the regional-scale preference analysis (Table 2), several of the class-specific burn rates of Table 1 differ significantly from each other. A partial ordering is obtained by counting the number of significantly positive entries in the rows of Table 2a. Black spruce is preferred to White spruce and to Other, both of which are preferred to Pine and Deciduous. Note that the burning preference is not the same as the *rate* of burning, a measure which incorporates both fire

composition and size. Thus, the regional preference ordering is not completely consistent with Table 1. Inverting the analysis, by counting significantly negative entries in the Table, we may say that class Deciduous is the most avoided regionally.

The regional pattern of fire preference is partially conserved at the scale of individual fires within their locales (Table 3). Locally, Black spruce is preferred to White spruce, which is preferred to the other three classes, all of which are equivalent. The proportion of class Black spruce in individual burns is greatly in excess of what might be expected, given the composition of the locale, and this preference is more pronounced locally than regionally. Again, by inverting the analysis as above, and counting significantly negative values in the rows of Table 3a, class Deciduous is locally the most avoided.

Forest management and fire composition

Let $\mathbf{a}, \mathbf{z}, \mathbf{x}, \mathbf{y}$, and $\hat{\Theta}$ be defined as in *Statistical analysis*, above. Then $\mathbf{y} = \mathbf{a}\hat{\Theta}$ may be regarded as a general transformation \mathbf{T} from \mathbb{R}^5 to \mathbb{R}^4 . The differential $d\mathbf{T}$ is a 4×5 matrix of partial derivatives:

$$\frac{\partial y_i}{\partial x_j} = \frac{\partial(1, \mathbf{z}) \cdot \boldsymbol{\theta}_i}{\partial x_j}$$

where " \cdot " is the vector dot product and $\boldsymbol{\theta}_i$ is the i th column of $\hat{\Theta}$; $d\mathbf{T}$ specifies the response $d\mathbf{y}$ in predicted fire composition to a small change $d\mathbf{x}$ in the locale. From the definition of \mathbf{z} and the equalities $\log(u/v) = \log u - \log v$ and $d \log u = 1/u du$,

$$\frac{\partial y_i}{\partial x_j} = \begin{cases} \theta_{i,j} & \text{if } j \in 1, 2, 3, 5, \\ x_j & \\ -\sum_{k=0}^4 \theta_{i,k} & \text{if } j = 4. \\ x_j & \end{cases}$$

By definition (see, e.g., Buck 1978: section 7.4), for a given \mathbf{x}' ,

$$\Delta \mathbf{y} = \mathbf{T}(\mathbf{x}' + \Delta \mathbf{x}) - \mathbf{T}(\mathbf{x}') \approx d\mathbf{T}|_{\mathbf{x}}(\Delta \mathbf{x}).$$

In particular, if a proportion $0 \leq p \leq 1$ of the white spruce stands in the locale are harvested and regenerate to deciduous, $\Delta \mathbf{x} = (px_2, -px_2, 0, 0, 0)$, and

$$\Delta y_i \approx \left(\theta_{i,1} \frac{x_2'}{x_1'} - \theta_{i,2} \right) p.$$

The treatment effect depends only on p and the preharvest ratio of the areas in the White spruce and Deciduous classes. Where this ratio is small (e.g., $x_2/x_1 = 0.278$ in Eq. 4), numerical evaluation at the sample mean of 48 locales shows the effect to be negligible. However, after the first pass of a two-pass clear-cut system ($p = 0.5$) is applied to the white spruce component of a locale where $x_1 = x_2$,

$$\Delta \mathbf{y} \approx (0.295, -0.82, -0.25, -0.385).$$

This implies that future fires in the locale will burn relatively less of the Black spruce, Other, and the remainder of the White spruce classes, and relatively more of the Deciduous and/or Pine classes than would have been the case preharvest. The effect magnitude is greatest for class White spruce.

