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BIOTIC AND ABIOTIC REGULATION OF LIGHTNING FIRE INITIATION IN THE MIXEDWOOD BOREAL FOREST

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Abstract. Lightning fire is the dominant natural disturbance of the western mixedwood boreal forest of North America. We quantified the independent effects of weather and forest composition on lightning fire initiation (a detected and recorded fire start) patterns in Alberta, Canada, to demonstrate how these biotic and abiotic components contribute to ecosystem dynamics in the mixedwood boreal forest. We used logistic regression to describe variation in annual initiation occurrence among 10 000-ha landscape units (voxels) covering a 9 million-ha study region over 11 years.

At a voxel scale, forest composition explained more variation in annual initiation than did weather indices. Initiations occurred more frequently in landscapes with more conifer fuels (*Picea* spp.), and less in aspen-dominated (*Populus* spp.) ones. Initiations were less frequent in landscapes that had recently burned. Variation in initiation was also influenced by joint weather–lightning indices, but to a lesser degree. For each voxel, these indices quantified the number of days in the fire season when moisture levels were low and lightning was detected. Regional indices of fire weather severity explained substantial interannual variation of initiation, and the effect of forest composition was stronger in years with more severe fire weather. Our study is a conclusive demonstration of biotic and abiotic regulation of lightning fire initiation in the mixedwood boreal forest. The independent effects of forest composition emphasize that vegetation feedbacks strongly regulate disturbance dynamics in the region.

Key words: abiotic and biotic regulation; boreal forest; fire; fuel; lightning; mixedwood forest; natural disturbance; weather.

Introduction

Natural disturbances are characteristic of all ecosystems, stimulating a cycle of release, reorganization, and regeneration (Gunderson and Holling 2002). Biotic and abiotic processes regulate disturbance events (e.g., Paine and Levin 1981), and the dynamics of an ecosystem depend on the comparative endogeny or exogeny of these processes (Didham and Watts 2005). Lightning fires are the dominant natural disturbance in much of the North American boreal forest (Stocks et al. 2003). The relative importance of biotic and abiotic factors regulating these fires is controversial (Bessie and Johnson 1995, Hély et al. 2001, Schoennagel et al. 2004). Our study considers one aspect of lightning fire behavior: initiation. Here, initiation is the outcome of a sequence of physical events and a detection system, resulting in the record of a fire caused by lightning (Cunningham and Martell 1976).

An initiation can be described mechanistically as the interaction between atmospheric and terrestrial conditions. Broad-scale weather patterns determine the location of lightning events that will provide the energy for ignition to occur. The efficiency of individual lightning strikes in igniting a fire is affected by variation in lightning properties such as polarity, multiplicity, or current (Fuquay et al. 1979); moisture properties of forest fuel resulting from recent weather conditions including precipitation, temperature, wind, and humidity (Van Wagner 1987); or rates of combustion that vary with fuel type (Rothermel 1972). Laboratory studies have shown that moisture content and fuel depth are important elements of ignition (Latham and Schlieter 1989). Fuel type can influence initiation through variation in cellular structure of the fiber and moisture content as well as the size and shape of fuel on the forest floor (Anderson et al. 2000). Survival from smoldering to an active fire is dependent on organic and soil properties (Hartford 1989). Under appropriate joint conditions a strike may ignite fuels, continue to combust, and persist to become a fire large enough to be detected: an initiation. Given a large sample, we view initiation as a random spatiotemporal point process with parameters conditional on covariates for each limiting factor. These include: lightning strike data to determine where initiation potential existed, weather data

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to assess fuel moisture conditions, and land cover data to assess the fuel types existing at the time of initiation.

Many previous studies (e.g., Fowler and Asleson 1984, Flannigan and Wotton 1991, Renkin and Despain 1992, Nash and Johnson 1996, Diaz-Avalos et al. 2001, Wierzchowski et al. 2002, Podur et al. 2003) have quantified the initiation process using some of the relevant covariates measured at various spatial and temporal scales. However, none incorporated the full complement of features critical to identifying independent correlates of initiation. The objective of our study was to quantify the relative contribution of weather and fuel composition to the initiation process in the western mixedwood boreal forest ecosystem. We considered weather as an abiotic, exogenous factor and fuel composition as a biotic, endogenous factor contributing to a disturbance event. By advancing our understanding of the environmental patterns influencing the distribution of initiations, we contribute insight to the processes regulating natural dynamics in the boreal forest and to scenarios that could arise from the interaction of unprecedented changes in climate (Flannigan et al. 2001) and land cover (Schneider et al. 2003) anticipated for the region in the near future.

