The outbreak history of Dothistroma needle blight: an emerging forest disease in northwestern British Columbia, Canada

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Abstract: Native pathogens are normally limited in the damage they cause by host resistance and (or) environmental conditions that limit one or more phases of the disease cycle. Changes to host or environmental conditions can relax these limits and result in disease emergence. Until recently, Dothistroma needle blight (Dothistroma), caused by *Dothistroma septosporum* (Dorog.) Morelet, has had only minor impacts on native forest trees in western North America. Over the past decade in the forests of northwestern British Columbia, Canada, Dothistroma has caused extensive mortality in managed plantations of lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.), and even mature pine trees are succumbing. We used dendrochronological techniques to reconstruct the temporal patterns of past Dothistroma outbreaks in the area using tree-ring series from sites with documented outbreaks. We found that Dothistroma outbreaks in northwest British Columbia have occurred periodically over the last 174 years, with an increase in outbreak incidence and extent since the 1940s. The most distinct change observed in the outbreak history has been the greater severity and synchrony among the sites affected during the current outbreak. A recently observed climate change trend over the study area may represent an environmental trigger that synchronized the current outbreak causing the widespread emergence of the disease.

Résumé : Les agents pathogènes indigènes causent normalement peu de dommages parce que la résistance de l'hôte et les conditions environnementales freinent le développement d'une ou plusieurs phases du cycle de la maladie. Des changements chez l'hôte ou dans les conditions environnementales peuvent réduire l'effet de ces facteurs limitants et entraîner l'émergence de la maladie. Jusqu'à récemment, la brûlure en bandes rouges causée par *Dothistroma septosporum* (Dorog.) Morelet avait eu peu d'impact sur les arbres forestiers indigènes de l'ouest de l'Amérique du Nord. Au cours de la dernière décennie dans les forêts du nord-ouest de la Colombie-Britannique, au Canada, cette maladie a causé beaucoup de mortalité dans les plantations aménagées de pin tordu (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) et même des pins matures meurent. Nous avons utilisé des méthodes dendrochronologiques pour reconstituer les patrons temporels des épidémies passées de cette maladie dans la région en utilisant des séries dendrochronologiques provenant de stations où les épidémies ont été répertoriées. Nous avons découvert que des épidémies sont survenues périodiquement au cours des 174 dernières années dans le nord-ouest de la Colombie-Britannique et que l'incidence et l'étendue des épidémies ont augmenté depuis les années 1940. Le changement le plus frappant observé dans l'historique des épidémies a été l'augmentation de la sévérité et de la synchronicité parmi les stations touchées par l'épidémie actuelle. La tendance vers un changement du climat observée récemment dans la région étudiée peut constituer un déclencheur environnemental qui synchronise l'épidémie actuelle causant ainsi une émergence généralisée de la maladie.

[Traduit par la Rédaction]

Introduction

Anthropogenic introductions of plant pathogens have resulted in widespread disease outbreaks affecting food crops (e.g., the introduction of *Phytophthora infestans* (Mont.) de Bary causal agent of potato late blight to Europe resulted in the Irish potato famine; Goodwin et al. 1994) and forest species (e.g., the introduction of *Cryphonectria parasitica* (Murrill) M.E. Barr to North America resulted in almost to-tal mortality of mature chestnut trees; Milgroom et al. 1996) with serious economic and ecological impacts. Pathogen introductions are a main cause of emerging infectious diseases, a term that has been adapted from medical and veterinary fields and applied to pathogens of plants (Anderson et al. 2004). Alien pathogens are introduced into an area where endemic hosts have little or no resistance. If conditions are favourable, the pathogen can become established and cause disease emergence and serious consequen-

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ces. As a result, significant attention has been paid to diseases of crop plants and economically important wild species caused by introduced pathogens. In some cases, however, native pathogens can cause emerging infectious diseases. The main drivers behind emergence of native pathogens include changes in cultural practices and weather (Anderson et al. 2004). Much less is known about native emerging pathogens and the diseases that they cause, largely because they were historically recognized as benign and therefore did not attract much attention. As emerging pathogens, their impacts may not be as sudden as those caused by introduced pathogens. Under the influence of climate change, emerging native pathogens may become more common and more devastating. Pathogens dependent on specific weather conditions for infection and reproductive success (e.g., foliar pathogens and rust fungi) may be most susceptible to changes in climate.

The identification of native pathogens as causal agents of emerging diseases first requires that the pathogen is known to be endemic to the area. Secondly, knowledge of the historical effects of the pathogen is required to separate emerging infectious diseases from outbreaks resulting from relatively rare combinations of specific weather events and host conditions. Understanding the drivers behind native emerging pathogens requires comprehensive knowledge of the pathogen and host interactions. Such knowledge is often not available because of the historically benign nature of the pathogen.

A recent outbreak of Dothistroma needle blight (Dothistroma) in northwestern British Columbia presented an opportunity to study a potentially emerging disease of an economically and ecologically important forest species. Dothistroma has been well studied as an introduced pathogen in the Southern Hemisphere responsible for widespread serious damage to native and exotic pines (Harrington and Wingfield 1998; Barnes et al. 2004). The fungus responsible for the disease, *Dothistroma septosporum* (Dorog.) Morelet (previously called *Dothistroma pini* Hulbary), infects the needles, causing necrotic lesions and premature needle drop (Bradshaw et al. 1997). The severity of attack remains low except at warm temperatures (15–20 °C) under regimes of continuous moisture (Peterson 1967; Gadgil 1974). The incidence of infection is highly sensitive to annual variation in weather (Peterson 1973). Rapid development of outbreaks can occur during periods of prolonged wet weather during the growing season (Harrington and Wingfield 1998). The fungus has a sexual state (*Mycosphaerella pini* Rostr.) but is more commonly observed in its conidial or asexual state (*D. septosporum*). The life cycle of the pathogen generally requires 1–2 years to complete.

Until recently, Dothistroma has been of little concern in lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) stands in western North America. The first published record of the disease in British Columbia, Canada, was from the Skeena–Stikine Forest District in 1963 (Parker and Collis 1966), an observation that coincides with greater worldwide recognition of the pathogen in the early 1960s (Murray and Batko 1962; Gibson et al. 1964). Annual Forest Insect and Disease Surveys (FIDS) monitored insect and disease conditions throughout the province up to 1995 and recorded past Dothistroma outbreaks (e.g., Unger and

Humphreys 1984). Damage to native species was normally 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 2003; Bradshaw 2004) in both managed and natural stands of lodgepole pine in northwestern British Columbia (Woods et al. 2005). The first instance of severe damage to a lodgepole pine stand was identified in 1997. The magnitude of the current outbreak was not fully appreciated until 2002, when low-level aerial flights identified widespread occurrence of the disease in the area (Woods 2003). The situation in British Columbia is unique because unlike plantations of exotic pines in the Southern Hemisphere, both the host lodgepole pine and the pathogen *D. septosporum* are native species in the area. Mortality in mature trees as well is unprecedented and we hypothesized that Dothistroma is an emerging disease that has recently been released, by global climate change, from environmental limits on spread and severity (Woods et al. 2005).

Although *D. septosporum* is considered native in the Northern Hemisphere, little is known about the history or long-term dynamics of the disease in northern temperate forests. A longer temporal and spatial perspective on outbreak patterns is needed to determine if Dothistroma is an emerging infectious disease and to identify drivers behind its emergence. We used dendrochronological techniques adapted from studies of insect outbreaks (Swetnam et al. 1985; Swetnam and Lynch 1989) to gain this long-term view of past outbreaks. Relationships between insect infestation and specific climate events have also been determined from long-term reconstructions of insect outbreaks (Zhang et al. 1999; Case and MacDonald 2003; Campbell et al. 2005). This study is the first to use dendrochronology to examine the history and dynamics of a fungal defoliator.

The objectives of the study are to (*i*) determine if Dothistroma is a native emerging infectious disease in northwestern British Columbia by reconstructing the outbreak history of Dothistroma at multicentury time scales, (*ii*) evaluate the temporal dynamics of the disease in lodgepole pine dominated forests of northwestern British Columbia using tree-ring analysis, (*iii*) investigate differences in outbreak patterns between distinct ecological forest types, and (*iv*) determine if changes in weather could be an underlying driver behind disease emergence.

