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Regional outbreak dynamics of *Dothistroma* needle blight linked to weather patterns in British Columbia, Canada

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Abstract: *Dothistroma* needle blight (DNB) has caused extensive mortality in plantations of lodgepole pine in northwestern British Columbia, Canada, and even mature pine trees in natural forests are succumbing. We examined a number of explanatory models to determine which temperature or precipitation variable is most important in explaining DNB outbreak occurrence. We compared a multicentury tree-ring outbreak reconstruction with mean monthly temperature and total monthly precipitation during the individual and seasonal spring (April, May, June) and summer (July, August, September) months. A trend towards increased August minimum temperatures appears to be an important climate factor contributing to the spread of the disease. Graphical comparisons of total April precipitation reveal that periods of above-average precipitation coincided with periods of outbreak increase. Decreases in August minimum temperature also correspond to decreases in outbreak severity. Even more pronounced was a spike in spring precipitation and its association with the current epidemic. The correspondence of past outbreaks with periods of wet and warm conditions suggests that regional climate trends drive DNB behavior. The extent and severity of the current disease epidemic raises the possibility that the key factors that drive outbreaks have become more frequent, enabling the emergence of DNB as a serious disease.

Key words: *Dothistroma* needle blight, climate change, dendrochronology, disease emergence, British Columbia.

Résumé : La brûlure en bandes rouges des aiguilles a causé beaucoup de mortalité dans les plantations de pin tordu latifolié du nord-ouest de la Colombie-Britannique, au Canada; il y a même des pins matures qui meurent dans les forêts naturelles. Nous avons examiné plusieurs modèles explicatifs pour déterminer quelle variable de température ou de précipitation est la plus importante pour expliquer le déclenchement des épidémies de brûlure. Nous avons comparé une reconstitution dendro-chronologique des épidémies sur plusieurs siècles avec la température mensuelle moyenne et la précipitation mensuelle totale durant chaque mois de printemps (avril, mai, juin) et d'été (juillet, août, septembre) et durant chacune de ces saisons. Une tendance à l'augmentation des températures minimum au mois d'août semble être un facteur climatique important qui favorise la propagation de la maladie. Des comparaisons graphiques de la précipitation totale du mois d'avril révèlent que les périodes durant lesquelles la précipitation est supérieure à la moyenne coïncident avec les périodes durant lesquelles il y a une augmentation des épidémies. Les diminutions de la température minimum du mois d'août correspondent aussi à des diminutions de la sévérité des épidémies. L'association entre une augmentation des précipitations printanières et l'épidémie actuelle était encore plus prononcée. La correspondance des épidémies passées avec des périodes caractérisées par des conditions chaudes et humides indique que les tendances du climat régional déterminent le comportement de la brûlure. L'étendue et la sévérité de l'épidémie actuelle de la maladie soulève la possibilité que les facteurs déterminants responsables des épidémies soient devenus plus fréquents faisant de la brûlure des aiguilles une maladie importante. [Traduit par la Rédaction]

Mots-clés : brûlure en bandes rouges des aiguilles, changements climatiques, dendrochronologie, apparition de maladies, Colombie-Britannique.

Introduction

Dothistroma needle blight (DNB) has a long history in the northern temperate forests of British Columbia (BC). Recent work using tree-ring analysis identified probable DNB outbreaks in northwestern BC, Canada, occurring as early as the 1830s (Welsh et al. 2009). DNB has been well studied as an introduced pathogen in the Southern Hemisphere responsible for widespread damage to exotic pines (Harrington and Wingfield 1998; Barnes et al. 2004). The fungus responsible for the disease, *Dothistroma septosporum* (Dorog.) Morelet, infects the needles, causing necrotic lesions and premature needle drop (Bradshaw et al. 1997). Damage to native species has normally been limited to a reduction in annual growth approximately proportional to the severity of defoliation (Gibson

1972; Ades et al. 1992). During the past decade, however, the prevalence of the disease and the severity of damage appear to have increased (Woods et al. 2005; Bradshaw 2004). Severe damage to managed and natural stands of lodgepole pine in northwestern BC has been reported (Woods et al. 2005). The situation in BC is unique, because unlike plantations of exotic pines in the Southern Hemisphere, the host lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) is a native species. The equal frequency of mating types and genetic patterns found in the study area also provides evidence of an endemic pathogen population (Dale et al. 2011). The ability of the pathogen to cause mortality in natural stands of mature trees, as well as in plantations, is an unprecedented phenomenon, and it has been suggested that this recent

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emergence may be linked to global climate change (Woods et al. 2005; Welsh et al. 2009).

Since the mid- to late-1990s, a trend towards increased summer precipitation and, more specifically, warm rain events has been recorded in northwestern BC. Woods et al. (2005) found a clear spatial correlation between areas subjected to increased mean summer precipitation and the area affected by the current epidemic. They also found that spikes in warm rain events that occurred in the early 1960s and 1980s corresponded to the timing of the first published record of the disease in the area (Parker and Collis 1966) and a 1984 outbreak identified by the Forest Insect and Disease Survey (FIDS) report. These precipitation events have increased markedly from earlier decades and appear to be due to directional climate change rather than influence of the Pacific Decadal Oscillation (Woods et al. 2005). A regional tree-ring reconstruction has shown that DNB has had a long history in northwestern BC and has persisted at low levels in the area, with a recent increase in outbreak spread (defined as disease intensification within the known study area) and severity since the mid-1990s (Welsh et al. 2009). It appears probable that the recent emergence of *Dothistroma*, given the broad-scale spatial synchrony of the outbreak (Welsh et al. 2009), is due to a deviation from average weather conditions consistent with climate-driven change in the area.

