The Relationship Between Climate And Outbreak Dynamics Of Dothistroma Needle Blight In Northwest British Columbia, Canada

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B.Sc., Trent University, 2004

Thesis Submitted In Partial Fulfillment Of

The Requirements For The Degree Of

Master Of Science

in

Natural Resources And Environmental Studies

(Biology)

The University Of Northern British Columbia

March 2007

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ISBN: 978-0-494-28456-8
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ISBN: 978-0-494-28456-8

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ABSTRACT

Until recently, Dothistroma needle blight caused by *Dothistroma septosporum* (Dorog.) Morelet has been uncommon and of little concern in lodgepole pine (*Pinus contorta* var. *latifolia*) stands in western North America. Since the mid-1990s, severe damage to managed and natural stands of lodgepole pine has been reported from northwest British Columbia. We used dendrochronological techniques to reconstruct the spatial and temporal patterns of the outbreak histories of Dothistroma needle blight in the area. We collected and analyzed tree-ring samples from sites where the disease had been identified in past survey records. By comparing the radial-growth response of spruce (non-host) with that of lodgepole pine (host) in nearby spruce-dominated stands, a characteristic tree-ring signature was identified and applied to tree-ring series from 19 additional sites throughout the study area. Our reconstructions suggest that Dothistroma needle blight 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 was the greater severity and synchronicity among the sites during the current outbreak.

Because yearly differences in weather are known to result in considerable annual variations in the amount of infection by Dothistroma needle blight, it was important to focus on the impacts of local climate variability on disease incidence. Comparisons of climate reconstructed from tree rings of lodgepole pine and distant, long-term weather station data were used to determine whether our climate reconstructions represent climate variability differently than more regional climatic patterns. We found that climate data from long-term weather stations though geographically distant, were equally

representative of climate variability in the study area, and we used this data to evaluate relationships between climate and Dothistroma needle blight outbreaks.

A trend towards increased minimum temperatures appears to be the most important climate factor contributing to outbreaks of the disease; peaks in the outbreaks directly coincide with peaks in August minimum temperature. It also appears that peaks in these warm periods correspond to increases in spring precipitation levels, and both show an increasing trend over the last ~40 years. Since 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. This suggests that climate in northwest British Columbia 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 Dothistroma needle blight resulting in widespread, synchronous outbreaks. If this is due to climate change, as has been suggested, this has serious implications for the future extent of Dothistroma needle blight and the health of lodgepole pine in British Columbia.

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ACKNOWLEDGEMENT

I would like to thank my committee members for all their support and encouragement. Special thanks to Alex Woods for all the help in the field and willingness to share his knowledge. Most importantly, I would like to thank my supervisor Kathy Lewis for her guidance and persistent help throughout my thesis, a true mentor. I would also like to acknowledge my external examiner James Speer whose previous work on Pandora moth was instrumental in the development of the methods for this research project.

I acknowledge the Forest Science Program and Ministry of Forests for their financial support for the project.

Finally, I would like to thank my partner Todd for his emotional support throughout my masters, as well as my dog Copper who was my most reliable field assistant.

To Nana and Popeye.

PREFACE

Dothistroma needle blight is an economically important forest disease, which causes serious defoliation of exotic pine. The fungus responsible for the disease, *Dothistroma septosporum* (Dorog.) Morlet infects the needles, leading to needle death and reduced yield. Until recently, Dothistroma needle blight has been uncommon and of little concern in lodgepole pine (*Pinus contorta* var. *latifolia*) stands in western North America. Since the late-1990s, severe damage to managed and natural stands of lodgepole pine has been reported from northwest British Columbia. Historically, the effect of defoliation on native host trees was a reduction in growth, and decline in tree vigor. Recently, however, this has dramatically changed in British Columbia where high levels of mortality have been documented.

Dothistroma needle blight poses a significant threat to the growth and yield of lodgepole pine in northwest British Columbia. Both increased host density and favourable weather patterns have been suggested as major catalysts of the current spread and severity of the disease. More extensive and longer records of past Dothistroma needle blight outbreaks are imperative to assess how outbreak dynamics have changed through time. The purpose of this research is to compare the influence of climate on the extent and nature of past Dothistroma needle blight outbreaks to understand the spatial and temporal variations of the disease in lodgepole pine-dominated forests of northwest British Columbia. The main objectives of this thesis were: (1) to reconstruct the outbreak history of Dothistroma needle blight at multicentury time scales through dendrochronological techniques; (2) to identify the best climate or proxy data to document historical climate; and (3) to determine the relationship between climate and the historical outbreak dynamics of the disease.

Chapter 1 introduces the current impacts of the disease worldwide, with emphasis on the severity and spread of the disease in northwest British Columbia. Possible factors involved in the current epidemic, such as recent changes in climate and forest structure, are also discussed. The importance of long-term outbreak reconstructions to improve our understanding of the pathogen is outlined.

Chapter 2 is a review of the general biology, geographic distribution of damage, and management and control strategies of the disease. The methods and techniques used to reconstruct disturbance histories of Dothistroma needle blight are also discussed.

Chapter 3 examines the extent and nature of past Dothistroma needle blight outbreaks in the forests of northwestern British Columbia. Dothistroma-specific criteria are developed and used to reconstruct outbreak histories using dendrochronological techniques. Basic outbreak characteristics, including frequency, magnitude, and longevity are used to determine the temporal and spatial variation of the disease. Differences in outbreak patterns between two distinct ecological zones are compared: Interior Cedar Hemlock zone (ICH) and Sub-boreal Spruce zone (SBS). Disease dynamics in highly managed areas where inoculum loads may be high due to the prevalence of young pine are compared to more remote sites to examine whether differences in outbreak frequency may be a result of industrial forest management practices.

In Chapter 4, climate is reconstructed using tree-rings from lodgepole pine trees from a number of sites in northwest British Columbia. The reconstructions are compared to long-term weather station data to determine whether the climate reconstructions recorded climate variability that was locally unique. The purpose of this study is to identify the longest and most spatially representative climate records available.

Chapter 5 documents the relationship between historical Dothistroma needle blight outbreaks and climate variables conducive to disease spread and severity, and to relate these to observed regional outbreak patterns. It was anticipated that these findings could provide an opportunity to present further perspectives on the likely responses of Dothistroma needle blight to climate change in northwest British Columbia.