Methods

Study area description

This study was conducted in northwestern British Columbia, Canada. Sample areas were selected from three biogeoclimatic variants: Nass Moist Cold Interior Cedar–Hemlock (ICHmc1), Hazelton Moist Cold Interior Cedar–Hemlock (ICHmc2), and Babine Moist Cold Sub-Boreal Spruce (SBSmc2) (Pojar et al. 1987).

The Interior Cedar–Hemlock (ICH) zone consists of low- to midelevation northern temperate forests in an area transitional between the coastal rainforests to the west and the more continental sub-boreal forests to the east. The climate of the ICH zone is intermediate and characterized by warm, moist summers, wet falls, and cold winters. Average annual

Fig. 1. Study area map showing the sampling distribution of the six known outbreak sites and 16 inferred outbreak sites. Map A shows the distribution of site locations in northwestern British Columbia and map B shows the site locations in the central interior of British Columbia.
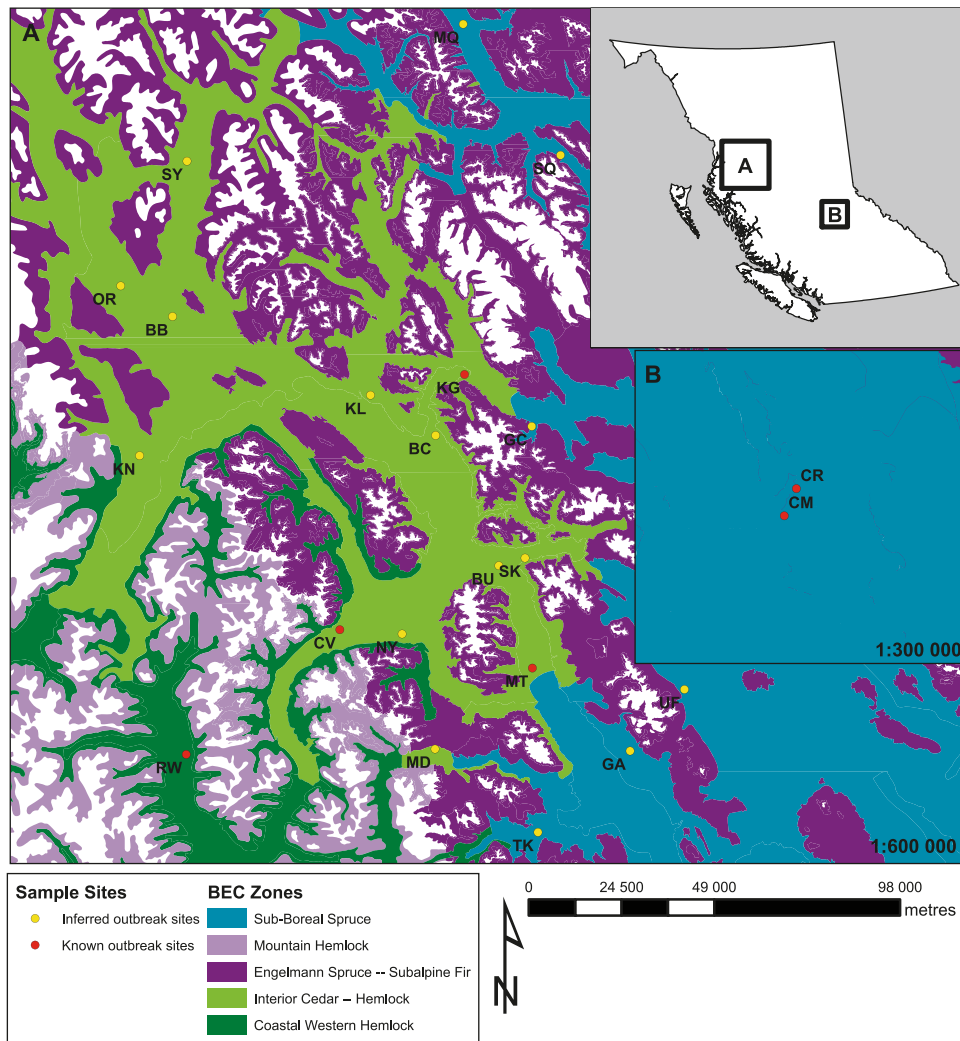
precipitation ranges from 500 to 1200 mm (Banner et al. 1993). The ICHmc1 has a mild, humid climate with very infrequent disturbance from fire, permitting growth of coastal tree species. The ICHmc2 occupies the lower-elevation forests and has a warmer and drier climate. Lodgepole pine is a component of both ICH subzones making up less than 10% of the dominant forest cover (Woods 2003).

The Sub-Boreal Spruce (SBS) zone covers most of the interior lowland forest to the east of the ICH zone. The climate of the SBS zone is continental with long cold winters and relatively short warm and moist summers. Annual precipitation is 440–650 mm; less than half falls as snow. Upland coniferous forests dominate the SBS zone landscape. Hybrid spruce, a cross of white spruce (*Picea glauca* (Moench) Voss) and Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), and subalpine fir (*Abies lasicocarpa* (Hook.) Nutt.) are the major climax tree species in the SBS zone. Lodgepole pine and trembling aspen (*Populus tremuloides* Michx.) pioneer extensive seral stands. Lodgepole pine is common in mature forests in the drier parts of the

zone (Banner et al. 1993). The SBSmc2 variant is found at higher elevations and has wetter climate.

Site and tree selection

FIDS and Canadian Forest Service (CFS) herbarium records were used to locate sites where past occurrences of Dothistroma had been recorded. Six sites with sufficient location information were identified, four in the northwest and two (both near Cinema, British Columbia) in the central interior (Fig. 1). Disease severity details were included for only two of the recorded outbreaks (Funk and Parker 1966; Unger and Humphreys 1984).

In addition, 16 sample sites were located within the study area based on the following criteria: (*i*) within the ICHmc1, ICHmc2, or SBSmc2, (*ii*) between 0.5 and 5 ha in size to ensure an adequate number of trees sampled and to minimize differences in tree growth due to site factors, (*iii*) contained older (>50 years) lodgepole trees dominant in the canopy to provide longer outbreak reconstructions for identifying past disease occurrences, (*iv*) close proximity to non-

Table 1. Master chronology statistics for lodgepole pine (PL) and spruce (SX) for the six known outbreak sites (bold) and 16 sites used to study outbreak patterns of Dothistroma needle blight in northwestern British Columbia.

Site	Designation	BEC variant[a]	Species	No. of tree cores	Series intercorrelation	Mean sensitivity	Start	End
Cedarvale	**CV**	**ICHmc1**	**PL**	**24**	**0.649**	**0.179**	**1921**	**2004**
			SX	**17**	**0.53**	**0.118**	**1868**	**2004**
Kisgegas Canyon	**KG**	**ICHmc1**	**PL**	**15**	**0.492**	**0.197**	**1879**	**2004**
			SX	**19**	**0.677**	**0.175**	**1926**	**2004**
Moricetown	**MT**	**ICHmc2**	**PL**	**17**	**0.517**	**0.152**	**1932**	**2004**
			SX	**19**	**0.635**	**0.163**	**1944**	**2004**
Rosswood	**RW**	**CWHws1**	**PL**	**20**	**0.542**	**0.173**	**1905**	**2004**
			SX	**20**	**0.605**	**0.144**	**1930**	**2004**
Cinema	**CM**	**SBSmh**	**PL**	**16**	**0.595**	**0.137**	**1949**	**2004**
			SX	**20**	**0.543**	**0.140**	**1927**	**2004**
Cottonwood	**CR**	**SBSmh**	**PL**	**19**	**0.626**	**0.221**	**1918**	**2004**
			SX	**20**	**0.543**	**0.140**	**1927**	**2004**
Brown Bear	BB	ICHmc1	PL	16	0.480	0.134	1624	2004
			SX	19	0.527	0.152	1719	2004
Orendo	OR	ICHmc1	PL	16	0.524	0.134	1899	2004
			SX	19	0.516	0.128	1903	2004
Sanyam	SY	ICHmc1	PL	16	0.521	0.164	1913	2005
			SX	19	0.578	0.220	1897	2005
Kinscuch	KN	ICHmc1	PL	15	0.438	0.119	1898	2004
			SX	18	0.579	0.136	1900	2004
Kuldo	KL	ICHmc1	PL	17	0.522	0.116	1923	2004
			SX	14	0.465	0.114	1894	2004
Gail Creek	GC	ICHmc1	PL	20	0.527	0.117	1872	2004
			SX	18	0.455	0.118	1874	2004
McDonell Lake	MD	ICHmc1	PL	16	0.466	0.107	1811	2004
			SX	17	0.451	0.098	1849	2005
Suskwa	SK	ICHmc2	PL	19	0.476	0.124	1918	2004
			SX	16	0.493	0.111	1919	2004
Bretson Creek	BC	ICHmc2	PL	16	0.506	0.164	1936	2004
			SX	18	0.577	0.117	1922	2005
Bulkley Canyon	BU	ICHmc2	PL	17	0.575	0.132	1900	2004
			SX	16	0.493	0.096	1919	2004
Nash Y	NY	ICHmc2	PL	20	0.531	0.167	1918	2004
			SX	14	0.490	0.103	1891	2004
Mosque River	MQ	SBSmc2	PL	17	0.533	0.174	1926	2004
			SX	15	0.538	0.137	1933	2004
Squingula River	SQ	SBSmc2	PL	14	0.516	0.137	1937	2004
			SX	13	0.423	0.105	1950	2004
Upper Fulton	UF	SBSmc2	PL	13	0.460	0.119	1788	2003
			SX	18	0.507	0.117	1820	2004
Telkwa	TK	SBSmc2	PL	16	0.541	0.141	1883	2004
			SX	15	0.417	0.099	1882	2004
Ganokwa	GA	SBSmc2	PL	13	0.461	0.120	1806	2003
			SX	16	0.440	0.107	1787	2004