Methods

Study region

Our study region was 91 000 km^2 of mixedwood boreal forest (Rowe 1972) in central-eastern Alberta, Canada (Appendix A). The regional climate is continental with mean winter and summer temperatures of −13.2°C and +13.5°C, respectively, and total precipitation in summer and winter in the range of 240 mm and 64 mm, respectively (Strong and Leggat 1992). Elevation varies gradually from ~200 m to 1000 m. Glacial movement through the region has resulted in rolling morainic deposits on the uplands and smoother glaciolacustrine deposits on the lowlands (Rowe 1972). The mixedwood is the most productive and diverse of boreal ecosystems in North America (see Chen and Popadiouk 2002 for a review). Forest tree communities (Appendix B) are stratified by soil moisture regime (Strong and Leggat 1992). Upland mesic sites are dominated by mixtures of trembling aspen (*Populus tremuloides* Michx.), balsam (aspen) poplar (*Populus balsamifera* L.), or white spruce (*Picea glauca* (Moench) Voss). Community development at these sites depends on variation in disturbance history, composition, and spatial context (e.g., stochastic availability of propagules from neighboring stands). Paper birch (*Betula papyrifera* Marsh) is present but pure stands are rare. White spruce and balsam fir (*Abies balsamea* (L.) Mill) dominate older stands but pure stands are not currently abundant. Xeric sites are vegetated by jack pine (*Pinus banksiana* Lamb), sometimes in association with aspen. Moist, poorly drained hygric sites are vegetated by black spruce (*Picea mariana* (Mill.) B.S.P.). There are extensive wetlands including open areas of bog, fens, swamps, and marshes. Tamarack (*Larix laricina* (Du Roi) Koch) is the dominant tree species in wetlands.

Data and exploratory analysis

The study region was divided into three-dimensional space–time samples, called voxels, with the units landscape and year. The Province of Alberta is partitioned using an administrative grid system of townships each measuring ~ 9600 ha and varying slightly due to geographic corrections. Each township in the study region was considered as the spatial sampling unit, hereafter referred to as a landscape (Appendix A). Data were collected for each landscape between 1983 and 1993 and summarized for each year providing the annual, temporal dimension to the voxel.

We described the relationship between the occurrence (point [1] below) of an initiation in a voxel with respect to a suite of biotic and abiotic variables [2–7] described by indices of: fire weather (weather reflecting fuel moisture relevant to fire initiation and behavior), climate, lightning, joint fire weather–lightning, geography, and forest composition using logistic regression. A summary of variables is available in Appendix B. Daily meteorological data were collected during the fire season and summarized to describe weather-related variation per voxel. The exception was the climate index, where daily meteorological data were summarized over the entire region for each year. Geography was a static description of landscape location and did not vary through time. Forest composition was described for each voxel and varied through time as a result of natural and anthropogenic disturbance. The 11 years of data represented a time series prior to a marked, intensified forest harvesting in the study region (Schneider et al. 2003).

1. *Lightning fire initiation*.—Alberta Sustainable Resources and Development (ASRD) provided data describing the location and date of initiations. Un-detected or un-recorded fires may have occurred in the region but fire detection efficiency appears to have been constant over the study interval (Cumming 2005). A binary response variable was selected to describe the presence or absence of an initiation in each voxel, such that $y_{ij} = 1$ if at least one initiation occurred in landscape i in year j. Multiple initiations were infrequently detected, but these events were omitted to preclude the statistical dependence of events resulting from the same weather/forest conditions.

The $\Sigma y_{ij} = 1280$ over the study period, and $p_{ij} = 0.12$. There were 116 ± 59 annual number of initiations in the region (mean ± SD). We expected spatial and/or temporal structure might exist in the processes generating all variables (Legendre et al. 2004); however, Bonferroni-corrected Mantel r statistics (Mantel 1967, Legendre and Legendre 1998) indicated there was no significant autocorrelation of y_i within each year j.

2. *Fire weather*.—We summarized daily weather and fuel moisture conditions relevant to fire ignition provided by the Canadian Forest Fire Weather Index System (FWI; Van Wagner 1987) to produce three fire weather indices for each voxel. We selected the Fine Fuel Moisture Code (FFMC), Duff Moisture Code (DMC), and Initial Spread Index (ISI). FFMC and DMC represent moisture content of litter or fast-drying fine fuels and loosely compacted organic layers of moderate depth, respectively. ISI includes wind speed in calculation and is theoretically relevant to the initial spread rate of a fire independent of fuel effects (Van Wagner 1987). These codes were calculated from daily measurements of temperature, relative humidity, wind speed, and precipitation taken from an array of 65 provincial weather stations operated and calibrated by ASRD in and around the region and interpolated across the region. We estimated a critical value where fuel moisture was ''receptive'' to fire propagation by assessing the cumulative distribution of the recorded daily FFMC, DMC, and ISI codes for each initiation in the data set. The critical value was selected as the code above which 85% of initiations were detected. We tallied the sum number of days per voxel when the code exceeded the critical value to create three fire weather indices. These indices, $FFMC_{DAYS}$, DMC_{DAYS}, and ISI_{DAYS} (Appendix B) were used to describe variation in receptive fire weather and fuel moisture.