The causal agent of DNB belongs to the group of Ascomycete fungi. *Dothistroma septosporum* reproduces by both sexual (ascospores) and asexual (conidiospores) spores, with conidia reported as the dominant state of the pathogen (Gibson 1972). In a study from Nebraska, the first splash-dispersed conidiospores were released in the spring (Peterson 1973), and under conditions of prolonged leaf wetness and temperatures above 5 °C, spores were released for up to seven months (Sinclair et al. 1987). In northwestern BC, where severe damage from DNB has been recorded, dispersal of conidia began in early to mid-June and ceased in mid-September (Boateng 2011). Infection can occur over a wide range of temperatures, but the severity of infection remains low except at warm temperatures (15–20 °C) under continuous moisture regimes (Peterson 1967; Gadgil 1974). In BC, where the sexual stage has been observed and where sexual reproduction occurs regularly in the pathogen population (Dale et al. 2011), ascospore production occurs in early June and continues for approximately one month (Funk and Parker 1966). The severity of infection by *D. septosporum* is thus highly sensitive to yearly differences in weather (Peterson 1973). Rapid development of outbreaks can occur during periods of prolonged wet weather during the growing season (Harrington and Wingfield 1998).

It is predicted that impending climate changes are likely to increase the risk of forest diseases (Coakley 1995; Chakraborty et al. 1998; Coakley et al. 1999). Tree species most vulnerable to damage may be those in which the associated pathogens are at low disease levels because of unfavourable climate conditions (Coakley et al. 1999; Woods et al. 2005). Woods et al. (2005) have emphasized the importance of climate change in the form of increased summer precipitation on the current DNB epidemic in northwestern BC. The objectives of this research were to document the relationship between historic DNB outbreaks and climate variables conducive to disease spread and severity and relate these to observed regional outbreak patterns. In this study, multicentury tree-ring reconstructions of DNB outbreaks were compared with the longest available temperature and precipitation records to investigate the influence of climate on outbreak occurrence. We considered a number of biological models to provide insight into which temperature or precipitation variable is most important in explaining DNB outbreak occurrence. We also examined the influence of time-lagged responses to assess delay in outbreak occurrence. It is possible that favourable weather patterns in previous years determine when an outbreak occurs. It is hoped that these findings could provide an opportunity to better

understand the likely responses of DNB to climate change in northwestern BC.

Materials and methods

Historical reconstructions of DNB outbreaks

A previously reconstructed tree ring based regional chronology of historical DNB outbreaks developed for northwestern BC (Welsh et al. 2009) was used for our comparisons with local climate records. This regional outbreak chronology was developed from specific criteria based on the timing, duration, and magnitude of the ring width reductions using tree-ring series from sites with documented outbreaks. FIDS reports and Canadian Forest Service (CFS) herbarium collection records were used to locate sites where past occurrences of DNB had been recorded. Six sites with sufficient location (i.e., road kilometre or UTM, etc.) information were identified, four in northwestern BC and two in central-interior BC. Increment cores were collected (at 0.3 m) from both host lodgepole pine and non-host Roche spruce (*Picea glauca* (Moench) Voss × *sitchensis* (Bong.) Carrière) or hybrid white spruce (*Picea glauca* (Moench) Voss × *engelmannii* Parry ex Engelm.) trees at each site. All cores were processed according to the methods of Stokes and Smiley (1968). Annual ring widths were measured using the Velmex "TA" System in conjunction with MeasureJ2X, crossdated using COFECHA (Holmes 1983), and standardized using ARSTAN version 40 (Cook and Holmes 1984). A host – non-host correction procedure was performed to separate the observed reduced growth in the host due to disease from climate variations (Swetnam et al. 1985). The resulting growth reductions associated with the documented outbreak periods were quantified and used to calibrate the software program OUTBREAK (Holmes and Swetnam 1996).

The resulting criteria were applied simultaneously to identify probable prerecord outbreak periods at 16 individual sites. Outbreaks in the regional series were based on criteria in which more than 40% of host trees in each site had to show a specific reduction pattern identified by the program OUTBREAK to be included as an outbreak in a given year. A regional time series was developed by summing the number of trees recording an outbreak as defined by the statistical criteria and the 40% threshold for each year across all sites. The regional time series was then standardized by computing the percentage of trees recording an outbreak each year. The regional outbreak chronology indicated periodic outbreak events since 1831 (total chronology length AD 1771 to AD 2004). Refer to Welsh et al. (2009) for more details.

Climate records

Weather records for northwestern BC were limited. Although a number of weather stations were established in the area, few records extended the necessary length for meaningful analysis. Climate data extracted from archives of daily weather records for Fort St. James, BC (Environment Canada 2011), provide the longest climate record for north-central BC. Climate records at the Fort St. James station are considered representative of broad-scale regional climate variability in our immediate study area (i.e., northwestern BC) (Woods et al. 2005). Temperature records at the Fort St. James weather station extend from 1896 to 2010, but because of missing data, precipitation records were shorter, extending from 1900 to 2010. As the outbreak chronology only extended to 2004, the precipitation and temperature data were truncated accordingly.