[a]Biogeoclimatic Ecological Classification system.

host spruce stands where lodgepole pine was largely absent to eliminate positive effects on spruce growth from the sudden availability of additional resources (e.g., light), and (v) at least 20 m away from any source of apparent intermediate-scale disturbance such as roads and blow-down to decrease the amount of ring width variation due to such disturbances.

Increment cores were collected from 20 lodgepole pine (host) and 20 spruce (nonhost) trees at each site (one core per tree). Trees were selected based on evidence of longev-

ity and diameter (DBH >15 cm). All trees were cored at 0.3 m in height, unless the tree had substantial butt rot, in which case it was cored at 1.3 m in height. Where available, cross-sectional discs from dead trees were also sampled to extend the chronologies.

Crossdating and standardizing

All cores were mounted and cores and discs were sanded with progressively finer sandpaper grits according to the methods of Stokes and Smiley (1968). Calendar dates were

Fig. 2. Standardized ring width indices of the six known outbreak sites. The black line represents the pine host chronology and the grey line represents the nonhost spruce chronology. Arrows indicate the year that the FIDS recorded disease occurrence or the date of collection of a CFS herbarium specimen. Both MT and CV dates were identified from herbarium collections. Site designations at the top right corner of each graph are defined in Table 1. Data not shown for the additional 16 sites.
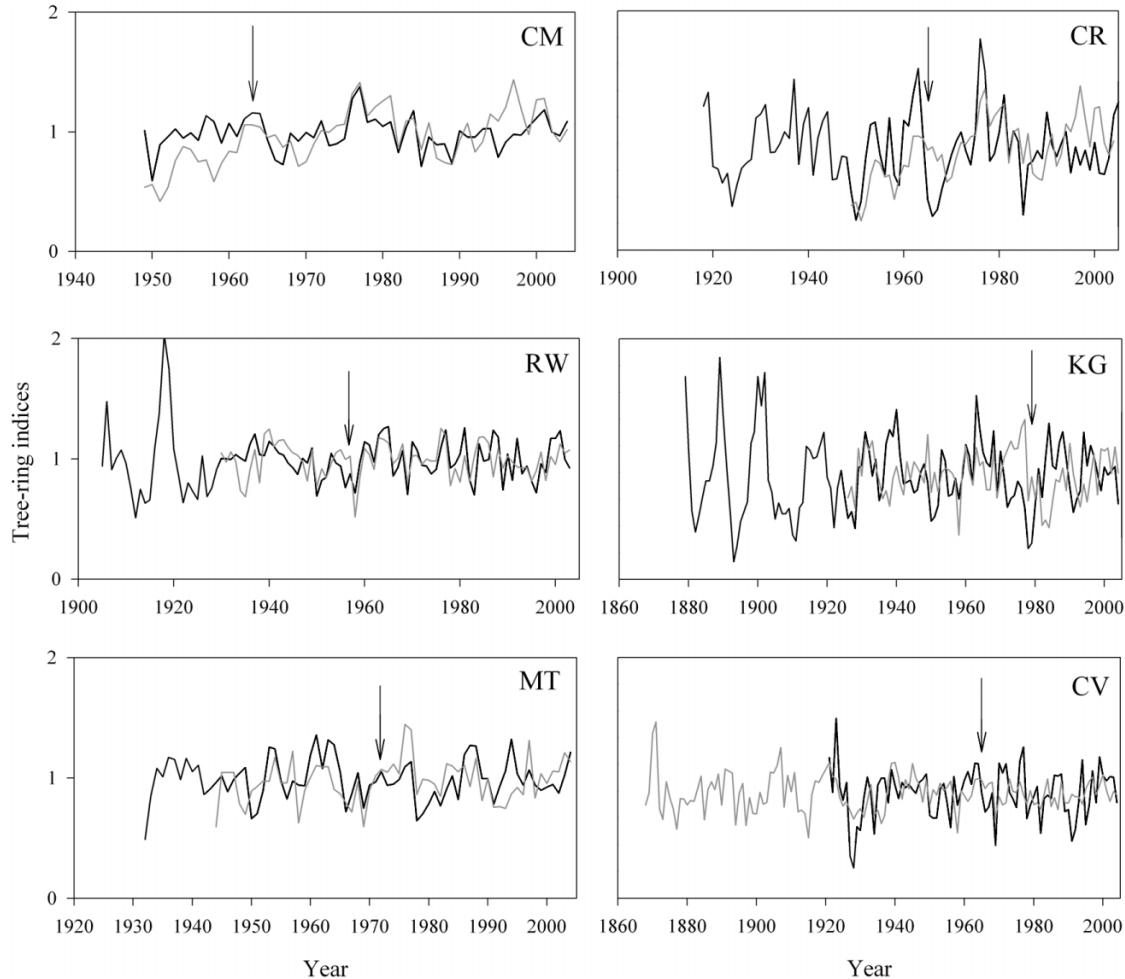
assigned to the cores and discs and visually crossdated using Yamaguchi plots (Yamaguchi 1991). Annual ring widths were measured to the nearest 0.001 mm using the Velmex "TA" System in conjunction with MeasureJ2X (1999–2004) and the crossdating verified with the computer program COFECHA (Holmes 1983). To remove age-related trends in growth, the dated ring width series were standardized with a cubic smoothing spline with a 50% frequency response cutoff of 40 years using ARSTAN version 40 (Cook and Holmes 1984).

Signal development and inferred outbreaks

Similarity of climate response in the host and nonhost species is required to separate the effects on growth caused by defoliator outbreaks from those caused by climate (Ryerson et al. 2003). Responses to climate in the host and nonhost species were compared using mean sensitivity statistics, graphical plots, correlation coefficients, and response function analyses using PRECONK version 5.17C (Fritts 1994), which involves a multiple regression after extracting principal components to estimate the response of tree growth to climate variables (Cook and Kairiukstis 1992). The signif-

icance of these associations was tested using bootstrap methods (Guiot 1991). The climate variables that we used were monthly mean temperature and total monthly precipitation for the period 1950–2003. Climate data for each site was interpolated as functions of latitude, longitude, and elevations using the program ANUSPLIN (McKenney et al. 2006). The resulting regression coefficients from the individual monthly climate variables of the host and the corresponding nonhost chronologies were compared.

To separate the observed reduced growth in the host due to disease from climate variation, the nonhost chronology was subtracted from each individual host index series to create "climate-corrected" series (Swetnam et al. 1985). The corrected indices were calculated with the following equation:

$$\text{Corrected index} = I_{\text{h}t} - \left[\frac{\text{SD}_\text{h}}{\text{SD}_\text{n}} (I_{\text{n}t} - \bar{I}_\text{n}) \right]$$

where $I_{\text{h}t}$ was the host index at year t, SD_h is the standard deviation of the individual host tree series for the period common to both series, SD_n is the standard deviation of the

Table 2. Correlation coefficients showing the strength of the relationship between each lodgepole pine and nonhost spruce site chronology.