In Chapter 6, the results of the individual studies are integrated, drawing final conclusions regarding the effects of climate on disease occurrence and the possible management implications to mitigate further risk of Dothistroma needle blight to lodgepole pine-dominated forests in British Columbia.

CHAPTER 1

INTRODUCTION

1.1 Global distribution and severity of Dothistroma needle blight

Dothistroma needle blight is an economically important forest disease which causes serious defoliation of many coniferous trees, particularly pine when planted out of their native range (Bradshaw *et al.* 2000). The fungus responsible for the disease, *Dothistroma septosporum* (Dorog.) Morelet infects the needles, causing premature needle death and reduced tree growth (Bradshaw *et al.* 1997). Defoliation caused by this fungus has resulted in complete failure of many exotic pine plantings in New Zealand, South Africa and South America (Peterson 1967, Gibson 1972, Bradshaw *et al.* 1997).

Until recently, Dothistroma needle blight has been uncommon and of little concern in lodgepole pine (*Pinus contorta* var. *latifolia*) stands in western North America. During the past decade, however, the frequency of observations of the disease has increased and it is affecting pine species in their native ranges in addition to those planted as exotics (Bradshaw 2004). Currently, the disease has been reported to affect over 60 *Pinus* species in 45 countries (Ivory 1994). In particular, reports from northwestern British Columbia show severe damage to managed and natural stands of lodgepole pine. For instance, recent low-level aerial surveys conducted over 40,000 ha of lodgepole-dominated managed stands showed 92% to be suffering varying degrees of damage. The foliar disease is now so prevalent and chronic that entire plantations of lodgepole pine are failing (Woods 2003), and the severity is such that mature pine trees are also succumbing (Woods *et al.* 2005).

The situation in British Columbia is unique. Dothistroma needle blight is internationally considered a serious forest pathogen only in exotic plantations in the Southern Hemisphere (Gibson 1972, Bradshaw *et al.* 2000). The damage being reported in British Columbia is an example of disease severity in the Northern Hemisphere, where hosts are native, and mature stands are affected (Woods *et al.* 2005). Historically, the effect of defoliation on native host trees was a reduction in growth, and decline in tree vigor (Ades *et al.* 1992). Recently, however, this has dramatically changed in the northern temperate forests of British Columbia where high levels of mortality have been documented. It is imperative that these changes in the extent and nature of Dothistroma needle blight outbreaks be better understood to try to avoid future epidemics and to develop comprehensive strategies for management of lodgepole pine in British Columbia.

1.2 Changes in climate conditions

The current outbreak of Dothistroma needle blight in northwest British Columbia is much larger than what has been observed in the recorded past. Woods *et al.* (2005) found that directional climate change towards an increased frequency of warm rain in the mid-to-late 1990s coincided with the sharp increase in the severity of the current epidemic. Peaks in mean summer precipitation were also shown to correspond with the timing of two documented outbreaks of the disease during the 1960s and 1980s. In general, very few studies have quantified the potential impact of climate change on forest pathogens and the diseases they cause. This is despite the fact that forest diseases are heavily dependent on prevailing weather events and no disease can develop in the absence of conducive weather conditions (Chakraborty *et al.* 1998). Foliar disease fungi may be some of the most responsive pathogens to climate change (Woods *et al.* 2005). Therefore, it is imperative that we quantify the effects of climate variability on the occurrence of past Dothistroma needle blight outbreaks to allow better predictions of future impacts of climate change on forest health.

1.3 Changes in forest structure

Some argue that current Dothistroma needle blight outbreak levels in northwest British Columbia are largely a consequence of forest management policies and practices in the area (Woods *et al.* 2005). Forest management practices over the past five decades in temperate and boreal forests of Canada have concentrated on even-aged, single-species stands. Many have argued that these attempts to simplify ecosystems and reduce their variability have caused managed ecosystems to become less resilient to disturbance or stress (Holling and Meffe 1996, Lewis and Lindgren 2000, Woods 2003). This is most evident in the Interior Cedar-Hemlock (ICH) zone (Pojar *et al.* 1987) of northwest British Columbia. Since the early 1980s, management policies have attempted to convert a landscape comprised primarily of western hemlock and true firs to one dominated by spruce and lodgepole pine (Woods 2003). For instance, prior to 1975 lodgepole pine represented <10% of the landbase in northwest British Columbia compared to the current 40% of reforested harvest area. Undoubtedly extensive planting of lodgepole pine has increased host abundance in the area (Woods 2003, Woods *et al.* 2005), but the influence of forest management practices and host availability on the incidence of Dothistroma needle blight is unknown. The increase in host abundance may have allowed a build up of inoculum over time which, until now, had not reached epidemic levels because of unfavourable climate conditions.

1.4 Historical records of past outbreaks

Few survey records of Dothistroma needle blight exist for northwest British Columbia. The first published survey recording the incidence of the disease occurred in the Skeena-Stikine Forest District in 1963 (Parker and Collis 1966). Annual Forest, Insect, and Disease Survey reports (FIDS) for 1984 described a small but intense infestation in a young lodgepole pine stand in the Interior Cedar Hemlock zone (ICH) in the same forest district (Unger and Humphreys 1984). By 1986 the disease was recorded as subsiding in the area. No more records of the disease were identified in the FIDS surveys up to 1995, when the survey program was discontinued. The first lodgepole pine plantation failure resulting from the current Dothistroma needle blight epidemic was identified in1997. Since 2002, aerial surveys have identified close to 4000 hectares of lodgepole pine plantation failures due to the disease in northwest British Columbia (Woods *et al.* 2005). Current damage in these plantations is recorded as most severe in the ICH zone where climate is characterized by a warm and humid temperate weather system. In addition to plantations, scattered mortality has been recorded among isolated mature pine trees in mixed-species stands, where pine represents only a small proportion of the stand composition (Woods *et al.* 2005).

Historical reports from the Canadian Forest Service (CFS), Forest Pathology Herbarium database also indicate a number of recorded observations of the foliar fungus in the study area. The earliest of these collections was near Terrace, British Columbia in 1941. Two additional collections were made near Hazelton in 1976 and 1977. The purpose of this database was to document and assist in the identification of fungi occurring on native plants in the province of British Columbia. Therefore, rarely did these reports list information about the magnitude or severity of the infection, and location coordinates for earlier records were never precise.