Modeling selection: analysis of climate and outbreak history

The climate variables were screened for collinearity using Pearson correlations. Correlations in which $r > 0.60$ were deemed to be collinear. Collinear variables were included separately in a Spearman's rank-order correlation analysis with the outbreak chronology. The correlate with the higher coefficient was retained for

Table 1. Model equations used to examine the influence of selected climate variables on the *Dothistroma* needle blight (DNB) outbreak chronology.

Model scenarios	Equations
Global model	APRP + MAYP + JUNP + JULP + AUGP + SEPP + APRT + MAYT + JUNT + JULT + AUGT + SEPT + AUGTmin
(*i*) DNB outbreak chronology is influenced by present monthly total precipitation (8 models)	APRP ($t - 0$) + MAYP ($t - 0$) + JUNP ($t - 0$) JULP ($t - 0$) + AUGP ($t - 0$) + SEPP ($t - 0$)
	APRP ($t - 0$)
	MAYP ($t - 0$)
	JUNP ($t - 0$)
	JULP ($t - 0$)
	AUGP ($t - 0$)
	SEPP ($t - 0$)
(*ii*) DNB outbreak chronology is influenced by 1-year past monthly total precipitation (8 models)	APRP ($t - 1$) + MAYP ($t - 1$) + JUNP ($t - 1$)
	APRP ($t - 1$)
	MAYP ($t - 1$)
	JUNP ($t - 1$)
	JULP ($t - 1$)
	AUGP ($t - 1$)
	SEPP ($t - 1$)
(*iii*) DNB outbreak chronology is influenced by 2-year past monthly total precipitation (8 models)	APRP ($t - 2$) + MAYP ($t - 2$) + JUNP ($t - 2$) JULP ($t - 2$) + AUGP ($t - 2$) + SEPP ($t - 2$)
	APRP ($t - 2$)
	MAYP ($t - 2$)
	JUNP ($t - 2$)
	JULP ($t - 2$)
	AUGP ($t - 2$)
	SEPP ($t - 2$)
(*iv*) DNB outbreak chronology is influenced by present monthly mean temperature (3 models)	AUGTmin ($t - 0$)
	APRT ($t - 0$) + MAYT ($t - 0$) + JUNT ($t - 0$)
	JULT ($t - 0$) + AUGT ($t - 0$) + SEPT ($t - 0$)
(*v*) DNB outbreak chronology is influenced by 1-year past monthly mean temperature (3 models)	AUGT min ($t - 1$)
	APRT ($t - 1$) + MAYT ($t - 1$) + JUNT ($t - 1$)
	JULT ($t - 1$) + AUGT ($t - 1$) + SEPT ($t - 1$)
(*vi*) DNB outbreak chronology is influenced by 2-year past monthly mean temperature (3 models)	AUGTmin ($t - 2$)
	APRT ($t - 2$) + MAYT ($t - 2$) + JUNT ($t - 2$)
	JULT ($t - 2$) + AUGT ($t - 2$) + SEPT ($t - 2$)

Note: Individual months are denoted by the first three letters in their name; P, precipitation; T, temperature; Tmin, minimum temperature. Time lags for climate variables are indicated as follows: $t - 0$, no lag (or present); $t - 1$, 1-year lag; and $t - 2$, 2-year lag.

further use in our analysis. The remaining variables were used to construct a global model (i.e., heavily parameterized model) that contained noncorrelated variables. For our candidate set, correlated variables were included separately in identical, but mutually exclusive, models. Multinomial logistic regression was used to assess model fitting of our global and candidate sets of models.

We used the information-theoretic approach of model selection to evaluate several models and scenarios (Burnham and Anderson 1998). A suite of biologically relevant models were developed a priori from climate variables to develop inferences concerning climate patterns affecting DNB outbreak occurrence (Table 1). The influence of past and present climate conditions was incorporated in the analysis to test the existence of time lags in the outbreak chronology.

To identify the best model for each climate and time-lag scenario, we used the Akaike information criterion (AIC; Burnham and Anderson 2002) with the small sample correction (AIC$_c$) proposed by Hurvich and Tsai (1989), which generates a rank of the models according to their support of the data. The lowest AIC or AIC$_c$ value in a model set indicates the model that achieves the best parsimony or trade-off between bias in the number of parameters (K) and amount of variance captured in the model. We then calculated the delta AIC$_c$ (ΔAIC$_c$) and Akaike weights (*w*AIC$_c$) to provide a probability measure of the strength of evidence for each model. As a rule of thumb, a ΔAIC$_c$ < 2 suggests substantial support for the model, values between 3 and 7 indicate that the model

has considerably less support, and ΔAIC$_c$ > 10 indicates that the model is very unlikely (Burnham and Anderson 2002). The *w*AIC$_c$ was used to choose the best model by providing an estimate of the relative probability that the top model was the best from the suite of proposed models. The *w*AIC$_c$ in a model set sum to one and provide a measure of the weight of evidence in favour of one model over the others (Burnham and Anderson 2002). Inferences were only made using best models with *w*AIC$_c$ ≥ 0.95. The predictive strength of the best models in each climate and time-lag scenario was compared to determine the best overall fit to the data. We then graphically compared the best temperature and precipitation models to determine whether temporal changes in outbreak occurrence were related to favourable climate variations.