Site	r
CV	**0.361**
KG	**0.248**
RW	**0.518**
MT	**0.345**
CM	**0.409**
CR	**0.288**
BB	0.350
OR	0.473
SY	0.362
KN	0.420
KL	0.581
GC	0.292
MD	0.408
SK	0.484
BC	0.572
BU	0.225
NY	0.226
MQ	0.361
SQ	0.374
UF	0.302
TK	0.252
GA	0.185

Note: See Table 1 for site names. All correlation coefficients were significant ($P < 0.05$). The six known outbreak sample sites are in bold.

nonhost composite chronology for the period common to both series, I_{nt} is the nonhost index at year t, and $\bar{I}_n$ is the mean of the nonhost index for the period common to both series (Swetnam et al. 1985; Ryerson et al. 2003). Each individually corrected host series was then averaged and subsequently normalized by subtracting the mean and dividing by the standard deviation. We used the software program OUTBREAK to automate the correction procedure in accordance with Holmes and Swetnam (1996).

Because little was known about outbreak patterns of Dothistroma in northwestern British Columbia, the development of criteria was necessary to identify prerecord growth reductions as Dothistroma outbreaks. Pandora moth outbreak parameters previously developed by Speer et al. (2001) were modified based on the timing, duration, and magnitude of the ring width reductions of the known Dothistroma outbreak periods. Growth reduction values from the initiation of the current outbreak were also quantified and set as initial criteria to calibrate OUTBREAK, which applies a set of user-defined criteria to identify outbreaks (Ryerson et al. 2003). All negative values in the corrected series were identified, and these periods were checked for compliance with the criteria and eliminated as a possible outbreak if the specified thresholds were not attained. If OUTBREAK did not initially identify the confirmed historical defoliation episodes from FIDS and CFS herbarium collection records, the parameters were changed in an iterative process until OUTBREAK did replicate the observed periods. The following criteria were applied simultaneously to the normalized corrected series to identify Dothistroma outbreaks: (*i*) the index

must reach at least −1.20 SD units (10th percentile) for at least 1 year, (*ii*) negative growth values must last between 5 and 10 years consecutively, and (*iii*) the beginning year of the outbreak must show a reduction of at least 70% of that of the previous year.

To reduce the chance of identifying a minor outbreak, or a reduction in pine growth caused by agents other than *D. septosporum*, the percentage of trees that met the above criteria during each possible outbreak period at each site was calculated. Only those periods where ≥40% of the trees met the criteria were recorded as Dothistroma outbreaks for each of the 16 sites.

Analysis of outbreak characteristics

The identified outbreak periods were compared across all stands to determine if outbreaks were synchronous at the stand level. A regional time series of outbreaks was developed by summing the number of trees recording an outbreak as defined by OUTBREAK and the 40% threshold for each year across all sites. To minimize sampling artifacts, only sites from the selected biogeoclimatic variants (ICHmc1, ICHmc2, and SBSmc2) were included in the regional time series. The numbers of trees included in the reconstruction decreased with increasing tree age, so we standardized the time series by computing the percentage of trees recording an outbreak for each year. The regional time series was used to examine periodicity of the recorded outbreaks and to further examine outbreak synchrony at the regional scale by combining tree-level data.

The duration and return intervals of the inferred Dothistroma outbreaks at the site level were calculated. The duration of the outbreaks was the number of years between the first and last years of an identified outbreak exceeding the 40% threshold. The return interval was recorded as the time between the end of one outbreak and the beginning of the next. Radial growth reductions during each outbreak were computed as the difference between the observed mean corrected index values and the expected index value (1.0 for a tree-ring index series) for each year of the outbreak. Mean percent growth reduction during each outbreak period was calculated as the sum of yearly growth reductions during an outbreak divided by the number of years in the period multiplied by 100 (Swetnam and Lynch 1989).

Sites were grouped by their respective biogeoclimatic variants (ICHmc1, ICHmc2, and SBSmc2) and temporal outbreak patterns were compared. Correlation analyses were used to determine whether outbreak incidence differed between the variants.

Results

Host and nonhost comparisons

A total of 851 cores and discs (421 host and 430 nonhost) from 22 sites were successfully crossdated. The mean sensitivity values (interannual variation in the ring width as a proportion of the local mean ring width) for lodgepole pine chronologies were generally similar to those of spruce chronologies (Table 1).

Graphical comparisons (not shown) indicate a general agreement in growth trends between the host and nonhost chronologies during most years for all sites. The graphical

Fig. 3. Response function coefficients for mean temperature and precipitation for lodgepole pine and nonhost spruce over the chosen 14-month window. The coefficients (or weights) describe the nature of the relationship of ring width growth with variables of monthly climate. Months associated with "1" indicate the previous year and those with "0" the current year. The solid line represents the mean temperature variable and the broken line represents precipitation. Site designations at the top right corner of each graph are defined in Table 1. Data not shown for RW.
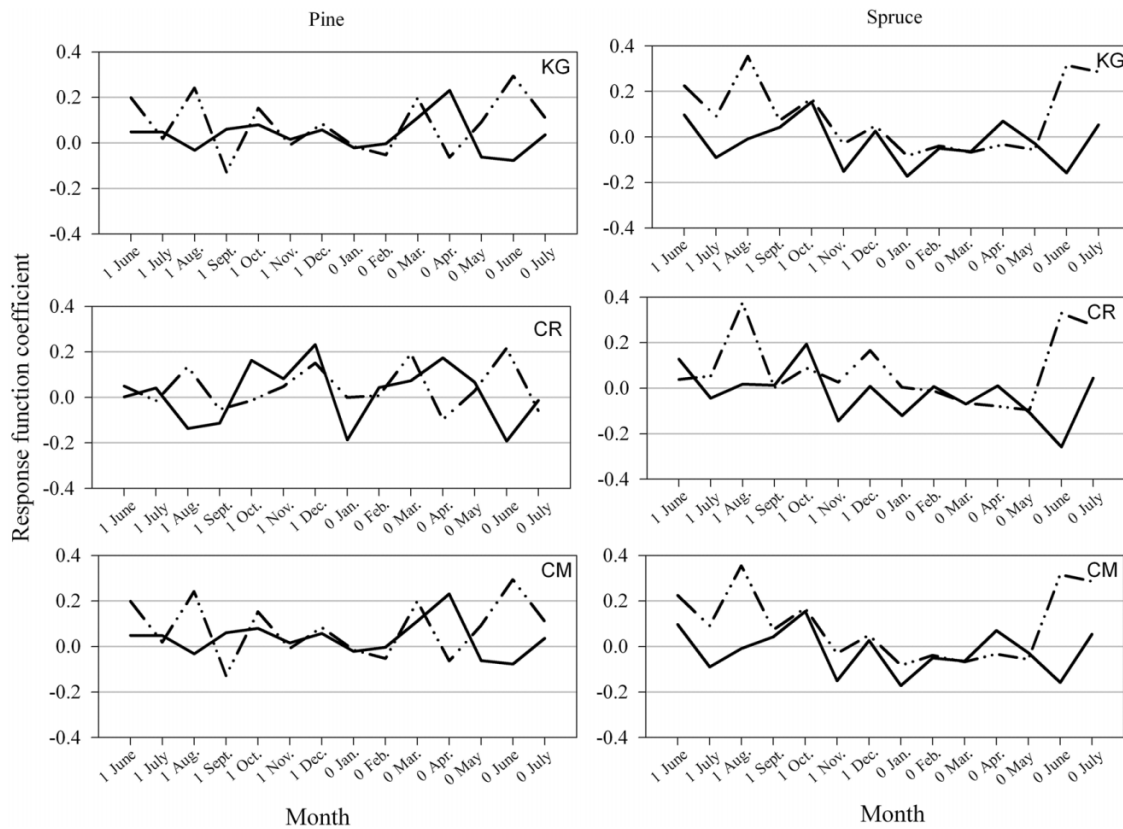
plots of the host chronologies for the six known outbreak sites showed periods of radial growth reduction corresponding to the timing of the documented disease outbreak years, with no corresponding growth reduction in the nonhost. Lodgepole pine cores from the MT and CV sites and plots of growth did not show a period of growth reduction that corresponded to the herbarium collection dates (Fig. 2). Because the timing of the defoliation events at these sites was based only on herbarium collections, without indication of the severity of the foliar disease, the MT and CV chronologies were removed from our criteria development. Pearson's correlation coefficients of the host and nonhost chronologies were statistically significant ($P < 0.05$) for all sites, indicating the presence of a common high-frequency climate signal across the length of the series between the host and nonhost chronologies (Table 2).