1.5 Problem statement and research questions

Dothistroma needle blight poses a significant threat to the growth and yield of lodgepole pine in northwest British Columbia. Studies suggest that the current outbreak is much larger than what has been observed in the recorded past (Bradshaw 2004, Woods *et al.* 2005). Changes in weather conditions towards more frequent warm rain events appear to be the principal cause of the current epidemic (Woods *et al.* 2005). However, there are no studies investigating multicentury histories of Dothistroma needle blight outbreaks and their relationship with climate. More numerous and longer reconstructions of past Dothistroma needle blight outbreaks are clearly needed to improve our understanding of this disturbance agent. The purpose of this research was to compare the influence of climate on the extent and nature of past Dothistroma needle blight outbreaks to understand the spatial and temporal variations of the disease in the forests of northwest British Columbia.

This study will address several important questions concerning the dynamics of Dothistroma needle blight and its relationship to climate. Specifically:

- Are past outbreaks evident in the tree-ring record?
- How has the frequency, magnitude (i.e., spatial extent and intensity), and longevity of outbreaks varied over time?
- How do outbreaks differ between the sub-boreal and coast-interior transition ecosystems?

- Have climate conditions conducive to disease incidence existed in the past, and if so are they accompanied by an outbreak?

1.6 Study objectives

The specific objectives of this study were as follows:

- Determine if Dothistroma needle blight caused a distinguishable suppression pattern in lodgepole pine tree-ring width.
- Reconstruct the outbreak history of Dothistroma needle blight using dendrochronological techniques over multicentury time scales.
- Investigate the dynamics of past outbreaks.
- Determine the relationship between outbreak history and climate, using the longest and most spatially representative climate information available.

1.7 Overview of methodology

To reconstruct a record of past Dothistroma needle blight outbreaks host (lodgepole pine) and non-host (spruce) increment cores were collected from five known historic outbreak sites. Radial growth was compared between host and non-host species to remove variation due to shared factors such as climate, and to identify periods of reduced growth observed only in the host species as possible periods of disease outbreak. A characteristic ring-width suppression pattern from the known outbreaks was used to calibrate the program OUTBREAK (Holmes and Swetnam 1996) to consistently and confidently identify periods of host growth suppression as evidence of Dothistroma needle blight outbreaks. The percentage of trees affected by each of the identified outbreaks was calculated, and a ≥ 40% threshold was set to separate significant outbreaks from apparent smaller defoliation events. The resulting criteria were applied simultaneously to identify probable pre-record outbreak signals in 19 individual sites. The regional composite time series presented in this study is the first reconstruction of outbreaks caused by a foliar pathogen in North America.

In northwest British Columbia, the required temporal and spatial coverage of meteorological data is limited. Therefore, the climate sensitivity of long-lived tree species offered an opportunity to develop histories of past climate fluctuations preserved in the tree-ring record. Areas sensitive to climate fluctuations, such as rocky outcrops and valley slopes, were selected as sites for our climate reconstructions. Transfer function models predicting climate from the residual chronologies were calibrated using a linear regression. The modeled relationships were confirmed using various statistical verification techniques. Statistically stable models were then used to reconstruct a record of climate prior to the period of instrumental climate data. Each climate reconstruction was compared to meteorological data extracted from geographically distant, long-term weather stations at Fort St. James and Terrace, British Columbia (Environment Canada 2006) to determine whether the climate reconstructions recorded climate variability that was locally unique to the study area. These results were used to determine the best available record of climate variability for comparisons with our outbreak reconstructions.

The regional outbreak chronology was then compared with the climate records to determine whether temporal changes in the outbreak patterns may be related to favourable climate variations. A stepwise regression and graphical comparisons were used to identify relationships between climate and outbreak occurrence.

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CHAPTER 2

LITERATURE REVIEW

2.1. Life history and ecology of Dothistroma needle blight

2.1.1 The pathogen and disease cycle

The causal agent of Dothistroma needle blight is an Ascomycete fungus characterized by both sexual (teleomorphic) and asexual (anamorphic) forms. The teleomorphic form, *Mycosphaerella pini* E. Rostrup apud Monk, originally placed in the genus *Scirrhia* (Ivory 1967), is less prevalent than the asexual form, *Dothistroma septosporum* (Dorog.) Morelet. *M. pini* was first reported in Europe, and more recently in Alaska, California, and Oregon (Patton 1997). In 1962 it appeared on *Pinus radiata* D. Don growing in high rainfall areas of East Africa and shortly after in New Zealand (Gibson 1972, Marks *et al.* 1989). However, many of these reports remain unconfirmed (Bradshaw 2004). Both forms are found in British Columbia, which has lead to speculation of its indigenous origins in the area (Funk and Parker 1966).

Dothistroma septosporum is a primary pathogen that invades and kills pine foliage (Gibson 1972). The disease is characterized by distinct brick-red bands (1-3mm wide) around the needles that can appear within weeks of infection (Shain and Franich 1981). The red colour is due to the production of a toxin, dothistromin. The toxin diffuses into tissue in advance of the hyphae, killing cells and resulting in their collapse (Shain and Franich 1981). Sporulation occurs shortly after the death of the needle tissue, by the formation of minute black stromata (fruiting bodies), which emerge through the dead epidermis. Conidial masses are borne on the stromata that typically begin to mature during the spring and are passively transported by rain splash during the growing season.

The teleomorphic state of the pathogen is formed in a similar way, but consists of linear black ascostromata bearing ascospores (Gibson 1972). New infection occurs on current year or 1-year-old needles. Under optimal conditions, germination occurs and is accompanied by the emergence of a germ tube. During the early stages of infection, the germ tube undergoes a precise and genetically programmed series of morphological changes. There are conflicting reports about whether the direction of growth is random or targeted towards a stomatal pore (Peterson 1966, Gadgil 1967). The resulting morphogenic events form an appressorium, a swollen structure that adheres strongly to the leaf surface and facilitates penetration (Peterson and Walla 1978). From this, hyphae branch into intra- and intercellular regions of the mesophyll layer of the needle tissue (Ivory 1972). Hyphae growth is restricted to necrotic tissue, suggesting the necessity of dothistromin production during colonization, and subsequent massive proliferation. The host cells collapse after 32-114 days and needle symptoms appear (Bradshaw 2004). The stromata generally mature and produce conidia a year or two after infection. Difference in cycle completion are often associated with geographic area (Peterson 1966), which could have implications for the disease's relationship with climate.