Model inputs

We evaluated specific a priori combinations of biologically relevant climate variables based on previous work (e.g., Peterson 1967; Gibson 1972; Parker 1972; Gadgil 1977; Boateng 2011). We considered precipitation, humidity, and temperature to be the most important climatic factors in relation to disease occurrence. Relative humidity data were not available for our study area; therefore, for our modeling approach, we used only monthly mean temperature and monthly total precipitation during spring (April, May, June) and summer (July, August, September) as variables in our analysis.

Table 2. Regression models of *Dothistroma* needle blight (DNB) outbreak occurrence explained by climate variables at different time lags.

Variables	K	n	AIC$_c$[a]	ΔAIC$_c$[b]	wAIC$_c$[c]	Predictive strength (%)
(*i*) Present precipitation						
APRP ($t - 0$)	8	105	291.387	0.000	0.969	35.20
JULP ($t - 0$)	8	105	298.500	7.113	0.028	—
SEPP ($t - 0$)	8	105	304.663	13.276	0.001	—
MAYP ($t - 0$)	8	105	305.093	13.706	0.001	—
AUGP ($t - 0$)	8	105	305.776	14.389	0.001	—
JUNP ($t - 0$)	8	105	306.172	14.785	0.001	—
JULP ($t - 0$) + AUGP ($t - 0$) + SEPP ($t - 0$)	16	105	313.056	21.669	0.000	—
APRP ($t - 0$) + MAYP ($t - 0$) + JUNP ($t - 0$)	16	105	324.102	32.715	0.000	—
Global model ($t - 0$)	52	105	419.277	127.890	0.000	—
(*ii*) 1-year past precipitation						
APRP ($t - 1$)	8	104	289.403	0.000	0.956	34.60
MAYP ($t - 1$)	8	104	296.460	7.057	0.028	—
JULP ($t - 1$)	8	104	299.453	10.050	0.006	—
SEPP ($t - 1$)	8	104	299.700	10.297	0.006	—
JUNP ($t - 1$)	8	104	300.944	11.541	0.003	—
AUGP ($t - 1$)	8	104	303.793	14.390	0.001	—
JULP ($t - 1$) + AUGP ($t - 1$) + SEPP ($t - 1$)	16	104	316.701	27.298	0.000	—
APRP ($t - 1$) + MAYP ($t - 1$) + JUNP ($t - 1$)	16	104	321.875	32.472	0.000	—
Global model ($t - 1$)	52	105	423.976	134.573	0.000	—
(*iii*) 2-year past precipitation						
APRP ($t - 2$)	8	107	288.847	0.000	0.830	—
MAYP ($t - 2$)	8	107	292.261	3.414	0.150	—
JULP ($t - 2$)	8	107	296.959	8.112	0.014	—
SEPP ($t - 2$)	8	107	299.214	10.367	0.005	—
AUGP ($t - 2$)	8	107	303.151	14.304	0.001	—
JUNP ($t - 2$)	8	107	304.389	15.542	0.000	—
JULP ($t - 2$) + AUGP ($t - 2$) + SEPP ($t - 2$)	16	107	317.925	29.078	0.000	—
APRP ($t - 2$) + MAYP ($t - 2$) + JUNP ($t - 2$)	16	107	323.027	34.180	0.000	—
Global model ($t - 2$)	52	105	427.239	138.392	0.000	—
(*iv*) Present temperature						
AUGTmin ($t - 0$)	8	108	229.795	0.000	1.000	46.80
APRT ($t - 0$) + MAYT ($t - 0$) + JUNT ($t - 0$)	16	108	299.183	69.388	0.000	—
JULT ($t - 0$) + AUGT ($t - 0$) + SEPT ($t - 0$)	16	108	305.151	75.356	0.000	—
Global model ($t - 0$)	52	105	419.277	189.482	0.000	—
(*v*) 1-year past temperature						
AUGTmin (t-1)	8	104	289.403	0.000	1.000	47.20
JULT ($t - 1$) + AUGT ($t - 1$) + SEPT ($t - 1$)	16	104	294.701	5.298084	0.000	—
APRT ($t - 1$) + MAYT ($t - 1$) + JUNT ($t - 1$)	16	104	321.875	32.47208	0.000	—
Global model ($t - 1$)	52	105	423.976	134.5732	0.000	—
(*vi*) 2-year past temperature						
AUGTmin ($t - 2$)	8	107	214.987	0.000	1.000	47.70
JULT ($t - 2$) + AUGT ($t - 2$) + SEPT ($t - 2$)	16	107	291.931	76.944	0.000	—
APRT ($t - 2$) + MAYT ($t - 2$) + JUNT ($t - 2$)	16	107	323.033	108.046	0.000	—
Global model ($t - 2$)	52	105	427.239	212.252	0.000	—

Note: Models were ranked from best to worst for each scenario according to the Akaike information criterion weights (wAIC$_c$). K indicates the number of model parameters, and n indicates the number of observations in the model. Individual months are denoted by the first three letters in their name; P, precipitation; T, temperature; Tmin, minimum temperature. Time lags: $t - 0$, no lag (or present); $t - 1$, 1-year lag; and $t - 2$, 2-year lag.