The three daily codes were interpolated at a resolution of 1 km across the study region on each day of the fire season over 11 years ($n = 3$ codes $\times$ 155 days $\times$ 11 years = 5115) by inverse-distance weighting (Flannigan and Wotton 1989) in ARC-GIS (ESRI 2002) using the six nearest weather stations. The interpolation of each code was cross-validated at 20 stations that covered a range in elevation. Data from randomly selected days were removed, and the codes were interpolated for these weather stations. For each code we used linear regression to test if the slope of the relationship between interpolated and measured values was significantly different from unity ($\alpha = 0.05$). To test the sensitivity of the generic interpolation to known adiabatic lapse rates, we used regression residuals from above to test if the slope of their relationship with elevation was different from zero ($\alpha = 0.05$). Interpolations underestimated ISI, but the relationship was linear. Otherwise, all tests indicated that the inverse-distance-weighting technique was adequate (Appendix C).

Threshold values of receptive fire weather calculated for FFMC, DMC, and ISI were 87, 34, and 4, respectively. We lowered the critical ISI from four to three as a simple adjustment for the bias in interpolation described in the previous paragraph. These values agree closely with analyses from a similar forest region in Saskatchewan, Canada (Anderson and Englefield 2001).

3. *Climate*.—A synopsis of annual variation in regional atmospheric conditions (e.g., a ''dry year'') was quantified using the seasonal severity rating (SSR) from the FWI system (Van Wagner 1987). SSR was calculated as the mean annual Daily Severity Rating of all weather stations in the region. SSR varied from 0.8 to 1.4 (mean = 1.06, SD = 0.17). A generalized linear regression model using a Poisson family suggested a log-linear relationship between counts of annual initiations and SSR ($\beta = 2.12$, SE = 0.13, $n = 11$).

4. *Lightning indices*.—We created two indices to describe the spatiotemporal distribution of lightning activity among voxels (Appendix B). Lightning data were obtained from ASRD detection stations across the province (Appendix A). The location of each lightning flash is estimated using time difference and triangulation techniques along with estimates of the polarity, multiplicity of strokes (number of return strokes in a flash), time, and peak current. The relationship between lightning characteristics and ignition probability is incompletely understood, and not all strikes have characteristics required to initiate a fire (Rakov and Huffines 2003). A long continuous current cannot be detected with current technology, and not all lightning strikes are recorded. As such, we considered all strikes equally in this study. The first index was the summed number of days in a voxel where at least one lightning flash was detected (L_{DAYS}), the second index was the cumulative number of detected lightning strikes (L_{COUNT}) in a voxel.

Nimchuk (1989) estimated spatial error of Alberta's lightning detection system at 4–14 km. This error is larger than the spatial resolution of each landscape. We assumed that if detected lightning events were autocorrelated across multiple landscapes and the direction of error was unbiased, the overall effect of spatial error and misclassification at the voxel scale is dampened. Variogram analysis (Cressie 1991) illustrated that daily lightning activity was spatially structured within years across the study region, suggesting that the influence of positional inaccuracy reported for strikes could be buffered by the spatial extent of storm activity and the resolution of our study voxels. Both indices varied weakly with elevation (Appendix D). There was no evidence to suggest the location of lightning detectors (Appendix A) influenced lightning indices.

5. *Joint weather–lightning indices (JWL)*.—We were motivated to create the joint fire weather–lightning indices from studies documenting an inverse relationship between lightning efficiency (number of fires/number of strikes) and fuel moisture (Nash and Johnson 1996) suggesting the co-occurrence of ''appropriate'' daily fire weather conditions and daily lightning should better explain the distribution of initiations than the independent distributions of each. Three joint weather–lightning indices (Appendix B: $FFMC_{JWL}$, DMC_{JWL}, ISI_{JWL}) were calculated for each voxel to de-

scribe the sum number of days when fuel moisture conditions were receptive to ignition and lightning was detected. This index joins the ''fire weather'' indices with the L_{DAYS} ''lightning index.'' Previous studies (Kourtz and Todd 1991) have suggested that large storms produce more lightning but also more precipitation. We calculated weighted JWL indices ($wFFMC_{JWL}$, $wDMC_{JWL}$) to account for this convex relationship between daily lightning density and ignition potential. For each day during the fire season, landscapes with no lightning and/or sub-threshold fire weather were classified as zero, between one and five strikes of lightning and above-threshold fire weather as one, and five or more strikes and above-threshold fire weather with a value of 0.2. Values for the lightning cut-points were based on Kourtz and Todd (1991).

6. *Geography*.—We described the elevation (ELEV) of each landscape at its centroid using a Digital Elevation Model (DEM). The DEM was a 100-m resolution grid created from digitized 1:20 000 topographic base-maps with 10-m contours provided by Alberta Pacific Forest Products (Boyle, Alberta, Canada). The NAD 27 Universal Trans Mercator measure of northing (NORTH) was included in analyses as a spatial proxy for unmeasured gradients. Northing ranged from a UTM of 6 100 565 to 6 428 588.