2.1.2 Effects of environment on disease development

Temperature is an important factor influencing the occurrence and development of many diseases (Colhoun 1973). Although infection by *D. septosporum* is largely dependent on wet conditions, optimal temperatures during extended periods of high humidity have the ability to increase disease severity (Peterson 1967). Favourable temperatures may shorten the period between infection and the production of new spores and so influence the number of spore generations occurring during a season (Colhoun

1973). This effect on the supply of inoculum may determine whether or not an epidemic can develop. Gadgil (1974) showed that highest conidia germination percentages were recorded on needles collected four days after inoculation during continuous wetness periods and warm temperature regimes (20/12°C and 24/16°C). In the same study, temperature seemed to have an appreciable effect on infection structures. For instance, mycelial growth on needles of *Pinus radiata* at the 24/16°C regime increased after eight days compared to those observed under a lower temperature regime. In a separate study, germination was near optimal at 22°C, but decreased rapidly below 22°C or above 24°C on water agar (Peterson and Walla 1978). In contrast, Parker (1972) showed that in late incubation treatments *P. radiata* had a greater number of needles infected at lower temperatures of 21/16°C and 16/13°C, at high humidity regimes (91-100% RH) compared to the 24/21°C regime. Similarly, Ivory (1972) showed that the optimum temperature for conidia germination and apparent stomatal pit entry was approximately 17°C. The combined effects of temperature and humidity on infection vary with the stage of infection. Infection by *D. septosporum* can occur at a wide range of temperatures, but severity of the infection remains low except at warmer temperatures under continuous moisture. Thus, it appears that temperature influences disease initiation and development. It has also been suggested that temperature may affect survival of the pathogen, and subsequent development of disease (Colhoun 1973).

Wet weather is required for the release of large number of *D. septosporum* spores. Spore trap experiments are often used to examine the influence of wet weather on the quantity of spores released. For instance, Peterson (1973) used spore counts to show that the majority of conidia were released during periods of rain or heavy mist. The length of the wetness period has also been shown to have a marked effect on the severity of infection and the length of the pre-reproduction period (Gadgil 1977). For example, Gadgil (1974) showed that disease severity (% visibly infected foliage) was much higher and the pre-reproductive period of Dothistroma needle blight shorter when foliage was kept moist continuously for only 8, 24, or 48 hr after inoculation. In contrast, the process of germination and penetration by conidia may occur under dry conditions. Gadgil (1977) showed that the length of the dry period (up to 60 days after inoculation) had no direct effect on the germination percentages following deposition. These results confirm observations from a 1984 survey conducted in eastern Australia. The survey showed that a severe drought in 1982 and 1983 had not eliminated the disease in several plantations and could be attributed to the drought tolerance of spore germination (Marks *et al.* 1989). In contrast, stromata formation shows an exponential increase with decreasing number of dry days (Gadgil 1977). These results support observations in northwest British Columbia of Woods *et al.* 2005. Between June-September the amount of rainfall and temperature is a good predictive indicator of disease development (appearance of infection) (Peterson 1973). For instance, long dry periods after Dothistroma needle blight infection leads to low disease development and slower disease expression than during wet conditions. Provided the conditions necessary for initial outbreak development are present (i.e., prolonged periods of warm, wet weather) Dothistroma needle blight appears capable of subsequently tolerating much less favorable environmental conditions for extended periods of time.

Light intensity has also been shown to have a strong influence on the severity of disease (Gadgil and Holden 1976, Bradshaw 2004). For instance, the development of

Dothistroma-induced symptoms has shown to be reduced under low light conditions (Gadil and Holden 1976). Indeed, if foliage is shaded for 5-20 days after inoculation, no symptoms are seen, although soon after removal from the shade treatment symptoms develop. It has been suggested that the reduced disease seen in low light conditions is due to the nature of the host response, rather than that if the fungus or its toxin. There is no direct evidence to support this suggestion but there is some tentative evidence for the role of photosynthetically active tissue in augmenting the toxicity of dothistromin (Bradshaw 2004).

Disease development may also be influenced by host quality. Environmental stress can predispose individual pines towards greater disease susceptibility by reducing host vigor. Local environment due to topography and soil conditions has a significant impact on the quality of the host. For example, Ades *et al.* (1992) reported variation in the severity of Dothistroma needle blight among provenances and families of *Pinus muricata* in New South Wales, Australia. Two sites were chosen to represent extremes in soil types (infertile sediments) among trees planted in the area. Soil parent material was shown to be a major factor affecting severity of infection. The most extreme soil type (i.e., most infertile) was recorded as having 40% more infection and lower host growth than the less extreme site. In contrast, an observed increase in infection severity was found in lodgepole pine plantations treated with a nitrogen fertilizer east of Prince George, British Columbia, compared to nearby untreated sites (*unpublished*, K. Lewis[1]). Much of this infection variability can also be attributed to the stability of resistance among tree provenances and seed sources. Earlier studies of damage in lodgepole pine provenance

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trials showed that although provenances exhibit considerable variability in susceptibility to forest disease, resistance to disease is related to seed source of different geographic origins (Ying and Hunt 1987). For example, Ying and Hunt (1987) assessed 41 lodgepole pine provenance sites in the central and southern interior of British Columbia for stability of resistance to *Lophodermella concolor* (needle cast). As a result, it was evident that resistance of pine to *L. concolor* was essentially a population characteristic under strong genetic control. That is, elevation of seed origin had a significant effect on the level of resistance to infection; susceptibility increased with seed source elevation. Therefore, seed transfers of distinct geographical origins can compromise the resistance stability of the host by exposing individuals to below optimal environmental conditions. Reduced host productivity and physiological performance, such as disease resistance, may be a factor contributing to disease incidence and severity of Dothistroma needle blight.

2.2 Geographic distribution and damage

The most widespread and extensively studied foliar disease in temperate forests is Dothistroma needle blight of pines (Harrington and Wingfield 1998, Bradshaw 2004, Woods *et al.* 2005). Severe outbreaks of the disease have threatened the forest industry in a number of exotic pine plantations (Peterson 1966, Gibson 1974). Dothistroma needle blight first gained prominence as a pest of *Pinus radiata* plantations in the Southern Hemisphere, devastating extensive plantations in Brazil, Kenya, Zimbabwe, New Zealand, and South Africa (Gibson 1972). In New Zealand, this highly susceptible host species was planted on 400,000 ha, which resulted in considerable crop failure due to Dothistroma needle blight (Marks *et al.* 1989). In the 1940s, *P. radiata* was planted extensively in East and Central Africa, but due to severe infection by Dothistroma needle blight further plantings were suspended (Gibson *et al.* 1964). Today, sporadic outbreaks of the disease continue to reduce productivity of the *P. radiata* plantations in various parts of the Eastern Cape Province, South Africa. In North America, the disease gained some notoriety after the failure of ornamental, shelterbelt, and Christmas tree plantings (Peterson 1966), but was not deemed important enough for large-scale surveys of damage and impact (Patton 1997). Since 1992 there have been reports of increased incidence in Europe and the United States, as well as new outbreaks in other parts of the world (Bradshaw 2004), such as in northwest British Columbia (Woods 2003, Woods *et al.* 2005).