[a]AIC$_c$ is the second-order AIC or small sample size bias correction term for AIC.

[b]ΔAIC$_c$ is the difference between the AIC$_c$ of a given model and the model with the lowest AIC$_c$ value.

[c]wAIC$_c$ represents the ratio of the delta AIC of a given model relative to the whole set of candidate models.

Monthly mean seasonal (spring, summer) temperature and monthly total seasonal (spring, summer) precipitation were used to test the cumulative effects of seasonal climate. We also chose models that included individual monthly climate variables to account for the importance of short-term, warm rain events during disease development. A previous exploratory study indicated that the variation in our outbreak reconstruction had a significant association with August minimum temperature (Welsh 2007); therefore, we included it in our modeling approach.

The outbreak response variable was transformed from a proportional dataset into a polytomous outcome variable representing five different categories of outbreak occurrences: 0%, <10%, ≥10 to <20%, ≥20 to <40%, and ≥40% outbreak occurrence. The transformation of our outbreak data was performed to meet the requirements of our model testing approach.

Results

The set of climate variables produced by the collinearity screening process was used to parameterize the global model. As expected, August minimum temperatures and mean August temperatures were highly correlated ($r = 0.778$). The rank order relationship was higher for August minimum temperatures (data not shown) and was retained in the global model and for further analysis. No climate variables in our candidate models were correlated.

The resulting models showed that outbreak periods were associated with wet and warm episodes. August minimum temperatures were consistently selected as the best model for each time-lag scenario (Table 2; wAIC$_c$ = 1.000). The 2-year previous time-lag scenario for the August minimum temperatures model had the highest predictive strength compared with the other

Fig. 1. Comparison of total April precipitation (mm) (AD 1900–2005) with *Dothistroma* needle blight outbreak periods (vertical bars). The horizontal line indicates the mean of the climate variable. The yearly weather records are represented by the gray line. A 10-year spline was added to help visualize trends (black line).
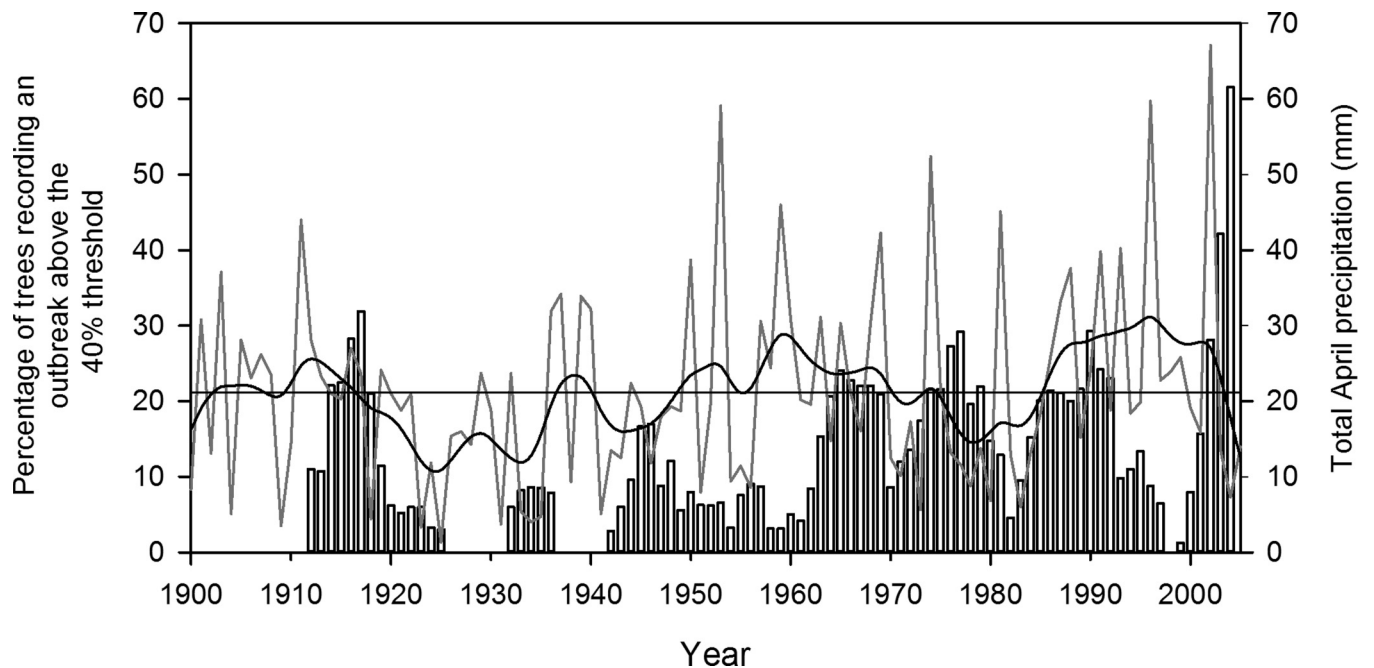
models (i.e., 47.7%). However, the predictive strength compared with the other August time-lag scenarios does not differ greatly. Among the precipitation models, total April precipitation was selected as the best model in both the present (wAIC$_c$ = 0.969) and 1-year past (wAIC$_c$ = 0.956) time-lag scenarios. Precipitation models for the 2-year past time-lag scenario did not reach the wAIC$_c$ ≥ 0.95 criteria and were therefore removed from further inference. Overall, present total April precipitation had the best AIC results among the candidate precipitation models and the best predictive strength compared with the other time-lag precipitation models (i.e., 35.2%).