7. *Forest composition*.—We used the Alberta Phase 3 Forest Inventory (Anonymous 1985) circa 2000 to describe forest composition within each voxel as a broad-scale indicator of fuel availability and variability. The inventory was carried out between 1970 and 1984 based on the interpretation of 1:50 000 leaf-on aerial photographs, supplemented by ground-truthing (Anonymous 1985). The inventory has been updated annually by the province for fire, harvesting, and other land conversion since its compilation. We simplified the inventory classification to 10 stand types based on dominant canopy species, composition, and stand density. We used the seven most-common stand types to describe the compositional area (ha) of each voxel (Appendix B). These included low-density aspen–deciduous (A_L), high-density aspen–deciduous (A_H), white spruce (S_W), black spruce (S_B), jack pine (P_J), recently burned (B), and open wetland/low-density scrub (O). Remaining fuel types accounted for $<2\%$ of the study region and were omitted from the analyses. Landscape composition in years prior to fire and harvest was recovered from detailing in map annotations and notation used in the update process (as described in Cumming [2001]), enabling us to quantify changes in composition for each voxel resulting from disturbances. We assumed forest composition was otherwise constant over the study interval. Forest types varied across the region and provided the contrast required for this study (Appendix D). Of the 1056 landscapes within the region, 946 were selected for study where classifiable terrestrial surface area was >5000 ha. This criterion excluded landscapes with small area, large areas of water, or human development. These 946 landscapes were sampled over 11 years, providing 10 406 voxels.

Logistic regression

We described the response variable, initiation per voxel, as a function of fire weather and lightning indices, forest composition, and geography using logistic regression in a generalized linear model framework (McCullagh and Nelder 1989) using the R statistical language and environment (version. 2.0.1; R Development Core Team 2005). We verified the linearity of the relationship between initiation probability and all candidate covariates through the log odds. These relationships were linear with the exception of the JWL indices and the area of black spruce forest cover type. Log-transformations of JWL indices induced linearity (0.5 was added to each index to accommodate transformation of zeros). We included a linear and quadratic term to account for nonlinear relationship with black spruce composition. We found no relationship between the odds of initiation and landscape area (9140 $\pm$ 438 ha [mean $\pm$ SD]), so area was not considered in the remainder of this work.

We assessed the collinearity between and among covariate classes using Pearson's product-moment pairwise correlation. The correlation among forest types had a maximum absolute value of $r = 0.36$ exhibited between open areas (O) and high-density hardwood (A_H); remaining forest types were correlated within $\pm$0.3, indicating multi-collinearity in terms should not affect the analyses. Weather indices were inherently correlated, since they included combinations of the lightning and weather data. The correlation among forest composition, fire weather, and JWL indices among voxels did not exceed $\pm$0.1, indicating there was sufficient variability to assess the relative influence of forest composition and weather. Scatter plots illustrated low correlation among annual JWL indices, forest composition, geography, and elevation (Appendix D). Our exploratory analyses indicated that there was no spatial autocorrelation of initiations among voxels, suggesting that residuals should be spatially, independently distributed and that we had an effective sample size of 10 406 (Legendre et al. 2004). As such, we began our analyses using a fixed-effects logistic regression model and based selection of the most parsimonious model on Akaike's Information Criterion (AIC) using a backward elimination procedure (Burnham and Anderson 1998). A change in AIC among candidate models of >5 was used to indicate a substantial change in the systematic descriptive ability of each model.

Our primary objective was to determine the independent influence of variation in weather and fuel on initiation. We used a hierarchical model selection approach to determine the best weather model (W) and best fuel model (F), and then combined these to determine the best weather and fuel model (WF). First a global weather model (W_0) of all 10 weather-related

TABLE 1. Selection and diagnostics for logistic regression models of fire initiation.

Model	Model terms	ℓ	k	AIC	ROC	R^2
Null	intercept only (β_0)	3880	1	7762	NA	NA
W_0 global weather	$DMC_{DAYS} + FFMC_{DAYS} + FFMC_{JWL} + DMC_{JWL} + ISI_{JWL} + wFFMC_{JWL} + wDMC_{JWL} + SSR + L_{COUNT} + L_{DAYS}$	3736	11	7495	0.64	0.052
W_1 best weather	$\ln(FFMC_{JWL}) + \ln(DMC_{JWL}) + wFFMC_{JWL} + SSR + L_{DAYS}$	3738	6	7489	0.64	0.051
F_0 global fuel	$B + A_L + A_H + S_W + S_B + S_B^2 + O + P_J$	3705	9	7429	0.65	0.063
F_1 best fuel	$B + A_L + A_H + S_W + S_B + S_B^2$	3706	7	7427	0.65	0.063
WF_0 global	$B + A_L + A_H + S_W + S_B + S_B^2 + wFFMC_{JWL} + \ln(FFMC_{JWL}) + \ln(DMC_{JWL}) + SSR + L_{DAYS} + ELEV + NORTH$	3534	14	7097	0.71	0.12
WF_1 best	$B + A_H + S_W + S_B + S_B^2 + \ln(FFMC_{JWL}) + \ln(DMC_{JWL}) + SSR + ELEV + NORTH$	3537	11	7097	0.71	0.12
WF_2 best	$B + A_H + S_W + S_B + S_B^2 + \ln(FFMC_{JWL}) + \ln(DMC_{JWL}) + SSR + ELEV + NORTH$	3528	12	7081	NA	NA