Further resort to differential calculus leads to a more directly interpretable result. For \mathbf{y} , the predicted vector of log ratios for a fire in a locale of composition \mathbf{x} , let \mathbf{w} be the predicted composition obtained from \mathbf{y} via the inverse log-ratio transformation (Aitchison 1986: definition 6.1). Consider the differential operator $d\mathbf{S}$, the 5×5 matrix of partial derivatives $\partial w_i / \partial x_j$. From $d\mathbf{S}$ one may estimate the effect $\Delta \mathbf{w}$ of treatment $\Delta \mathbf{x}$ on the predicted fire composition. As the treatment effect on residual areas of white spruce is of most interest, I focus on the component

$$\Delta w_2 \approx \left(\frac{\partial w_2}{\partial x_1} - \frac{\partial w_2}{\partial x_2} \right) p x_2. \quad (8)$$

By definition, $w_2 = \exp(y_2) / (\exp(y_1) + \exp(y_2) + \exp(y_3) + \exp(y_4) + 1)$. Application of the chain and quotient rules to the expressions for $\partial y_i / \partial x_j$ derived above, yields an expansion of the right-hand side of Eq. 8 in terms of \mathbf{w} , $\hat{\Theta}$, \mathbf{x} , and p , from which some general results can be obtained. For example, a sufficient condition for $\Delta w_2 < 0$ is $0.75 < x_1/x_2 < 1.36$. Thus, in any locale where the ratio of areas in classes Deciduous and White spruce falls within these bounds, harvesting will reduce the expected proportion of class White spruce in the composition of postharvest fires, relative to the preharvest expectation. Assuming that the likelihood of fire is not increased by such treatments, the class-specific rate of burn for White spruce must decrease locally. That is, harvesting part of a locale's white spruce will confer some degree of protection upon the remainder. The stated condition on x_1/x_2 applies to 9% of townships in the study area, containing 17% of the total area of white spruce. Less strict conditions can be derived, but are not as simply ex-

pressed. However, Δw_2 is negative in most cases. The effect magnitude of any specific treatment–locale combination must be evaluated numerically.

DISCUSSION

Mean annual burn rates have been very low over the 36-yr study interval ($r = 0.0021$), relative to the longer-run values indirectly estimated for boreal regions—studies collated by Larsen (1997) indicate that $r = 0.01$ is typical. Two estimates exist that are specific to the Alberta mixedwood. Murphy (1985) applied Van Wagner's (1978) methods to an age-class structure derived from forest inventory data, and estimated that, prior to any efforts at fire suppression, $r = 0.022$. In contrast, in an earlier version of the present study, which extended the analysis to a 54-yr interval, I have estimated that $r = 0.0041$ (Cumming 1997). This estimate corrected for the effect of fire suppression by nonparametric analysis of recent changes in the fire-size distribution.

To interpret my empirical results as an estimate of the rate parameter(s) in theoretical fire-history models (Johnson and Van Wagner 1985) requires that one consider both the sampling limitations of indirect studies (Fox 1989, Finney 1995) and long-term variation in climatic drivers (Johnson and Larsen 1991) that could confound my direct but short-term study. Both issues are beyond the scope of this paper—but see Armstrong (1999) for a consideration of whether these model parameters can meaningfully be estimated at all. I note, however, that the present study interval included four severe fire years (1980–1982 and 1995) and is fairly representative of the interannual variability seen in the historical record (Weber and Stocks 1998: Fig. 2).

Statistical analysis of 48 mapped fires shows that their sample mean composition is not the same as the composition of the study area, and that the compositions of individual fires and their locales differ. Multivariate linear-regression analysis shows that fire composition is strongly related to, but not the same as, the composition of the locale. All components of the locale's composition are significant determinants of fire composition. However, interaction effects are not significant, e.g., the abundance of conifer classes in a locale does not influence the expected amount of the Deciduous class burned in a fire. I found no relationship between fire size and composition over the range of fire sizes studied. I conclude that variation in fire susceptibility between forest stand classes influences fire behavior at both the regional and local scales, and that this influence persists even under the extreme weather conditions associated with large fires. I did not sample the four largest fires that burned in the study interval. However, these fires account for only 20% of the total area burned (Fig. 5). Thus, even if included in the analysis, these fires would not much affect the results, unless a threshold exists, at some large size, in the relation between fire size and fire composition.