Response function analysis of the four remaining known outbreak sites revealed that the host and nonhost chronologies had a similar climate – tree growth relationship. Both pine and spruce responded positively to greater amounts of precipitation in the spring–summer of the current year (May, June, and July) and in August of the year preceding tree growth (Fig. 3). Negative growth responses to increases in mean temperatures were observed during June of the current year and August of the previous year for both species. These consistent relationships suggest the tendency for good growth to correspond to above-average summer precipitation (millimetres) and poor growth to be associated with warmer summer temperatures (degrees Celsius), especially above-average summer temperatures in the following year. Based on these observations, it was determined that spruce could provide a reasonable estimate of expected pine growth during an outbreak. This provided a logical basis for the application of the correction procedure.

Evidence of Dothistroma outbreaks in the tree-ring record

Preliminary ring width and earlywood to latewood ratios revealed a distinctive radial growth reduction pattern associated with most of the documented outbreak periods (Fig. 4). The pattern included reduced earlywood and latewood, with an overall pattern of reduced ring width that lasted 5–10 years. The corrected chronologies from the known outbreak sites showed strongly demarcated negative growth responses during the known outbreak periods. The 40% threshold distinguished between periods of reduced growth attributable to the documented defoliation events and smaller events (or "noise") expressed in the corrected host chronology (Fig. 5). The 1984 documented outbreak at the KG site had the highest percentage of host trees affected (reaching 100%) with the longest duration of 9 years. The timing of the outbreak complements reports of observed mortality at the site, suggesting that the disease was present before the 1984 survey. The current outbreak was also ob-

Fig. 4. Photographs of thin earlywood and latewood during two modernday outbreaks (initial years of 1972 and 1971, respectively, photographs A and B) and subsequent reduced growth (arrows) in an earlier outbreak (initial year of 1917, photograph C).
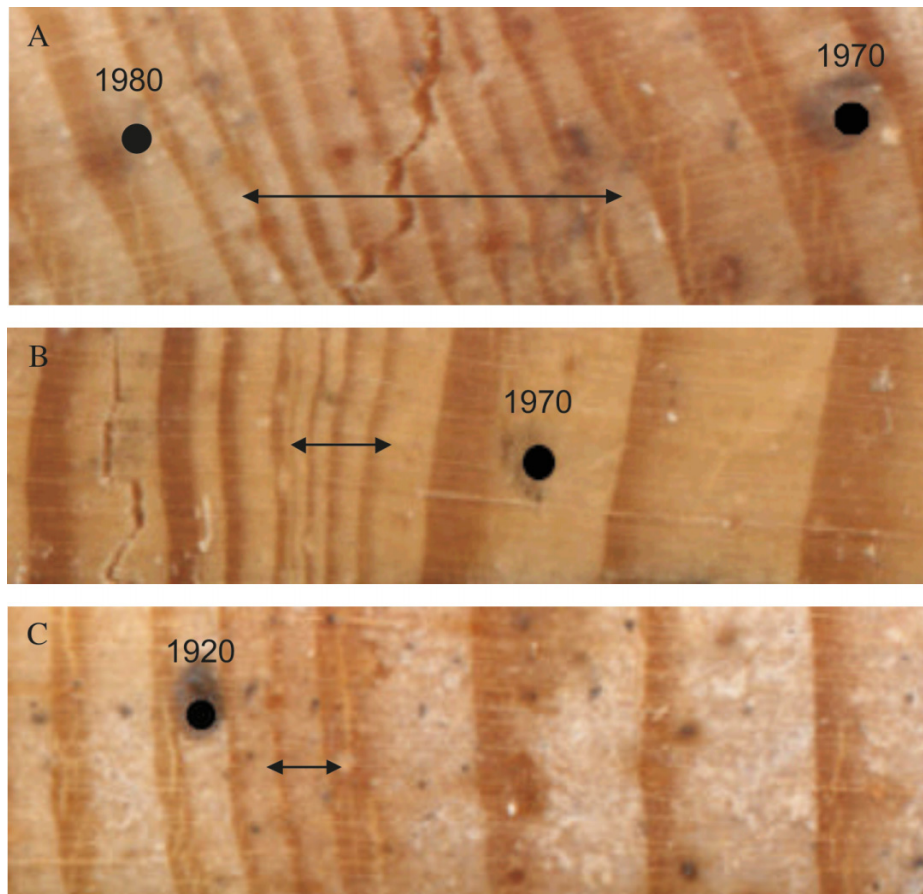
served at that site and exceeded the 40% threshold by 2001. At the RW site, the timing of the current outbreak coincided with dates identified at KG. An earlier outbreak during the late 1950s was also evident but did not reach the threshold. An inferred outbreak was recorded at the RW site, affecting 62.5% of the trees from 1939 to 1946. This coincides with herbarium samples collected in the area in 1941. Because the herbarium samples did not provide sufficient information regarding location of the collection or disease severity, the 1941 collection was not included as a known outbreak during the initial development of the outbreak criteria. The 1964 outbreak near Cinema in the Prince George Forest District was identified in both the CM and CR host chronologies. The most recent outbreak was identified at the CR site and occurred between 1994 and 2002, reaching 70.6% trees infected by 1997. A shorter outbreak was identified at the CM site between 1994 and 1998.

Outbreak dynamics

Inferred periods of Dothistroma defoliation based on the outbreak criteria were observed in host chronologies at all 16 individual stands. A compilation of the outbreak history revealed the presence of outbreak synchrony among the sites (Fig. 6). The current outbreak covered most of the study area (76% of the sites), with the first year appearing as a cluster of dates rather than a single year. An earlier outbreak

during the 1960s covered 40% of the study sites. A number of earlier outbreaks occurred, most notably between the 1970s and 1980s reaching 30% of the total study sites.

Over the 233-year record (AD 1771 to AD 2004), 10 outbreak periods were evident across all sample sites in the ICHmc1, ICHmc2, and SBSmc2 variants (Fig. 7) starting as early as 1831. The low number of trees recording an outbreak at the beginning of the chronology is due in part to reduced sample depth (Fig. 7a). The percentage time series (Fig. 7b) is less affected by sample size. Outbreaks identified after this low sample depth period started in mid-1910, mid-1930s, mid-1940s, mid-1960s, late 1970s, late 1980s, and ~2000. Peak percentages in outbreak incidence (i.e., defined by the outbreak criteria) were 32%, 9%, 17%, 24%, 29%, 29%, and 62%, respectively. Dothistroma outbreaks increased in frequency after 1960, and peaks in occurrence correspond to documented records of Dothistroma needle blight incidence in the area during the 1960s and 1980s. Between the 1940s and 1998, there is an outbreak recorded at one or more sites in every year. The percentage of trees affected is greatest during the current outbreak.

Dates of all inferred outbreaks, duration, and return intervals are listed in Table 3. The duration of outbreaks for all sites included in the composite time series ranged from 1 to 10 years, with a mean of 5.2 years. The interval between outbreaks ranged from 2 to 53 years, with a mean of