Historically, the most immediate effect of defoliation by Dothistroma needle blight was the reduction in growth (Ades *et al.* 1992). Wood yield loss is approximately proportional to disease severity (defoliation level), particularly when young photosynthetically active needle are affected (Gibson 1972). The ultimate effect of defoliation on growth is strongly influenced by the species, resistance, and the physiological condition of the tree (Ivory and Paterson 1969, Gibson 1972). Recently, however, this has dramatically changed in the northern temperate forests of British Columbia where high levels of mortality are now occurring in plantations that were affected earliest. The mortality found in mature lodgepole pine stands is globally unprecedented and illustrates the unpredictable nature of a changing climate on forest diseases (Woods *et al.* 2005).

2.3 Management and control

2.3.1 Host resistance

Resistance to *D. septosporum* infection has been observed within many species of pine. In East Africa, Ivory and Paterson (1969) observed 10 to 15-year-old *P. radiata* trees showing outstanding health, combined with acceptable size and form, in otherwise severely diseased plantations. Such trees are often regarded as carrying some inherent resistance to the blight, as their position in the midst of a severely infected crop make it most unlikely that they were chance escapes.

Disease susceptibility varies with host species. For example, *P. attenuata, P. ponderosa,* and *P. radiata* are highly susceptible, although *P. radiata* develops resistance at about 10-15 years of age. Species showing some level of natural resistance include *P. patula, P. tacda*, and *P. sylvestris* (Gibson 1972). Because lodgepole pine has never been considered to be at risk, little is known about its resistance capabilities. Surveys have documented severe levels of infection in northwest British Columbia, which may indicate that lodgepole pine is a highly susceptible species. However, much of this effect may be caused by a combination of exogenous factors rather than those that are genetic in nature, such as the larger numbers of hosts on the landscape and weather more suitable for disease development.

2.3.2 Control strategies

More than 60 pine species are known to be hosts, and in North America alone Dothistroma needle blight has been found on 29 pine species and hybrids, including two-, three-, and five-needle pines (Ivory 1994, Patton 1997). Control for Dothistroma needle blight in commercial forests has been practiced by breeding resistant plant stock and by spraying fungicide. In New Zealand, successful aerial spray programs were developed with copper-based fungicides in which sprays were applied when the overall infection level of unsuppressed green crowns reached >25%, and the total number of trees infected in the area reached 50% (Kershaw *et al.* 1988). As many as seven or eight applications were required until the plantations became resistant at approximately 20 years of age. Cost-benefit models did not determine whether there is a real financial benefit because of the high cost of spraying on a commercial scale (van der Pas *et al.* 1984). However, applications in many other countries have continued to prevent loss of wood yield and minimized potential human health hazards posed by the dothistromin toxin (Bradshaw 2004).

Breeding programs have achieved additional control, and a reduction in fungicide environmental impact and cost. Natural variation in resistance was noted within many species of pine, including *P. radiata.* As a result, breeding trials showed high heritability of a resistant trait in *P. radiata*, which lead to the development of a Dothistroma-resistant family (Carson 1989). In New Zealand, this family was estimated to have 15% less disease, and to cost 56% less in chemical spray compared with control trees (Bradshaw 2004). However, where site conditions are favourable for disease development, the degree of resistance observed in *P. radiata* was insufficient to contain the disease at economically acceptable levels (Ades *et al.* 1992). Therefore, recognizing those environmental conditions that cause an epidemic will help identify high-risk situations and aid in the development of sustainable management practices. A particular advantage of tree-ring reconstructions is that they provide the necessary temporal length for evaluating past relationships between climate and disease behaviour and whether any change in the pathogen's environment has played a role in the current epidemic.

2.4 Dendrochronology, crossdating, and standardization

In dating of past historical and natural events, the most common techniques are derived from the field of dendrochronology (Fritts 1976). Forest ecosystems are unique, because high-resolution histories of disturbance and other environmental variations can be preserved for centuries in the tree-ring record (Speer *et al.* 2001). Dendrochronological techniques have been used to reconstruct disturbance histories and environmental change over broad temporal and spatial scales (Fritts 1976, Speer *et al.* 2001, Ryerson *et al.* 2003). Tree-ring reconstructions are particularly important where instrumental records or historical observations of natural phenomena are limited (Case and McDonald 2003), such as with the limited records of climate and outbreaks of Dothistroma needle blight.

Crossdating is the most important principle of dendrochronology (Fritts 1976). The principle refers to a type of environmental control that ensures each ring-width is placed in its proper time sequence (Fritts and Swetnam 1989). That is, if there is sufficient covariation among rings in different trees and the sample is large enough, the year in which each ring was formed can be correctly ascertained. Crossdating is possible because all trees at a site are limited by the same or similar environmental conditions, and the year-to-year fluctuations in the limiting condition produce synchronous variations in ring structure (Fritts 1976). As a result, dendrochronology is the most accurate tool available for dating natural phenomena in forest systems; among other applications, it has been used to date historical objects (e.g. Dean 1978), fire scars (e.g. Swetnam and Betancourt 1990), and reconstructions of climate (e.g. Briffa *et al.* 1983).