Notes: Abbreviations are: ℓ, the negative of the log-likelihood from maximum-likelihood estimation; k, the number of parameters estimated in the model; ROC, Receiver Operating Characteristic; NA, not available. Appendix B provides descriptions of all variables. WF_2 includes a random intercept for landscape. Table 2 summarizes parameter estimates of WF_2.

indices (Table 1) was reduced to the most parsimonious (best) weather model (W_1). Similarly, a global fuel model (F_0) of all seven forest composition variables was reduced to the best fuel model (F_1). W_1 and F_1 were invited to the global weather and fuel model (WF_0; Table 1) where two geographic measures (ELEV and NORTH) were also included. WF_0 was reduced to the best fixed-effects model, WF_1. We then assessed the independence of residuals from (WF_1) to determine if additional, un-observed processes might have generated spatial or temporal autocorrelation. There was still no evidence of correlation in residuals among landscapes or as a function of year. Box plots of residuals grouped by landscape suggested correlation within a landscape throughout the study period, but this was not structured by time or time interval. We compared WF_1 to a logistic mixed-effects model (using Broström 2003) where a random effect with compound symmetry in the variance–covariance matrix was included to describe variation of the intercept for each landscape (WF_2). WF_2 assumes that stationary, yet unmeasured attributes influence the probability of initiation for voxels at a given landscape through time.

Our primary objective did not specify explicit hypotheses regarding interaction terms. We tested the hypothesis that the influence of fuel type would decrease in years with more extreme fire weather through interactions between forest composition terms and SSR using model WF_2. It has been suggested that all forest types are equally flammable under extreme fire weather conditions (Renkin and Despain 1992, Bessie and Johnson 1995). For a given forest composition term, a difference in sign between the main effect and the interaction terms would provide evidence that the influence of fuel type was diminished in more extreme fire years.

We assessed the relative influence of forest composition and weather/moisture on initiation by comparing the variation explained by W_1, F_1, and WF_1 using AIC scores and the Nagelkerke R^2. Model fits were assessed with the le Cessie-van Houwelingen-Copas-Hosmer unweighted sum of squares test (Hosmer et al. 1997) and Receiver Operating Characteristic (ROC) plots. The area under the ROC curve measured the ability of a logistic regression model to predict the occurrence of an event within the initial data set where values above 0.5 indicate increasingly substantial explanatory power (Fielding and Bell 1997). We evaluated model residuals using spatial, temporal, and unstructured diagnostics. We are not aware of any goodness-of-fit tests currently developed for logistic mixed-effects models, so we assumed those calculated from the fixed effects models provided conservative estimates for WF_2.

RESULTS

Model WF_1 offered the lowest fixed-effects AIC relative to the global model WF_0. WF_1 and WF_2 retained four forest composition terms, two JWL indices, SSR, elevation, and northing (Table 1). Inclusion of the quadratic term for black spruce (S_B^2) reduced the AIC by three, and this was retained in WF_2 due to evidence of nonlinearity. The maximum of this quadratic term occurred at a value of 3070 ha, and 68 landscapes had black spruce in excess of this value. The change in AIC for SSR was large enough ($\Delta AIC = 35$) to maintain it was significant at a regional scale, with an effective sample size of 11 rather than 10 406. A change in AIC of 16 between WF_1 and WF_2 suggested the inclusion of a random effect for landscape to the best fixed-effects model explained sufficiently more variation in the data (Table 2). We proposed that spatiotemporal structure in JWL indices could lead to stable initiation potential within each landscape and be responsible for the residual autocorrelation being quantified by the random effects. We detected significant positive autocorrelation in the 11-year cumulative sum of each JWL index up to 100 km (10 landscapes); however, we did not detect any corresponding spatial structure in the value of the random effects using variograms.

TABLE 2. Maximum-likelihood estimates and their standard errors for each term in WF_2 (see Table 1).

Term	β	SE	ΔAIC
β_0	+7.03	2.74	
B	−2.85	0.41	58
A_H	−2.52	0.26	93
S_W	+4.40	0.57	55
S_B	+2.91	0.87	9
S_B^2	−4.74	2.10	3
ln($FFMC_{JWL}$)	+0.23	0.050	20
ln(DMC_{JWL})	+0.27	0.048	31
ELEV	+0.0012	0.00032	12
SSR	+1.26	0.21	35
NORTH	−0.0000018	0.00000042	16
Random effect: landscape†	NA	NA	16

Note: ΔAIC is the increase of AIC when each term is removed from the mixed-effects model.
† Standard deviation for landscape = 0.44.

There was a significant, positive interaction between SSR and the S_W forest composition term when it was included in WF_2 (ΔAIC = 17, β = 11.48, SE = 2.71; Appendix E). We conclude that the effect of fuel variation on initiation was amplified in more extreme fire years, rather than decreased. The SSR values for three (1985, 1990, and 1991) of 11 years were more extreme than the third inter-quartile range of a 20-year series (1973–1993) of data from the same region, indicating these years could be considered extreme fire years in the region. There were no other significant interactions between forest composition types and SSR.