Variation in fire susceptibility

Estimated mean annual burn rates vary by an order of magnitude across classes (Table 1), with Deciduous burning at the lowest annual rate ($r = 0.0005$) and Black spruce at the highest rate ($r = 0.005$). A partial ordering of the classes by decreasing rate is Black spruce > Pine > White spruce and Other > Deciduous. By preference analysis, some of these differences are significant at both the regional scale (at which the mean rates were computed), and at the scale of individual fires within their locales. A partial ordering of classes by relative preference that is consistent at both scales is given by: Black spruce > White spruce and Other; White spruce > Pine and Deciduous. The relative preference for class Other differs across scales. At both scales, Black spruce is the most preferred, and the Deciduous class is the most avoided. The only inconsistency between the local and regional preference rankings and the overall rates of burn is that class Pine ranks high in rate, but low in preference. This is attributable to several large fires in the early 1980s that burned considerable areas of pine in association with black spruce, inflating the overall rate for this type.

These results contradict the most directly comparable known studies. Larsen (1997) estimated the time since last fire at 166 sample patches in Wood Buffalo National Park, a ~45 000-km² region that extends from 80 to 400 km due north of my study area. By survival analysis, he estimated an aspen "fire cycle" (equivalent, in this context, to the mean interval between fires) of 39 yr (corresponding to a mean annual burn rate of $r = 0.026$) and a black spruce fire cycle of 78 yr ($r = 0.013$). For boreal forests of interior Alaska, Yarie (1981) reports values of 20 yr for aspen, and 45 yr for black spruce. That, e.g., Larsen's (1997) estimated rates exceed mine by factors of 52 and 2.6, respectively, could be due to his longer term data set (estimated patch ages of up to 300 yr), to the more northerly location of the park, which seems to be associated with larger fires (Rowe and Scotter 1973), or to differences in fire-suppression history between the park and provincial jurisdictions (M. E. Alexander, *personal communication*). That both his and Yarie's (1981) relative orderings of burn rates are opposite to mine is harder to explain, and requires further investigation. Negative biases in estimating time since fire from small samples of stem ages may form part of the explanation (see *Ecological implications of preferential burning*, below). Yarie (1981) sampled only 3–5 stems per patch, while Larsen (1997) used sample maximum ages of between three and ten canopy trees. Successional changes may be another factor. To the extent that primarily coniferous stands revert to deciduous dominance after fire (see *Ecological implications of preferential burning*, below), survival analysis of the age distribution of deciduous stands will overestimate their rate of burn.

The relative fire preferences of the five forest classes are apparently controlled by different processes acting at different spatial scales. The regional effect could be related to spatial variation in climate, topography, or frequency of lightning strikes. However, I propose that the effect arises from class-specific ignition probabilities, such as reported by Renkin and Despain (1992). In my study area Poisson regression using forest composition data as independent variables explains ~20% of the deviance in detected ignitions per township over 26 yr (*unpublished data*), and the resultant rankings of ignition probabilities are consistent with the preference rankings reported here.

The regional effect is not necessarily inconsistent with the results of Renkin and Despain (1992) or Bessie and Johnson (1995) with respect to the relative importance of fire weather and fuels in the behavior of individual fires. However, the marked class preferences of fires within their locales, across all fire sizes, does contradict their conclusions. I suggest that a partial explanation of my findings lies in well-documented physical differences between stand classes that determine their relative ability to develop and sustain a crown fire, given that a surface fire is burning. I use aspen stands as my example, although similar arguments might be devised for mature pine stands (e.g., Renkin and Despain 1992:43) and for wetlands.

Crown fire initiation under varying conditions of fuel and weather was central to Bessie and Johnson's (1995) study. They used Eq. 4 of Van Wagner (1977) to model the critical surface fire intensity required to initiate crowning: $I_o = (Czh)^{1.5}$ where I_o is fire intensity (in kilowatts per meter), z is lower crown base height, h is the foliage ignition energy, and C is an empirical constant; h is related to foliar moisture content m , expressed as a percentage of dry mass, as $h = 460 + 26m$.