Fig. 5. Percentage of trees showing growth reductions due to defoliation by Dothistroma needle blight at four known outbreak sites in the northwestern British Columbia. The straight line represents a threshold of 40% that was chosen as a criterion for identifying an outbreak. Site designations at the top right corner of each graph are defined in Table 1. Arrows indicate documented outbreak years.
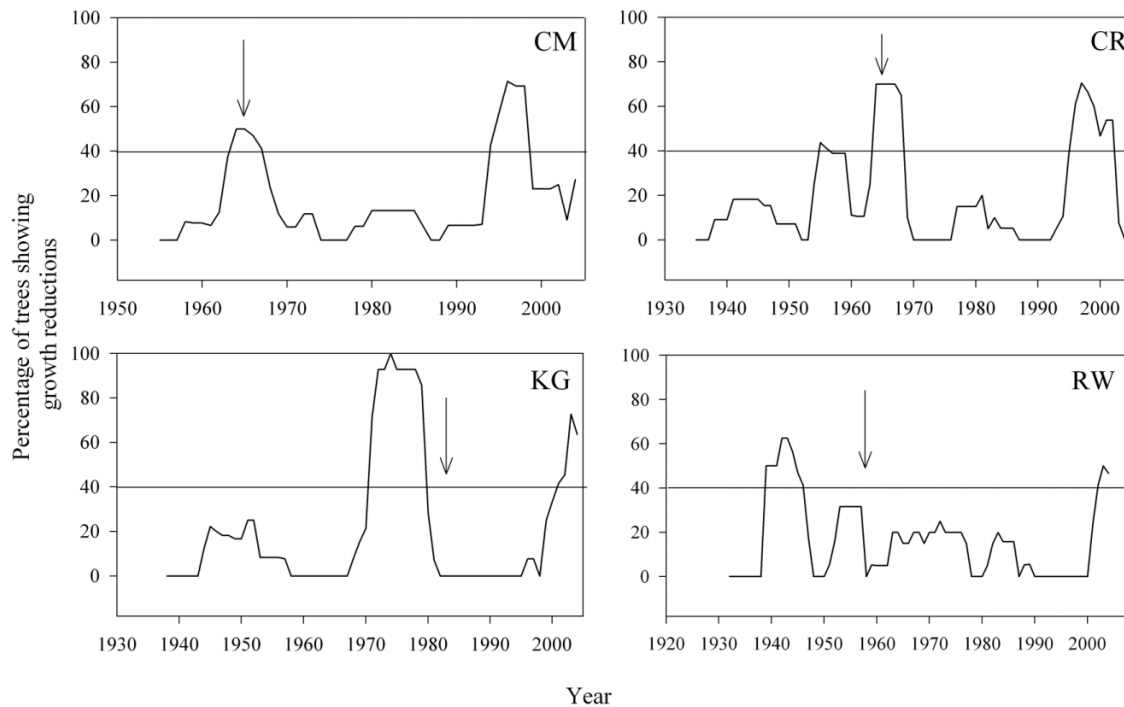
18.8 years. Mean percent growth reduction during the outbreaks ranged from 1% to 45%, with a mean value of 16% (data not shown).

Outbreak characteristics between ecological variants

A continuous time series of the percent trees recording outbreaks identified by the outbreak criteria was calculated for each variant. Outbreaks in the ICH zone appeared to affect more trees and last longer than those in the SBS zone, with a notable increase in intensity after the 1960s for the ICH zone (Fig. 8). Reconstructions of stands in the SBS zone showed a high frequency of outbreaks but all were less intense than those in the ICH zone. The current outbreak is similar across all variants and represents the largest outbreak to date. The magnitude of the outbreaks was highly correlated between ICH subzones ($P < 0.05$), whereas only the ICHmc1 was correlated with the SBS zone outbreaks.

Discussion

Quality and reliability of the Dothistroma signature

We found a distinct dendrochronological signature associated with Dothistroma needle blight defoliation. The annual ring width structure from documented outbreaks shows a sharp reduction in both earlywood and latewood production, persisting for more than 5 years and up to a maximum of 10 years. The formation of the earlywood in a ring is dependent primarily on older foliage, while the production of latewood is due primarily to current-year foliage (Onaka 1950). The reduction in earlywood production in the first year is likely a response to the cumulative loss of older needles that were infected in previous years. In the early stages of attack, infection by *D. septosporum* is concentrated in the

older needles and later spreads into younger foliage (Gibson 1972). The subsequent spread into younger and more photosynthetically active needles could explain the observed reduction in total annual growth. The observed reduction in total annual growth during the outbreak periods supports similar findings from New Zealand with *Pinus radiata* D. Don (Harris and McConchie 1978). Whyte (1968) found a minimal reduction in diameter increment during early stages of Dothistroma attack that increased in magnitude when more than 25% of the foliage was affected and the younger needles were involved. Diameter increment was reduced by one half when severe defoliation had affected half the foliage, and a further increase in disease to more than 85% needle loss resulted in almost complete cessation of diameter growth (Hocking and Etheridge 1967).

We believe it is unlikely that the outbreaks we have identified and attributed to Dothistroma were a result of other disturbance agents. The observed reduction in total annual growth during Dothistroma events is unique in comparison with studies on many insect defoliators, such as larch sawfly (*Pristiphora erichsonii* (Htg.)), gypsy moth (*Lymantria dispar* L.), and western spruce budworm (*Choristoneura occidentalis* Freeman). In these studies of insect-caused defoliation, the effects of defoliation in the first year of reduced growth manifests as only reduced latewood production (Jardon et al. 1994; Krause and Morin 1995; Muzika and Liebhold 1999). Numerous insect defoliators utilize lodgepole pine trees as a host in British Columbia; the most important include *Zelleria haimbachi* Busck (Lepidoptera: Yponomeutidae), *Coleotechnites* species (Lepidoptera: Gelechiidae), and *Neodiprion nanulus contortae* Ross (Hymenoptera: Diprionidae). All are regarded as common colonial defoliators that occasionally reach epidemic levels causing

Fig. 6. (A) Composite chronology of Dothistroma needle blight outbreaks in 20 lodgepole pine sites (known outbreak sites in bold). The arrowheads indicate the peak percentage of trees recording an outbreak. The vertical line indicates the innermost ring year. The solid line indicates the duration of each outbreak that met the 40% threshold. The broken line indicates the length of the corrected chronology. (B) Percentage of sites in the composite chronology recording an outbreak for each year.
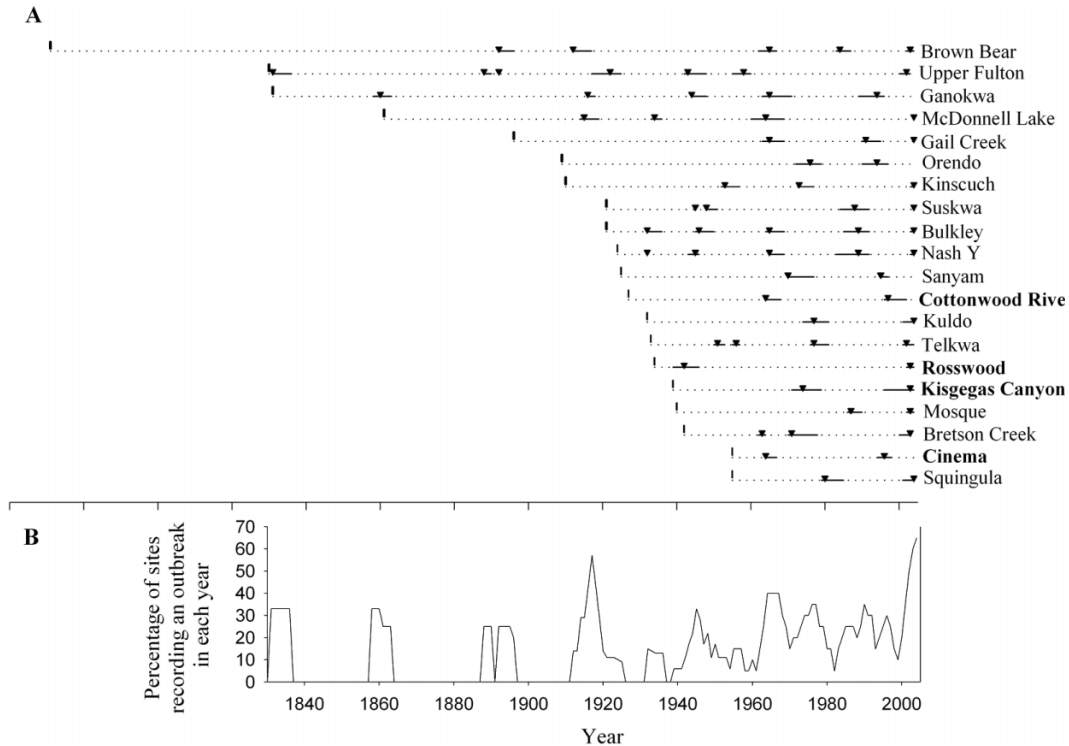
significant defoliation. Significant outbreaks have been recorded in many areas of southern British Columbia (Duncan 2006). The FIDS records indicated light defoliation caused by *Z. haimbachi* and *Coleotechnites* spp. ~70 km east of our study area in 1981, 1982, and 1983, but no outbreaks were recorded. We assume, therefore, that these insect defoliators are not common disturbance agents of the forests in this study area and can be eliminated as possible causes of the ring width pattern.