Absolute values of tree-ring widths are functions of multiple factors, including tree age, climate variations, endogenous and exogenous disturbances, and genetics (Ryerson *et al.* 2003). This is why dendrochronologists standardize tree-ring widths prior to quantitative analyses. For example, it is recognized that the relative effects of age-related impacts on growth must be removed and transformed into a stationary index prior to interpretation (Fritts and Swetnam 1989); otherwise the relative changes in other factors can be masked (Ryerson *et al.* 2003). This procedure reduces the variance among cores and transforms ring widths into dimensionless index values. Many deterministic and/or stochastic standardization methods are available. The deterministic methods typically involve fitting an *a priori* defined mathematical model of radial growth to the ring-width series, by the method of least squares. The stochastic methods are more data-adaptive, and often are chosen by *a posteriori* selection criteria (Fritts 1976, Fritts and Swetnam 1989). It is important that the estimation and removal of growth trends from tree-ring series are based on intended application of the tree-ring data. This means that there should be an expectation of what the signal of interest is in the ring-width measurement (i.e., outbreak). Given this expectation, the method of detrending should be chosen that reduces the low-frequency noise not associated with the signal (Cook and Kairiukstis 1990). With the variance stationary, the indices can be averaged with the indices from other cores and trees, to obtain an average chronology for a site.

2.5 Importance of sample size

To ensure that a chronology is representative of stand history rather than the idiosyncratic growth patterns of a few trees, it is desirable to include as many increment cores in the sample as possible. The number of cores included in a chronology generally decreases towards earlier dates (Veblen *et al.* 1991). Thus, to extend chronologies, cross-dated series from dead trees are combined with those of live trees. Numerous studies have found that incorporating cores from dead standing trees substantially improves the interpretability of a stand chronology (Veblen *et al.* 1991). For example, dead, downed tamarack and black spruce trees were sampled to increase the sample depth through periods prior to the 20th century. As a result, tamarack and black spruce ring-width series extended back 330 and 327 years, respectively. Increasing the number of radii assessed ensured accuracy of dating early larch sawfly outbreaks (Case and MacDonald 2003). In another study, the incorporation of samples from dead-standing trees was shown to increase sample size and reveal patterns in the early history of spruce beetle outbreaks that may have not been detected if samples only from live trees were used (Veblen *et al.* 1991).

2.6 Methods of outbreak reconstructions

2.6.1 Host and non-host chronology comparisons

The host and non-host comparison is a preliminary procedure carried out where climate variations are removed (or "corrected") from host tree-ring indices for outbreak reconstructions (Swetnam *et al.* 1985). Similarity in the host and non-host climate response is necessary to provide precise estimates of reduced growth for criteria development. This correction procedure is explained in the next section. The objectives of the host and non-host comparison are to determine if: (1) the effects of current or past outbreaks are detectable as a decrease in the growth of individual host trees with no corresponding decrease in the non-host chronology; (2) the growth trends of the host and non-host trees are generally similar; and (3) the chronology statistics of the host and non-host are generally similar, with exception of differences due to outbreak effects (Swetnam *et al.* 1985). These comparisons determine whether the non-host species is a good estimate of average expected growth of host tree during an outbreak (i.e., a suitable climate control species).

2.6.2 Correcting the host chronology

Climate variation contained in the host index series is corrected through the subtraction of the non-host index series. This technique is based on the assumption that non-host and host trees respond in a similar manner to climate variations. Therefore, the differences (or residuals) between standardized ring-width chronologies of the non-host and host trees will primarily reflect non-climatic environmental variables (Speer *et al.* 2001). As a result, the corrected host-tree indices served as a record of radial growth with the climate signal reduced or eliminated and can be used to quantify outbreak-induced growth reductions. Swetnam and Lynch (1989) found that this "correction" procedure was necessary to consistently and confidently identify western spruce budworm outbreaks within and among host trees and stands. The computer program OUTBREAK (Holmes and Swetnam 1996) automates the correction procedure.

To verify outbreaks, documented records must be compared with the timing of the periods of growth reduction. Historical outbreak documentation is often limited; therefore, screening criteria are developed from characteristics of known outbreaks years that can be used to identify earlier growth reductions as pre-record outbreaks. In selecting these criteria, it is also important to rely on published descriptions and comparisons of other possible disturbance agents in the area of study. The basis of the criteria, theoretically, would enable the researcher to partition outbreaks from other endogenous or exogenous disturbance pulses from the same trees by outbreak patterns typical of the disturbance agent (e.g., defoliator) (Swetnam *et al.* 1995).

2.7 Twentieth-century dynamics of outbreaks in a multicentury context

One of the most important uses of multicentury reconstructions of outbreak histories is to evaluate the hypothesis that outbreaks have become more frequent, widespread, or severe during the 20th century (Speer *et al.* 2001). The causes of these changes have been largely attributed to past management practices and the effects of climate shifts. These hypotheses speculate that: (1) human land uses have caused changes in the forest composition and/or structure that affect outbreak dynamics (Swetnam and Lynch 1989; Burleigh *et al.* 2002); and/or (2) climate changes may have caused an alteration in outbreak dynamics through changing weather effects on trees or an agents physiology (or a combination of the two) (Zhang *et al.* 1999, Case and MacDonald 2003). Both increased host density and favourable weather patterns have been suggested as a major catalyst of the current spread and severity of Dothistroma needle blight in northwest British Columbia (Woods *et al.* 2005). Multicentury histories of Dothistroma needle blight dynamics, however, have not been previously studied. A distinct advantage of having long time series for studying outbreak dynamics is that multiple examples of disease cycles or other behaviours through time may be obtained, and it may also be possible to assess how outbreak dynamics have changed through time (Speer *et al.* 2001).

This study will emphasize the importance of long time series for evaluating forest disease dynamics and their exogenous controls.

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CHAPTER 3

MULTICENTURY HISTORY OF DOTHISTROMA NEEDLE BLIGHT DYNAMICS IN NORTHWEST BRITISH COLUMBIA, CANADA

3.1 Abstract

Until recently, Dothistroma needle blight caused by *Dothistroma septosporum* (Dorog.) Morelet has been uncommon and of little concern in lodgepole pine (*Pinus contorta* var. *latifolia*) stands in western North America. Since the mid-1990s, severe damage to managed and natural stands of lodgepole pine has been reported from northwest British Columbia. We used dendrochronological techniques to reconstruct the spatial and temporal patterns of the outbreak histories of Dothistroma needle blight in the area. We collected and analyzed tree-ring samples from sites where the disease was present. By comparing the radial-growth response of spruce with that of lodgepole pine in nearby but separate stands, a characteristic tree-ring signature was identified and used to reconstruct the outbreak history of the foliar fungi. Our reconstructions suggest that Dothistroma needle blight 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 was the greater severity and synchronicity among the sites during the current outbreak. These findings support claims of a short-term directional change in climate as a factor causing the current epidemic. Differences in outbreak pattern and impact were also observed between three biogeoclimatic variants. The warmer and wetter climates of the two variants from the Interior Cedar Hemlock zone may explain the observed increases in outbreak severity and spread. It is clear from this study that more research is needed to

examine how past climate and forest management has increased the risk of Dothistroma needle blight in the area.