Bessie and Johnson (1995) sampled 47 stands in which z ranged from 0.1 m to 13.7 m, with $\bar{z} = 7.8$ m and $\sigma_z = 2.8$ m. In mature aspen stands, by contrast, z can range from 15 to 20 m (Peterson and Peterson 1992: Table 4). In aspen stands after leaf flush, m varies between 140% and 200% (Van Wagner 1977). However, for their conifer stands, Bessie and Johnson (1995) assumed a constant value of $m = 100\%$. Thus, I_o in a mature aspen stand could exceed their sample maximum by a factor of 1.8–4.4, and their sample mean by a factor of 4.1–10.3. It is likely that both the statistical and graphical analysis employed by Bessie and Johnson (1995) would be sensitive to this inflated variance. These remarks merely elaborate the physical basis of the informal observations of Rowe and Scotter (1973), who refer to the "built-in broadleaf fire-breaks" found in southern mixedwood forests as limiting fire sizes.

Bessie and Johnson's 1995 study area did not include deciduous or wetland areas. Their results evidently do not apply to the more heterogeneous landscape of the

boreal mixedwood. In particular, the low contrast in two key independent variables limits the generality of their study, as Johnson et al. (1998) recognize. As an aside, subalpine conifer stands show no relation between age and z for stands above 50 yr (Bessie and Johnson 1995: Appendix A). However, in aspen stands z tends to increase with stand age (Peterson and Peterson 1992). Thus aspen stands with low recruitment of white spruce may become less susceptible to crown fires as they age.

Aspen stands do burn. The forgoing argument merely shows that crown fires should be less easily started or sustained in aspen stands than in certain conifer types. However, the main front of a large fire could spread around an aspen stand, through the canopy of surrounding coniferous forests, or jump over it by spotting—a mechanism of fire propagation by wind-blown burning debris. The aspen stand could burn as a surface fire, after the main fire front has passed. My local-scale preference analysis indicates that this must happen comparatively seldom.

Ecological implications of preferential burning

In the mixedwood region, most sites that support aspen can also support white spruce (Kabzems et al. 1986). These mesic sites typically exhibit substantial postfire regeneration of aspen, by suckering from clonal root systems (Peterson and Peterson 1992). Although the amount of white spruce in these stands tends to increase with time, the temporal pattern of individual recruitment responsible for this increase is variable (Lieffers et al. 1996). When high seed input coincides with mineral-soil exposure by an intense fire (Kabzems et al. 1986), an even-aged mixed-species stand may establish. Despite aspen's much higher early growth rate, white spruce can dominate the canopy of these stands within ~ 100 yr, when the initial aspen cohort senesces (Kabzems et al. 1986). Other developmental pathways are biologically possible, including those with persistently low white spruce densities, or those where high densities of white spruce are attained over several centuries. Both of these represent relatively stable aspen stands, with continual replacement of canopy aspen from the understory, accompanied (or not) by low rates of white spruce recruitment. Although Kabzems et al. (1986:84) recognized such trajectories as an "extended mixedwood stage," their significance has been neglected. I attribute this to the uncritical acceptance of high and homogeneous estimated rates of disturbance in the mixedwood region, such as would preclude the existence of substantial areas of old forest. For example, the expected proportion of the forest exceeding 100 yr would be $< 11\%$, given Murphy's (1985) estimated disturbance rate of 0.022.

Cumming et al. (2000) have shown that gap-phase dynamics (Shugart 1984) begin at about 40 yr in aspen stands in the Alberta mixedwood, and that older stands showing evidence of such dynamics are abundant and

widespread. Thus, stable aspen stands could develop and persist. By simulation, they show that aspen stand ages estimated from the sample mean or small-sample maxima of stem ages are negatively biased in stands older than ~ 120 yr, and present evidence that these biases affect ages estimated by air-photo interpretation. In consequence, they argue that it is not valid to estimate disturbance rates from age structures derived from forest inventory data.