Graphical comparisons revealed an increase in the magnitude of yearly spikes in total April precipitation over the last 50 years (Fig. 1). Prior to the 1950s, April precipitation levels typically remained below the long-term average. This increase in wet spring weather appears to coincide with a period of sustained disease presence in the study area (starting in 1942). It is also apparent that there has been an increasing trend in April precipitation levels from the mid-1980s to the late-1990s, which corresponds to the timing of the most recent outbreak. In 2002, a peak in April precipitation that reached previously unrecorded levels coincided with the recent epidemic. A decrease in outbreak levels occurred during a period of high precipitation levels in the late 1990s.

The climate records indicate that there has been a clear increasing trend in August minimum temperature throughout the record period (Fig. 2). We examined graphical comparisons by using 2-year previous August minimum temperature, which showed that the regional outbreak series was generally in phase with August minimum temperature cycles. More specifically, increases in 2-year previous August minimum temperature in the 1960s, 1970s, and 1990s corresponded to peaks in outbreak levels in the regional chronology. In addition, outbreak peaks in the late 1910s were also associated with increases in August minimum temperature. Decreases in minimum temperature values were also often accompanied by decreases in outbreak levels. No outbreak was associated with an increase in August minimum temperatures during the 1920s.

Discussion

Our results suggest that DNB is limited by spring precipitation and low summer minimum temperature cycles. Comparisons of climate and the regional outbreak series show that significant DNB outbreak events in northwestern BC were in phase with 2-year previous August minimum temperature cycles but were temporally variable. We found that although outbreak events were not strongly related to increases in precipitation levels, outbreak events occurred during periods of greater precipitation during the month of April. Decreases in August minimum temperature levels were also accompanied by a collapse in the individual outbreak periods.

Yearly differences in weather are known to result in considerable yearly variations in the amount of infection by *D. septosporum* (Peterson 1973). The first splash-dispersed conidiospores of the fungus are released in the spring and can continue to be released throughout the year, provided that temperatures are above 5 °C and moisture is continually present (Sinclair et al. 1987). In eastern Nebraska, conidia of DNB have been found on stromata (fruiting bodies) on needles of Austrian (*Pinus nigra* Arnold) and ponderosa pine (*Pinus ponderosa* Laws.) as early as April, with first release occurring early in May (Peterson 1973). In the same study, spore counts showed that the majority of conidia were released during periods of rain or heavy mist, even when there had been a heavy dispersal only 1 or 2 days earlier. Marks et al. (1989) also found that the amount of defoliation increased to 75% of the tree's foliage in several plantations after 10 months of very wet weather. The temporal patterns of DNB spore production and dispersal in northwestern BC have been known to occur between June and mid-September, with peak periods of spore production during the months of July and August (Boateng 2011; Braun 2009). Woods et al. (2005) found a strong spatial correlation between the frequency of warm rain events and the area affected by the current epidemic in northwestern BC. Spikes in summer precipitation levels were also shown to correspond to the 1960s and 1980s documented outbreaks in the area. These observations support our findings that periods of increased spring precipitation were accompanied by increases in the extent and severity of outbreaks of