3.2 Introduction[1]

The most widespread and extensively studied foliar disease in temperate forests is Dothistroma needle blight of pines. The fungus responsible for the disease, *Dothistroma septosporum* (Dorog.), Morelet infects the needles, causing necrotic lesions and premature needle drop (Bradshaw *et al.* 1997). Severe outbreaks of the disease have caused complete failure of many exotic pine plantings in New Zealand, South Africa, and South America, especially those associated with *Pinus radiata* D. Don (Gibson 1972, Bradshaw *et al.* 1997). Because of its extensive geographic range and impact on exotic timber resources, Dothistroma needle blight is considered one of the most important diseases of pines in the world (Barnes *et al.* 2004).

Until recently, Dothistroma needle blight has been uncommon and of little concern in lodgepole pine (*Pinus contorta* var. *latifolia*) stands in western North America. During the past decade, however, prevalence of the disease has increased (Woods 2003, Bradshaw 2004). In particular, northwestern British Columbia has reported severe damage to managed and natural stands of lodgepole pine. For instance, recent low-level aerial surveys conducted over 40,000 ha of lodgepole-dominated managed stands showed 92% to be suffering varying degrees of damage. The foliar disease is now so prevalent and chronic that entire plantations of lodgepole pine are failing, and the severity of the

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[1] A version of this document will be submitted for publication under multiple authors. All data used in this study were collected by C. Welsh and a number of field and lab assistants. In this thesis I use 'we' and 'our' to reflect the involvement of others in various aspects of this work.

disease is such that mature pine trees are also succumbing (Woods 2003, Woods *et. al.* 2005).

The situation in British Columbia is unique. Dothistroma needle blight is internationally considered a serious forest pathogen only in exotic plantations in the Southern Hemisphere (Gibson 1972, Bradshaw *et al.* 2000). The damage being reported in British Columbia is an example of disease severity in the Northern Hemisphere, where hosts are native, and mature stands are affected. Historically, the most immediate effect of defoliation on native host trees is the reduction in growth, leading to substantial decline in tree vigour (Ades *et al.* 1992). Recently, however, this has dramatically changed in the northern temperate forests of British Columbia where high levels of mortality have been documented (Woods *et al.* 2005). It is imperative that these changes in the extent and nature of Dothistroma needle blight outbreaks be better understood to avoid future epidemics and to develop comprehensive strategies for management of lodgepole pine in British Columbia.

Few survey records of Dothistroma needle blight exist for northwest British Columbia. The first published survey recording the incidence of the disease occurred in the Skeena-Stikine Forest District in 1963 (Parker and Collis 1966). Annual Forest, Insect, and Disease Survey reports (FIDS) for 1984 described a small but intense infestation in a young lodgepole pine stand in the Interior Cedar Hemlock zone (ICH) (Pojar *et al.* 1987) in the same forest district (Unger and Humphreys 1984). By 1986 the disease was recorded as subsiding in the area. No more records of the disease were identified in the FIDS surveys up to 1995, when the survey program was discontinued. The first lodgepole pine plantation failure resulting from the current Dothistroma needle blight epidemic was identified in1997. Since 2002, aerial surveys have identified close to 4000 hectares of lodgepole pine plantation failures due to the disease in northwest British Columbia (Woods *et al* 2005). Current damage in these plantations is recorded as most severe in the ICH where climate is characterized by a warm and humid temperate weather system. In addition to plantations, scattered mortality has been recorded among isolated mature pine trees in mixed-species stands, where pine represents only a small proportion of the stand composition (Woods *et al.* 2005).

Historical reports from the Canadian Forest Service (CFS), Forest Pathology Herbarium database also indicate a number of recorded observations of the foliar fungus in the study area. The earliest of these collections was around Terrace, British Columbia in 1941. Two additional collections were made near Hazelton in 1976 and 1977. The purpose of this database was to document and assist in the identification of fungi occurring on native plants in the province of British Columbia. Therefore, rarely did these reports list information about the magnitude or severity of the infection. In addition, location coordinates for earlier records were never precise.

The current outbreak of Dothistroma needle blight is larger and more severe than has previously been documented. Two principle factors appear to have played a role in the development of the epidemic: (1) increased host abundance on the landscape, and (2) a shift towards weather patterns that are more conducive for disease spread. Woods *et al.* 2005 found that directional climate change towards an increased frequency of warm rain in the mid-to-late 1990s coincided with the sharp increase in the severity of the current epidemic. Peaks in mean summer precipitation were also shown to correspond to the timing of documented outbreaks of the disease. Establishing a causal relationship between host availability and disease is difficult. Extensive planting of lodgepole pine has increased host abundance in the area, starting since the early 1980s (Woods 2003, Woods *et al.* 2005). This increase may have allowed a build up of inoculum over time and, until now, had not reached epidemic levels because of unfavourable climate conditions. Although Dothistroma needle blight is considered native in the Northern Hemisphere, little is known about the history or dynamics of the disease in northern temperate forests. A longer temporal and spatial perspective of Dothistroma needle blight outbreak patterns is needed to identify factors that control episodic trends of the disease.

Dendrochronology has been used to study the response of host trees to defoliation by insects and the detection of past insect outbreaks (Veblen *et al.* 1991; Jardon *et al.* 1994; Weber and Schweingruber 1995; Girardin *et al.* 2001). Past episodes of defoliation are reflected by growth suppression in annual radial growth (Zhang *et al.* 1999). A record of disturbance histories is preserved in the tree-rings and can be unraveled by dendrochronological techniques (Fritts and Swetnam 1989). A particular advantage of tree-ring reconstructions is that they provide the necessary temporal length for evaluating outbreak dynamics, especially where instrumental records or historical observations are limited or absent (Speer *et al.* 2001, Case and McDonald 2003). This study is the first to attempt to create a dendrochronological reconstruction of a foliar pathogen.

Dothistroma needle blight poses a significant threat to the growth and yield of lodgepole pine in northwestern British Columbia. Reconstructions of past Dothistroma needle blight outbreaks are needed to improve our understanding of this disturbance agent. The purpose of this research is to determine the extent and nature of past Dothistroma needle blight outbreaks in the forests of northwestern British Columbia.