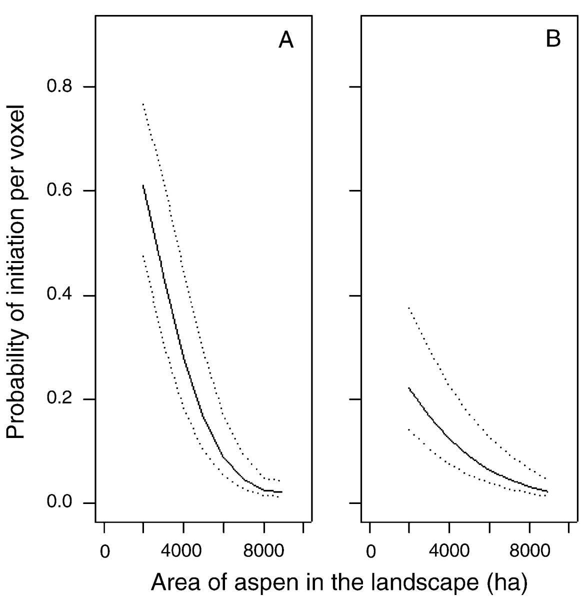

FIG. 1. The probability of fire initiation per voxel varies with forest composition and weather conditions; spruce- and aspen-dominated landscapes promote opposing initiation frequencies. The solid black lines illustrate the expected probability of initiation as the amount of aspen increases and the amount of (A) white spruce decreases or (B) black spruce decreases. The dotted black lines show the interval of expected probabilities calculated from the central 95% of values observed for $FFMC_{JWL}$ and DMC_{JWL}.

ROC area under the curve goodness-of-fit tests indicated WF_1 had substantial explanatory value (Table 1). The le Cessie-van Houwelingen-Copas-Hosmer unweighted sum of squares test for global goodness of fit also indicated that WF_1 was a well-fit model with a P value of 0.70. F_1 was a more parsimonious model than W_1 using AIC, although ROC-AUC values differed only slightly (Table 1). R^2 values from the fixed effects models supported the relative superiority of F_1 over W_1, and the ΔAIC and effect size of parameter estimates from WF_2 (Table 2, Fig. 1) demonstrated dominance in the magnitude of influence for forest composition relative to weather.

Fig. 1 illustrates that initiation is influenced by both fuel and weather, but that fuel has the dominant effect. Expected probabilities were calculated using parameter estimates from WF_1. Panel A illustrates a trade-off in the amount of aspen (A_H) and white spruce (S_W) in a landscape while maintaining 1000 ha of both burned (B) and black spruce (S_B) forest types, and all other covariates are maintained at their mean value (Appendix A); Panel B illustrates a similar trade between aspen (A_H) and black spruce (S_B).

DISCUSSION

We demonstrated that forest composition and weather conditions independently influenced the annual probability of lightning fire initiation within a large area of the mixedwood boreal forest. The fuel effects strongly predominated, even under extreme annual weather conditions. The probability of initiation was greater in spruce (*Picea*)-dominated landscapes than in deciduous, aspen (*Populus*) landscapes. This implies that initiation is more frequent in spruce and less frequent in deciduous stands. This effect was amplified for landscapes containing white spruce in years with more extreme fire weather, as measured by SSR.

The mixedwood boreal forest is a heterogeneous region characterized by its mixedwood stands that are typically composed of white spruce and trembling aspen. These stands develop through structural stages that

PLATE 1. Aspen (top) and spruce (bottom) are the dominant trees in the mixedwood boreal forest. Photo credit: Fiona Schmiegelow.

usually include a change in species composition. Multiple developmental pathways exist for mixedwood stands in mesic areas (Chen and Popadiouk 2002). The state of a stand is expressed from the interaction of stand condition, context, and disturbance history (Chen and Popadiouk 2002, Albani et al. 2005). Trembling aspen is the typical regenerating species in a stand when it is present in the pre-fire landscape (see Plate 1). This is a result of vegetative shoot development from root suckers. White spruce may establish at stand initiation depending on seed source, micro-site conditions, and interspecific competition (Greene et al. 2004, Albani et al. 2005; see Plate 1). White spruce is shade tolerant and will grow in the understory of aspen stands to be released to the overstory as aspen reaches maturity, dies, and provides gaps in the canopy. Through this pathway, stands may burn, regenerate along a successional trajectory with early deciduous dominance and lower probabilities of initiation, and then develop to spruce dominance and higher probabilities of initiation; a ''fire-prone'' white spruce can be seen as growing up in a protective aspen nursery. We must consider that initiation patterns (and fire regimes) change over long time scales (e.g., multiple disturbances) and reflect the intrinsic stochasticity of mixedwood boreal stand development.