Growth reduction measured in our study suggests a unique tree-ring pattern associated with fungal defoliators. Numerous foliar pathogens defoliate lodgepole pine in British Columbia, but only three are considered common in the northwest: *Lophodermella concolor* (Dearn.) Darker, *Lophodermella montivaga* Petr., and *D. septosporum*. Outbreaks of *L. concolor* and *L. montivaga* can be locally severe where cool, moist environmental conditions persist. However, *D. septosporum* has greater potential to cause serious and more widespread damage (Ying and Hunt 1987; Hunt 1995), in part because it can infect needles of all ages any time temperatures are above 5 °C and moisture is present (Sinclair et al. 1987). In contrast, *Lophodermella* species attack only current-year needles and are active only in the spring (Hunt 1995). Historical records suggest that only a few *L. concolor* defoliation events have occurred, and the only *L. montivaga* infections documented from the sampling area were at low levels. The criterion of 70% growth reduction during the first year of a possible outbreak eliminates defoliation events associated with weaker fungal pathogens. The consistent recurrence of the Dothistroma-specific signature in association

with the historically documented records enabled us to identify 10 peak outbreak periods in northwestern British Columbia since 1831.

Comparison of host and nonhost growth enables separation of growth effects due to climate from those caused by a host-specific biotic agent (Trotter et al. 2002). The reliability of this "correction" procedure is based on two major assumptions: (*i*) the nonhost species are unaffected by the agent causing the outbreak and (*ii*) the host and nonhost species respond similarly to environmental influences (Swetnam et al. 1985). False interpretations of outbreak histories are introduced by systematic differences in climatic responsiveness or sensitivities of the host and nonhost trees (Ryerson et al. 2003). The verified Dothistroma outbreaks consistently appeared as periods with declining trends in the pine chronologies and relatively unchanging growth trends in the nonhost spruce chronologies, suggesting that the observed periods of growth reduction in the host trees were not caused by a climate event. Furthermore, our climate – tree growth response function analyses showed that the host and nonhost series were generally similar (Fig. 3). Moreover, the strength of the precipitation and temperature responses, as reflected in the magnitude of the response coefficients, was not measurably different between the species. Chronology statistics and correlation analyses also indicated a general agreement between yearly growth of host and nonhost species.

Inevitably, there will be some species-related differences in response to climate or other environmental variations. Therefore, the corrected indices could retain varying

Fig. 7. (A) Time series of the number of trees from sites recording outbreaks identified by the outbreak criteria (i.e., statistical criteria and 40% threshold) and the sample size curve (or the number of trees included in the regional outbreak reconstruction for each year). (B) Percentage of trees from sites recording an outbreak identified by the outbreak criteria. Numbers indicate 10 outbreak periods.
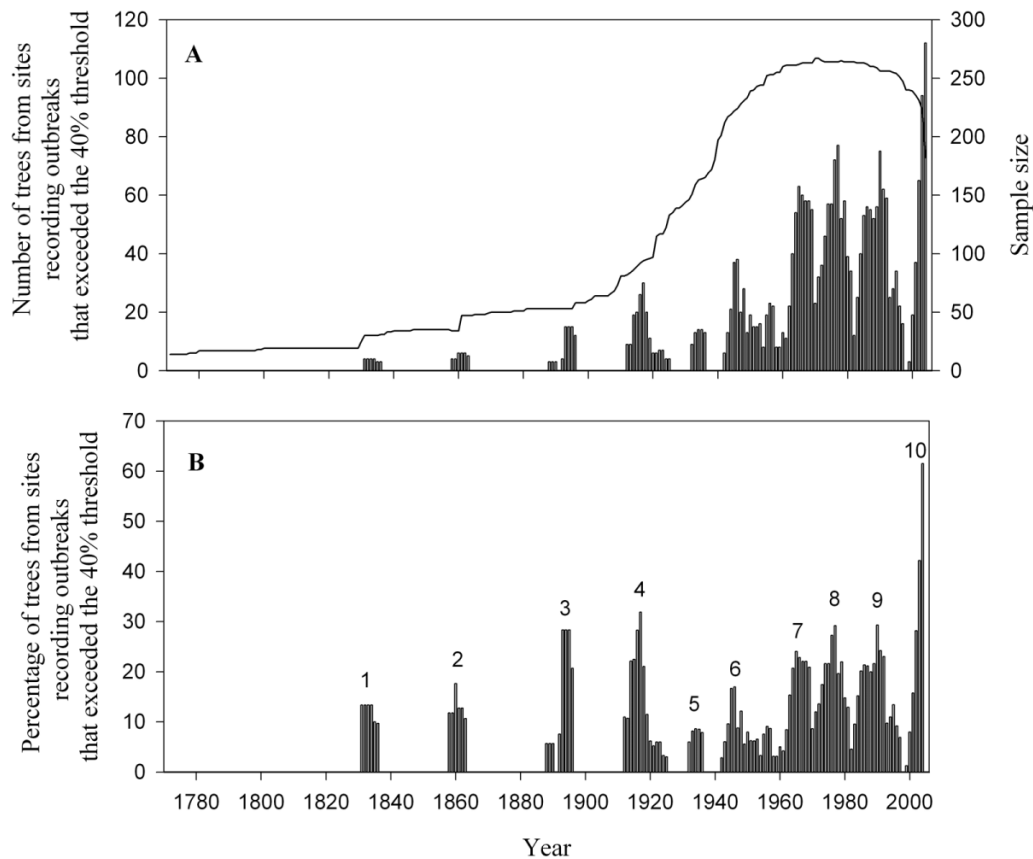
amounts of unwanted "noise" (Swetnam and Lynch 1989). Although we acknowledge the possibility that the correction procedure may create outbreak artifacts, we point to three lines of evidence suggesting that this is unlikely in our reconstructions. First, as previously mentioned, response function analyses showed a general agreement between climate and growth responses for both host and nonhost species. Second, low-growth periods from our known outbreaks were verified as Dothistroma outbreaks by comparing the timing of the growth reductions in the corrected series with the corresponding FIDS record. Our criteria were developed from these known outbreak periods and considered characteristic of the effects caused by the pathogen. Third, the addition of the threshold where ≥40% of trees had to meet the outbreak criteria helped to reduce error due to the correction procedure.

Outbreak dynamics and disease emergence

Our reconstructions demonstrate that Dothistroma outbreaks in northwestern British Columbia have occurred periodically over the last 174 years and that there has been a change in outbreak incidence within our sampled stands. We found an increase in the extent and severity of the outbreaks since the 1940s. Stand-replacing fires are likely the cause of the apparent shift in the sample depth curve (Fig. 7a) and not due to mortality caused by past Dothistroma outbreaks or any other forest health agent. Damage to native species caused by Dothistroma has historically been

Table 3. Dates of inferred and known outbreaks (bold), duration of ring width reductions, and return intervals between reductions in lodgepole pine during Dothistroma needle blight outbreaks.

Site	Dates	Duration (years)	Interval (years)
BB	1892–1896	5	
	1912–1917	6	16
	1962–1967	6	45
	1983–1987	5	16
	2002–2004	3	15
OR	1972–1979	8	
	1990–1997	8	11
SY	1970–1977	8	
	1995–1997	3	18
KN	1952–1957	6	
	1973–1977	5	16
	2003–2004	2	26
KL	1974–1981	8	
	2001–2004	4	20
GC	1963–1969	7	
	1990–1995	6	21
	2004	1	9
MD	1914–1919	6	
	1933–1936	4	14
	1960–1969	10	24
	2004	1	35

Table 3 (*concluded*).

| Site	Dates	Duration (years)	Interval (years)
SK	1945–1946	2	
	1948–1951	4	2
	1984–1992	9	33
	2004	1	12
BU	1932–1936	5	
	1945–1950	6	9
	1964–1969	6	14
	1985–1992	9	16
	2003–2004	2	11
NY	1932	1	
	1943–1946	4	11
	1965–1969	5	19
	1983–1992	10	14
	2003–2004	2	11
BC	1962–1964	3	
	1970–1978	9	6
	2000–2003	4	22
MQ	1986–1990	5	
	2002–2004	3	12
SQ	1979–1985	7	
	2001–2004	4	16
UF	1831–1836	6	
	1888–1890	3	52
	1892–1896	5	2
	1917–1925	9	21
	1942–1948	7	17
	1955–1960	6	7
	2000–2003	4	40
TK	1950–1953	4	
	1955–1957	3	2
	1976–1981	6	19
	2001–2004	4	20
GA	1858–1863	6	
	1916–1918	3	53
	1944–1948	5	26
	1963–1971	4	20
	1989–1996	8	18
CM	**1964–1967**	**4**	
	1994–1998	**5**	**27**
CR	**1964–1968**	**5**	
	1996–2002	**7**	**28**
RW	**1939–1946**	**8**	
	2002–2004	**3**	**56**
KG	**1971–1979**	**9**	
	1996–2004	**9**	**17**

Note: See Table 1 for site names.

limited to only a reduction in annual growth (Gibson 1972; Ades et al. 1992). Similarly, the FIDS records did not identify any economically important forest health agent in the immediate study area that would explain the decreasing trend in the sample size. Outbreaks identified in the regional time series reached peak percentages of 24% of trees infected during the mid-1960s and by the late 1970s and 1980s increased to 29% over the sampled stands. By 2003, peak percentages had surpassed previous recorded levels of infection and continued to increase to 62% of the sampled area by 2004. This suggests that the current outbreak is

more extensive than previous outbreaks. These findings support recent survey reports of an increase in disease spread and severity in the study area since the mid-1990s (Woods 2003). Our regional outbreak reconstruction shows that Dothistroma has had a long history in the study area and in the past has persisted at low levels in the host population. The recent increase in outbreak spread and severity provides evidence that Dothistroma is an emerging native disease.