Fig. 2. Comparison of 2-year past August minimum temperature (°C) (AD 1986–2004) with *Dothistroma* needle blight outbreak periods (vertical bars). The horizontal line indicates the mean of the climate variable. The yearly weather records are represented by the gray line. A 10-year spline was added to help visualize trends (black line).
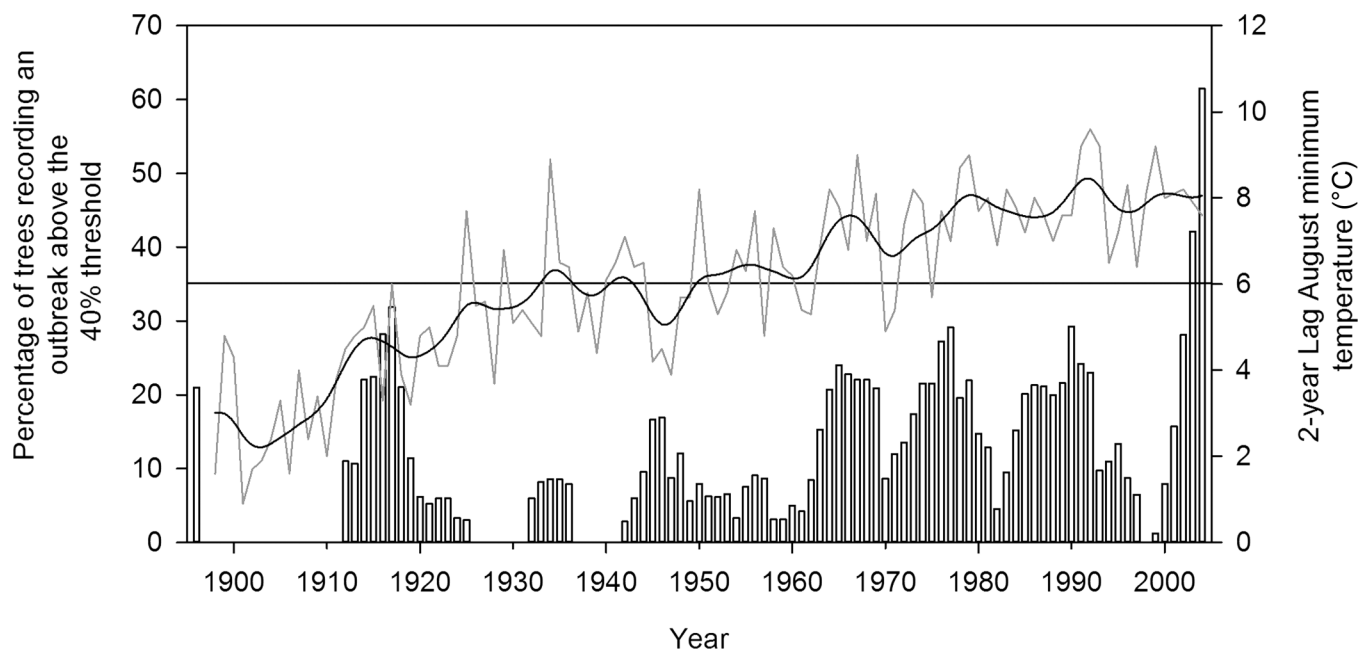
DNB in the regional chronology. Our results may also suggest that the influence of early spring precipitation (specifically, total April precipitation) may have more of an influence on disease development than previously documented. Because precipitation has an important influence on the amount of disease, it seems likely that increases in spring precipitation in the form of rainfall could have played a role in the observed increases in the historical outbreaks. This relationship has been exemplified over the last ~50 years, where peaks in spring precipitation were higher and the frequency of outbreaks increased.

A number of microclimate conditions such as temperature, relative humidity, and precipitation play an important role in DNB infection. In this study, we used a priori knowledge to select variables with biological relevance to DNB disease development. Leaf wetness is the most common indicator used to determine the severity of DNB infection in laboratory experiments. For instance, Gadgil (1977) examined *D. septosporum* infection severity under different leaf wetness periods and found that stromata development decreased substantially under short leaf wetness periods of up to 8 h interspersed with 24 h dry periods. This suggests that a relatively brief drying period could slow disease development and result in little infection. This could explain the period of low outbreak levels during seemingly high, mean spring precipitation levels during the late 1990s or suggest that other unidentified environmental factors have an influence on DNB. In a study on symptom development and weather in the same area as our study, Braun (2009) found that in 7-day mixed-effects models, nightly minimum temperatures above 10 °C, daily relative humidity above 70%, and daily leaf wetness above 40% significantly influenced development of red bands. For fruiting body development, daily minimum temperatures above 6 °C and 7 °C, relative humidity above 90%, and leaf wetness above 30% were the most influential. Clearly, factors other than precipitation alone help determine whether an outbreak can occur but can be considered a good indicator of the amount of infection to be expected. Woods et al. (2005) found that peaks in mean summer precipitation that occurred in the early 1960s and 1980s corresponded to the timing of the first published record of DNB in BC in 1963 and the 1984–1986 outbreak observed by the FIDS surveyors. Our comparisons of total April precipitation with the regional out-

break chronology support these findings that warm rain events influence disease development. During the mid-1950s, spring precipitation levels reached a record high and were later followed by an increase in the frequency of rain events above the long-term average during the 1960s through to the early 1980s. It is apparent that these events were accompanied by an increase in DNB activity. One can expect that this increase in precipitation events may have resulted in conditions favourable for large amounts of infection (Peterson 1973; Marks et al. 1989). We suggest that successive years of increased precipitation are one of the principle causes of the initial increase in the severity of DNB in the study area.

Temperature is also an important factor influencing the occurrence and development of disease. Boateng (2011) found a negative correlation between mean daily temperature and sporulation in DNB. Warm daily temperatures may contribute to the maturation of spores, but those conditions are considered unfavourable to spore release and dispersal (Boateng 2011). However, in this study, the trend towards increased summer minimum temperatures appears to be the most important climate factor contributing to outbreaks of the disease. Since the 1950s, the magnitude of peaks in August minimum temperatures has increased (Fig. 2). For instance, peaks in August minimum temperature have increased ~2 °C compared with temperature values prior to the 1950s. The level of disease since that time has not subsided to levels below the 40% threshold, and peaks in outbreaks appear to coincide with peaks in August minimum temperature. We speculate that increases in August minimum temperature approximate cloud cover, influencing nighttime humidity levels. The increase in humidity levels is known to have a significant effect on the biology of the pathogen (Braun 2009; Boateng 2011). Extended periods of high humidity levels may increase the amount of inoculum and infection late into the summer. As the disease and amount of inoculum increase, inoculum could spread to adjacent areas. It appears probable that higher August minimum temperatures, through the influence on nighttime humidity levels, have contributed to the development of the disease epidemic in northwestern BC.