The variation of initiation among forest types can be interpreted through variation in quality and quantity of fuels among them. Hély et al. (2000) provide a thorough review of variation in fuel characteristics among stand types similar to those in our study. They suggest that stand fire hazard increased via the quality of surface fuels as a result of species replacement through time. Spruce stands tend to contain more flammable fuel conditions (Van Wagner 1977) such as ladder fuels provided by basal conifer branches (Hély et al. 2000). Accordingly, we found that landscapes with more spruce had higher odds of initiation, and those with more aspen had lower odds. Flannigan and Wotton (1991) suggest the duff layer sheltered under conifers is more flammable in comparison to duff in hardwood stands. Duff moisture content also varies between open and canopy-sheltered areas in conifer stands (M. Wotton, *personal communication*); this suggests that the relative importance of moisture/weather and fuel type is scale dependent.

The decreased odds of initiation associated with recently burned forest may be explained by intense fires leaving lush, young trees or graminoid regeneration after fire. In mesic stands, early regeneration is typically dominated by aspen regardless of the subsequent developmental pathway. In xeric areas, burned jack pine stands typically regenerate to jack pine and aspen, the former as a result of seed release from serotinous cones (Greene et al. 2004). The inclusion of burned forest area in the models accounts for changes in the probability of subsequent initiations in a landscape after a fire and demonstrates age-dependent initiation frequency. The years 1980–1982 (prior to the study period) and 1990 were extreme fire years in the region; roughly 13 660 km^2 of the study area (0.2%) was burned in 1990. The forest composition variable for burned area was not stratified by year-since-burn in our analysis. These stands would vary in age from 1 to 12 years old. Chen and Popadiouk (2002) suggest that lightning strikes themselves would be less frequent in shorter, young stands, but lightning is thought to propagate down randomly from a cloud without influence of objects on the ground until it is 50–100 m above ground, when it chooses its target within a radius of about 100 m (M. Uman, *personal communication*), suggesting that stand age as a function of height did not influence initiation patterns at the landscape scale of our study. The dampening of initiation with burned and deciduous area and increasing initiation with spruce area suggests the probability of initiation increases with stand age as a function of stand composition in the mixedwood boreal. Ignoring these age- (Van Wagner 1978, Boychuk et al. 1997) or species-initiation feedbacks in natural disturbance regimes could result in an incomplete or misleading synthesis of boreal dynamics and the potential influences of forest management.

We detected a quadratic relationship between initiation and black spruce composition, suggesting that initiations were more likely in landscapes with intermediate amounts of black spruce. The relationship reached a maximum when 30% compositional area of the landscape was black spruce dominated. Since black spruce can occupy poorly drained sites, this may reflect regional hydrology such that soil landscapes where black spruce is most abundant are also very moist and less conducive to initiation. It could be argued that soil moisture gradients play a strong role in determining stand composition, so it would be more appropriate to compare the relative influence of two abiotic factors (soil landscapes and weather patterns) on fire initiation. Though this may be true at some spatial scales, the differences in forest composition effects estimated by our analyses were dominated by white spruce and aspen. Either of these species can each be expressed on the same mesic site through a range of development pathways. Because of our coarse scale of analysis, detailed heterogeneity among and within stands or within cover types could not be addressed.

Initiation did not vary with the amount of jack pine in a landscape. This was surprising, since *Pinus* is regarded as fire-adapted genus (Richardson 1998). Jack pine typically grows on rapidly draining soils with dry surface fuels readily flammable in match-ignited field trials (J. Beverly, *personal communication*). Perhaps ignition is successful in dry, fine fuels of a mature jack pine stand's understory, but a dearth of coarse fuel for sustained combustion on the forest floor results in a proportionate initiation frequency. In Alberta, mature pine is considered a ''go, no-go'' fuel type (assuming ladder fuels such as a spruce understory are not present) where fire behavior is considered low except under strong winds (C. Tymstra, *personal communication*). This may be further enhanced through the mixing of pine and aspen in the mixedwood region. Initiation was not sensitive to the amount of open (e.g., muskeg) area in a landscape.

Weather, representing fuel moisture conditions, explained substantial variation in initiation frequency demonstrated by a positive relationship with two JWL indices and SSR. The JWLs represented potential initiation conditions by combining appropriate fuel moisture levels and lightning activity. More variation was described by the JWLs than lightning and weather alone or together. The superior performance of transformed JWLs suggested the relationship with initiation was not additive, but that initiation efficiency decreased at higher values of JWL. This nonadditivity might be an artifact of the binary response data, since we were simply modeling the probability of a single initiation per year per landscape. We expected that weighted JWLs would be better descriptors of initiation than JWLs, since they represented a hypothesis that storms with high lightning density also produced more precipitation and would result in decreased initiation potential. Only one wJWL was selected in the model W_1, and this term dropped out in WF_1 and WF_2. The failure of the wJWLs might reflect a temporal disconnection between lightning and weather data. Weather data were collected at noon, whereas lightning ''days'' were 24 hours in duration from midnight; errors in lightning detection are discussed in *Methods*. The positive relationship with SSR indicated that the regional climate variability among years resulted in a change in initiation probability. The relationship with the JWLs and SSR were demonstrated at a voxel and regional scale, respectively, and together highlighted multi-scale influences of weather conditions on initiation.