Climate variability in British Columbia is thought to be driven by cyclic changes in ocean surface temperatures, specifically those related to the Pacific Decadal Oscillation (PDO) and the El Niño Southern Oscillation (Stahl et al. 2006). Warmer phases of the PDO are associated dry conditions in British Columbia and the cool phase with wet conditions (Mantua and Hare 2002). However, precipitation levels in the northwest have increased markedly from earlier decades and appear to be independent of the trends in the PDO (Woods et al. 2005). It has been suggested that the current trend in precipitation patterns is more likely a part of directional climate change rather than a result of the influence of the PDO (Woods et al. 2005). The complexities of climate change, and the biotic responses to this, make causation difficult and are seldom directly documented. Woods et al. (2005) found a clear spatial correlation between areas subjected to the recent increases in mean summer precipitation and those affected by the current epidemic. It is therefore likely that the current Dothistroma epidemic is due to a climate-driven change. Our results support these claims of a link between short-term directional climate change and increases in disease spread and severity.

The most distinct change that we observed in the outbreak history was the obvious synchrony among sampled sites during the current outbreak (Fig. 6). Examination of the regional time series showed a number of peak outbreak periods common among all of the trees, further demonstrating synchrony (Fig. 7). Spatial synchrony refers to changes in abundance that are coincident among geographically distant populations (Liebhold et al. 2004). While synchrony is easily detected, the causes can be elusive. Broad-scale spatial synchrony of population dynamics is often attributable to deviations from average weather conditions that tend to extend over large areas (Liebhold et al. 2006). Prolonged periods of warm and wet weather are considered to be optimal conditions for development of Dothistroma (Harrington and Wingfield 1998). Peterson (1973) found that the majority of *D. septosporum* spores were released during periods of warm rain or heavy mist. Longer wetness periods were also shown to relate to an increase in the severity of infection (Gadgil 1977). Since the 1970s, the frequency of warm rain events have been increasing in northwestern British Columbia (Woods et al. 2005). Woods et al. (2005) found that spikes in these weather events during the early 1960s and 1980s corresponded to the timing of two Dothistroma outbreaks identified by the FIDS. The 1960s, 1970s, and 1980s outbreak peaks in the regional time series coincide with the timing of the FIDS records and increases in precipitation levels identified by Woods et al. (2005). The current, much more severe epidemic is also thought to be a result of a marked increase in the frequency of these warm rain events observed during the mid- to late 1990s. These weather events may be a common trigger, called the Moran effect,

Fig. 8. Percentage of trees recording an outbreak for each variant: (A) ICHmc1, (B) ICHmc2, and (C) SBSmc2. Plots within each bar graph indicate the number of trees (or sample size) included in the reconstruction for each year.
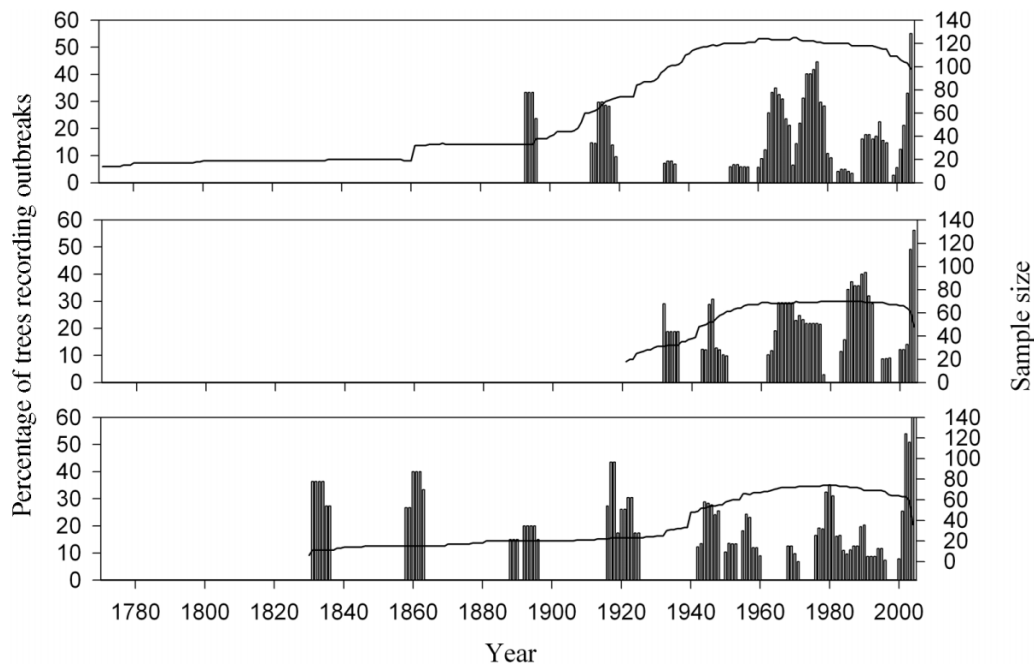
that acts sporadically to synchronize *D. septosporum* populations that are oscillating at different densities over the landscape (Myers 1998). It is likely, therefore, that recent increases in summer precipitation and, more specifically, warm rain events over large areas represent an environmental trigger that synchronized the current outbreak causing the widespread emergence of the disease. More detailed analyses on the relationship between climate and outbreak history will help quantify the effects of climate change on disease spread and development, which will allow better predictions of future impacts of climate change on forest health.

Differences in outbreak pattern and impact among ecological variants could be explained by environmental heterogeneity that leads to varying suitability for disease. The ICH zone is characterized by warm, moist summers and cold winters, while the SBS zone is more continental. The ICHmc1 is somewhat transitional between the ICHmc2 and SBSmc2, which may explain the similarity in outbreak pattern observed between the ICHmc1 and SBSmc2. The warmer and wetter climatic conditions of the ICH zone may explain the observed increases in the severity and spread in that zone compared with outbreaks recorded from sites in the SBS zone. Greater synchrony among sites from both the ICHmc1 and ICHmc2 was also observed. The notable increase in disease intensity and spread after the 1960s in the ICH zone corresponds to the onset of industrial forest management in the area. Forest management practices over the past 30 years have increased host abundance in the ICH zone. Lodgepole pine comprises ~40% of managed stands compared with 10% in natural, unmanaged forests (Woods 2003; Woods et al. 2005). The increase in available hosts on the landscape could have contributed to a buildup of inoculum that may explain the observed increase in severity and spread over time of Dothistroma needle blight. The involvement of human-mediated loss or modification of biodi-

versity is being increasingly recognized as a major factor in the recent increase in emerging diseases (Anderson et al. 2004). This same hypothesis has been raised repeatedly in the coastal forests of Oregon and Washington where an epidemic of the endemic Swiss needle cast (*Phaeocryptopus gaeumannii* (T. Rohde) Petr.) is causing severe defoliation in Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) plantations (Hansen et al. 2000). Strong economic incentives in recent decades have converted many lowland coastal areas previously occupied by a mixture of hardwoods, spruce, and hemlock to pure stands of Douglas-fir. This increase in the proportion of Douglas-fir, along with a documented increase in favourable climate conditions, has enabled *P. gaeumannii* to increase above historically normal levels, leading to an increase in inoculum pressure (Hansen et al. 2000). Similarly, high disease severity during the current outbreak of Dothistroma is probably due in part to a greater number of available hosts. Further research is needed to examine how forest management may have increased the risk of Dothistroma needle blight in the area.

Acknowledgements

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