The present study extends these results by providing, at a regional scale, empirical evidence that aspen stands are unlikely to burn, at least until they develop a significant amount of canopy spruce. Stands where white spruce recruitment is restricted by site conditions or by seed availability will likely be undisturbed by fire for extended periods, which provides the time needed for endogenous processes such as individual-tree replacement to become dominant within stands. These processes are characteristic of the old-growth condition (Kneeshaw and Burton 1997). I conclude that the age structure of the mixedwood's population of mesic stands is not directly controlled by fire, but rather by the rate of white spruce recruitment, perhaps in combination with other factors such as disease, drought, windthrow, and herbivory. The standard model of the boreal mixedwood as a young, fire-dominated ecosystem needs revision.

Management implications

Landscape-scale fuels management.—Forest managers in Alberta are exploring the possibility of "cooling" or "fire-proofing" (D. Quintilio, *personal communication*). Hopes are pinned on the use of aspen stands as natural fire breaks (see Fechner and Barrows [1976], cited in Jones and DeByle [1985]). In the study area, fire frequency in deciduous stands is low, presumably because these stands usually do not sustain crown fires. Crown fires that enter a deciduous canopy generally drop to the ground, and may continue to burn as surface fires, which are more safely and easily fought. Thus, the establishment and maintenance of deciduous stands in strategic locations could allow firefighters to limit individual fires to contiguous patches of conifer stands.

Omi (1996) has evaluated the potential of landscape-scale fuels manipulation to limit the impact of future high-intensity fires, and concluded that it might be justified for protecting communities and developed areas, and also parks and reserves that are small relative to the size of fires that may affect them. An additional concern in some jurisdiction is that large fires may seriously affect the viability of forest-products firms with area-based tenures. In the boreal mixedwood, where such tenures are usual, white spruce is a principal value at risk, as it is the most commercially valuable tree species, is difficult to regenerate, and has a relatively long rotation (Lieffers and Beck 1994).

In a working forest, exploitation of harvest patterns

may offer a cost-effective means of landscape-scale fuels management. My results show that, under many conditions, multi-pass harvesting of white spruce stands with subsequent regeneration to (at least temporary) aspen dominance will protect the remaining white spruce, at the cost of increased (but low) risk to the deciduous component. Specifically, the expected proportion of white spruce to burn in a future fire in the vicinity will decline. This implies that harvest schedules could be designed to manipulate the spatial distribution of these two stand classes so as to control the risk of white spruce losses due to fire. The relation between fire compositions and fire surroundings may serve as a step towards rational landscape management. Further progress requires that the effect, if any, of forest composition on ignition probabilities and fire-size distributions be quantified.

Natural disturbance management models.—Natural disturbance regimes (NDRs) have been proposed as models for the management of the circumpolar boreal forest (Hunter 1993, Haila et al. 1994). Hunter (1993) identified three features of NDRs that forest managers could seek to emulate: the spatial pattern and size of disturbances, the nature and amount of residual material, and the rate of disturbance. Hunter (1993) focused on spatial pattern, while Lee et al. (1997) focused on residual material. The present results bear on disturbance rates.

A maximum-sustained-yield harvesting regime on the mesic portion of my study area (classes Deciduous and White spruce) implies a disturbance rate of ~1% annually (Armstrong et al. 1999). Only stands at or exceeding rotation ages would be harvested in this way, although the age specificity of fire in this system, if any, is undocumented. Rotation ages for hardwoods and softwoods are roughly 70 yr and 120 yr, respectively, so the harvesting rate for the Deciduous class will exceed that of the White spruce class. In the study area at present, nonmesic forested sites (those containing pine and/or black spruce) are mostly not harvested at all. However, my results show that empirical values for disturbance rates and for fire preferences at both regional and local scales are rank ordered as Black spruce > White spruce > Deciduous. This ranking of disturbance rates is the inverse of that to be expected under current management plans.

In an earlier study (Cumming 1997) that corrected for the effects of fire suppression, I estimated natural fire frequencies (the inverse of disturbance rates) for the Deciduous and White spruce classes to be about 4 times longer than implied by Table 1. Even so, forest management plans that harvest at these longer intervals, assuming no additional losses to fire, produce only one quarter of the timber yield achievable under maximum-sustained-yield management (Armstrong et al. 1999). Current management plans are thus considerably at odds with at least one aspect of the natural-disturbance model, as regards the overall rate of harvest, and

how this harvest is distributed amongst populations of forest tree species.

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