Initiation probability increased with elevation despite a negative relationship between elevation and the JWL indices. In contrast, L_{COUNT} and L_{DAYS} increased with elevation, though these lightning indices did not explain sufficient variation to be kept in the WF_1 or WF_2 model. The critical value for creating the JWLs was set at weather conditions where 85% of initiations were recorded, so the range in conditions viable for initiation is not fully represented by the JWL indices. Initiation potential could increase with elevation through the integration of increased lightning activity and appropriate (yet subcritical) fuel moisture codes. We had no evidence for a relationship between elevation and initiation through variation in fuel, since elevation was not correlated with any forest types. Northing (latitude) was a potential proxy for growing-season length or additional unmeasured gradients in climate since fewer initiations were recorded in more northerly landscapes even after accounting for variation in elevation, weather, and forest composition.

Our best model, WF_2, included fixed effects and a random effect for landscape. We examined the spatial distribution of random effects to suggest processes responsible for this stability of initiation within the landscape scale; nothing was apparent. We had detected a stable pattern in cumulative JWLs, but these were structured at a much broader scale than a single landscape and were found to be a direct reflection of elevation. We did not include anthropogenic linear features such as roads and seismic lines, the distribution of mineral deposits, nor metallic structures such as compressor stations or oil and gas wells, which are abundant in the region (Schneider et al. 2003). It would be interesting to determine if these features could be responsible for local, stable variation of initiation or have an indirect influence on natural disturbance patterns in the boreal forest.

Our study is the first conclusive demonstration that variation in fuel type influences initiation patterns in the boreal forest. Though we only address the initiation phase of fire behavior in our study, the ecological consequence implies that variable flammability of species regulates this natural disturbance endogenously. Recent studies have illustrated that the frequency and size of boreal fires are related to vegetation. Bergeron et al. (2004) demonstrated the influence of landscape composition on burn rate in the mixedwood and coniferous boreal forests of northwestern Quebec. The effectiveness of deciduous stands as fire breaks that limit fire size has been proposed in simulation models on Alberta landscapes (Hirsch et al. 2001), and preferential burning of coniferous forest stands has been shown in the compositional analysis of area burned in this same study area (Cumming 2001).

The relationship between fire, weather, and forest composition may vary depending on heterogeneity, study scale, and the component of fire behavior. The boreal forest is circumpolar and its structure varies. We would expect similar patterns to those we identified here in other mixedwood boreal regions such as Saskatchewan, Ontario, and Quebec. Much of the more northerly and mountainous boreal regions are conifer-dominated, and it is difficult to infer how sensitive initiation patterns would be to the decreased heterogeneity in landscape composition found in such regions. Where fuel type is less variable, initiation patterns will likely be more strongly associated with heterogeneity in fuel moisture/weather conditions for any ecosystem. Bessie and Johnson (1995) used data from subalpine conifer stands exhibiting relatively limited heterogeneity and demonstrate that fire behavior was dominated by interannual weather variation rather than variation in fuel. Renkin and Despain (1992) demonstrated how the relationship with forest type varied between initiation and spread in the conifer-dominated region of Yellowstone National Park, and showed that the influence of forest cover type on fire activity decreased under drought conditions. However, we found that in more extreme fire weather years the detected effect of forest composition (amount of white spruce in a landscape) on fire initiation increased, as illustrated through a positive interaction between S_w and SSR. It is possible that climate change may precipitate even more extreme fire weather that could overwhelm any endogenous, biotic regulation of initiation patterns in the mixedwood study region; however, we issue a caveat that changes in forest composition (and heterogeneity) through development, exploration, forestry, and insect outbreaks could also trigger even more pronounced biotically regulated patterns of initiation.

Many existing models of natural disturbance integrate empirically derived stochastic initiation probabilities; however, estimates that allow spatiotemporal variation in environmental characteristics that influence fire initiation are critical to simulation models of ecosystem dynamics (He and Mladenoff 1999), since we (humans) insist on novel and dramatic alterations to our environment. We provide an example that answers a call to develop appropriate empirically based estimates from which to test ecological hypotheses (Yang et al. 2004). The statistical models used in this study provided parameter estimates relating initiation to biotic and abiotic sources; in this system these are endogenous and exogenous regulators to natural disturbance, respectively. Our study illustrates methods and results to enhance our understanding of weather–vegetation–disturbance interactions in boreal forest ecosystems and a framework to generate hypotheses about the integrated effects of ongoing changes in land cover, climate, and natural disturbance to ecosystem dynamics.

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APPENDIX A

A map of the study region showing the resolution and extent of data used for analyses (*Ecological Archives* E087-024-A1).

APPENDIX B

A summary table of variables used in logistic regression models (*Ecological Archives* E087-024-A2).

APPENDIX C

A table of results from the validation of fire weather index interpolations (*Ecological Archives* E087-024-A3).

APPENDIX D

A figure illustrating the intercorrelation and distribution of six study variables (*Ecological Archives* A087-024-A4).

APPENDIX E

A figure illustrating the increased effect of forest composition in years with more extreme fire weather (*Ecological Archives* E087-024-A5).