Although the predictive power of the 2-year previous August minimum temperature model did not greatly differ from the other time-lag scenarios, it was the more superior model. The

stronger relationship with the 2-year previous August minimum temperature model could suggest that DNB disease development in BC may be influenced by long-term changes in climate. Warm nighttime temperatures may extend the length of spore dispersal and spore production stages contributing to higher disease severity in successive years. Overall, temporal patterns in disease development are difficult to interpret as an explanation of lagged responses. Alternatively, the lag effect could have more to do with the nature of the tree-ring data. For instance, defoliation caused by DNB in any one year may have a lagged forcing on tree growth in subsequent years. The undesirable offshoot of this is that ring widths following years of high defoliation may not be synchronous with current infection levels. Therefore, we suggest that the observed lag effect could have more to do with the response of the trees to defoliation rather than a result of prereproduction factors of the pathogen. However, more research is necessary to fully understand whether lag responses are a result of DNB development factors or host-tree response.

Large-scale spatial synchrony of population dynamics is often attributable to deviations from average weather conditions that tend to extend over large geographical areas (Liebhold et al. 2006). In this study, periods of increased spring precipitation and 2-year previous August minimum temperatures were accompanied by increases in outbreak levels across the study area. More specifically, increases and decreases in the precipitation and temperature variables tended to occur simultaneously with the increases and collapse of outbreak levels. The correspondence of outbreaks with periods of wet and warmer conditions in our study area and, in particular, the increasing directional trend in overnight minimum temperature in August suggest that a climate change might be influencing the synchronicity of DNB on a regional scale. We suggest that for DNB outbreaks to be synchronized among the sampled sites, specific weather events must be present during specific stages of disease development. It is possible that wet summers in combination with warmer minimum temperatures extend the length of the infection period and could represent a common trigger for outbreak events.

Global circulation models (GCMs) suggest that increases in temperature are likely to be similar for daily maximum and minimum values, except where there are changes in rainfall and cloudiness (Chakraborty et al. 1998). Wetter, cloudier conditions lead to a greater increase in minimum temperature, whereas drier, clearer conditions produce a greater increase in maximum temperature (Chakraborty et al. 1998). This may explain why warmer minimum temperatures accompanied increases in precipitation in northwestern BC. Mechanisms of temperature and moisture control over DNB have been identified (Peterson 1973; Gadgil 1974). Through coupling this knowledge with downscaled GCM projections for BC, it appears probable that climate change may have more serious implications for the future extent of DNB in the province. Hamann and Wang (2006) predict that the northern portion of the current Sub-boreal Spruce (SBS) zone in central BC will experience a shift in climatic conditions to more closely resemble the Interior Cedar Hemlock (ICH) zone by 2025. As the current epidemic is largely concentrated in the ICH zone, this projection presents a concern for the SBS zone where pine is a dominant species. If this change in climate occurs in the SBS zone, lodgepole pine forests could be severely impacted by the associated foliar disease.

DNB has a long history of coexistence with lodgepole pine in northwestern BC (Funk and Parker 1966; Woods et al. 2005; Welsh et al. 2009). Regular outbreaks have recurred in the forests for at least the past 174 years (Welsh et al. 2009). Relationships between climate and reconstructed DNB outbreaks over the past ~100 years indicate that outbreaks prior to the 1950s were restricted by unfavourable climate conditions (i.e., low precipitation levels). These findings support survey records suggesting that, until recently, outbreaks of DNB have been uncommon and of little concern in these forests (Woods et al. 2005). Since the 1950s, summer precipitation levels have increased to previously unrecorded levels along with increases in August minimum temperatures. It appears that this climatic change has created conditions favourable for DNB to reach epidemic levels.

Conclusion

Our climate and outbreak comparisons indicated that increases in spring precipitation coincided with increases in the extent and severity of outbreaks. Because precipitation has an important influence on the amount of disease, it seems likely that increases in spring rainfall played a role in the increased severity of the historical outbreak periods. Woods et al. (2005) emphasized the importance of climate change in the form of increased summer precipitation on the current epidemic. Our results clearly indicate that an increase in disease severity and spread during the current outbreak coincided with recorded precipitation levels.

The trend towards increased minimum temperatures appears, however, to be the most important climate factor contributing to outbreaks of the disease; peaks in the outbreaks generally coincide with peaks in 2-year previous August minimum temperature. It also appears that peaks in these warm periods often correspond to increases in spring precipitation levels, and both show an increasing trend over the last ~50 years. This suggests that climate in northwestern BC has become increasingly warmer and wetter. The correspondence of outbreaks with periods of wet and warm conditions in our study area suggests that regional climate is becoming more favourable for DNB, resulting in widespread, synchronous outbreaks. This has serious implications for the spread of disease into new areas as climate change creates conditions that are more favourable for disease development. Lodgepole pine forests could be severely impacted on a wider geographical scale.

We have demonstrated that outbreaks of DNB over the last ~100 years in northwestern BC are generally in phase with April precipitation and August minimum temperature cycles. Woods et al. (2005) suggests that past outbreaks of DNB had not reached epidemic levels because of periods of unfavourable climatic conditions for the pathogen. It is apparent that decreases in the precipitation and temperature events coincided with decreases in past outbreak events. During the recent epidemic, however, precipitation levels reached record levels and it is unlikely that the disease will subside without a substantial decrease in the frequency of warm rain events occurring in the study area.

Acknowledgements

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