Basic outbreak characteristics, including frequency, magnitude, and longevity over time will be used to determine the temporal and spatial variation of the disease. Differences in outbreak patterns between two distinct ecological zones will be compared: Interior Cedar Hemlock zone (ICH) and Sub-boreal Spruce zone (SBS). We anticipate that outbreak patterns will differ because of differences in climatic patterns, ecological communities, and land-use histories. Disease dynamics in highly managed areas where inoculum loads may be high due to the prevalence of young pine will be compared to more remote sites to examine whether differences in outbreak frequency may be a result of industrial forest management practices.

3.3 Site Methods

3.3.1 Study area description

This study was conducted in northwest British Columbia, across four forest districts: Fort St. James, Nadina, Skeena-Stikine, and Kalum (Fig. 3.1). The study area included two biogeoclimatic zones: Interior Cedar Hemlock zone (ICH) and Sub-boreal Spruce zone (SBS). Sample areas were selected from three variants: ICHmc1, ICHmc2, and SBSmc2.

3.3.2 Biogeoclimatic classification system

The ICH zone consists of low-to mid-elevation 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 is intermediate, characterized by warm, moist summers, wet falls, and cold winters. Average annual precipitation ranges from 500 to 1200 mm (Banner *et al.* 1993).

The climax forests of the ICH are dominated by western hemlock (*Tsuga heterophylla* [Raf.] Sarg.). Lodgepole pine is typically a seral component of these forests, which occur together with subalpine fir (*Abies lasicocarpa* [Hook.] Nutt.); western redcedar (*Thuja plicata* Donn ex D. Don); hybrid spruce, a cross of white spruce (*Picea glauca* [Moench] Voss) and Sitka spruce (*Picea sitchensis* [Bong.] Carr.); paper birch (*Betula paprifera* Marsh.); trembling aspen (*Populus tremuloides* Michx); and black cottonwood (*Populus balsamifera* ssp. *Trichocarpa* Torr. & Gray). Amabilis fir (*Abies amabilis* Dougl. ex Forbes) is found at higher elevations of the zone.

The Nass Moist Cold Interior Cedar-Hemlock (ICHmc1) has a mild, humid climate, with very infrequent disturbance from fire, permitting growth of coastal tree species. The Hazelton Moist Cold Interior Cedar-Hemlock (ICHmc2) occupies the lower-elevation forests and has a warmer and drier climate. Industrial forest management is most evident in the ICH where forest management practices have caused a species shift in managed forests towards lodgepole pine and spruce (Woods 2003).

The SBS zone covers most of the interior lowland forest to the east of the ICH. The climate of the SBS zone is continental, characterized by long, cold winters and relatively short warm and moist summers. Annual precipitation is roughly 440-650 mm; less than half falls as snow. Upland coniferous forests dominate the SBS landscape. Hybrid spruce and subalpine fir are the major climax tree species in the SBS zone. Lodgepole pine and trembling aspen pioneer extensive seral stands. Lodgepole pine is common in mature forests in the drier parts of the zone (Banner *et al.* 1993).

There are three subzones of the SBS in the northwest. The SBSmc subzone is found at higher elevations and is characterized as areas of wetter climate. In the northwest, the SBSmc is represented by a single variant, the SBSmc2: the Babine Moist Cold Sub-Boreal Spruce.

3.3.3 Site selection

Five known historic Dothistroma needle blight outbreaks, with sufficient location information, were identified. Four were in the northwest and one in the Prince George Region. Two stands in close proximity located near Cinema, Prince George, were used to represent an outbreak recorded in the same year, giving a total of six known outbreak sites (Table 3.1). Detailed observational data was included for only two of the historical outbreaks (Funk and Parker 1966; Unger and Humphreys 1984). The most recent and detailed historical reference of a Dothistroma needle blight outbreak in the study area was in the FIDS annual reports for the years 1984-1986 at Kisgegas Canyon. The report stated that 20% of the trees were >80% defoliated. The outbreak was characterized as small but intense, with some mortality among the young trees. The fact that mortality had occurred suggests that the disease was present for several years prior to the identification of the outbreak (Woods *et al.* 2005). By 1986 the survey reports stated that the disease appeared to be subsiding. In the Prince George Forest District, near Cinema, death of a number of young lodgepole pine and a reduction in diameter growth of 10-year-old pines were attributed to repeated attacks by the fungus in 1964. Severe levels of infection were observed to be limited to one to two acres.

Reference to an earlier possible outbreak in 1957 near Rosswood, British Columbia, north of Terrace (N. Alexander *pers comm.*) was investigated. Dothistroma-like symptoms of infection and mortality of young pines had been observed in the area. According to the literature, Dothistroma needle blight had not yet been identified in

British Columbia. However, herbarium samples of Dothistroma were collected from the Terrace area around 1941, providing evidence of its possible occurrence during the late 1950s. Detailed records of Dothistroma needle blight at two additional sites, Moricetown and Cedarvale, were not available (1977 and 1976, respectively). Dates for these sites were obtained from herbarium collections with no record of infection level.

In addition, a total of 19 sites were located within the Fort St. James, Nadina, Skeena-Stikine, and Kalum Forest Districts to develop a long-term and widespread record of Dothistroma outbreaks in the area (Table 3.2). These sites fell within the three biogeoclimatic variants (ICHmc1, ICHmc2, SBSmc2), and were chosen based on the following criteria: (1) sites were 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, (2) contained older (>50 years) lodgepole trees dominant in the canopy to provide longer outbreak reconstructions for identifying past disease occurrences; (3) contained spruce nearby where lodgepole pine was largely absent so as to remove the possible outbreak effects on the non-host as a result of the sudden availability of additional resources (e.g., light); and (4) were approximately 20m away from any source of apparent intermediate-scale disturbance, such as roads and blowdown to decrease the amount of ring-width variation due to these disturbances.

3.3.4 Other defoliators

Historical herbarium collections and FIDS records of other common defoliators were examined for their possible occurrence in the study area. Five fungal defoliators of lodgepole pine recorded in the area were *Lophodermella concolor* (Dearn.) Darker, *Lophodermella montivaga* Petre., *Hendersonia pinicola* Wehm., *Phaeoseptoria contortae*

Parmelee and Hiratsuka, and Dothistroma needle blight (*D. septosporum*), but only *L. concolor*, *L. montivaga,* and Dothistroma needle blight could have caused enough damage to suppress radial growth of the host trees (Hunt *et al.* 1987, FIDS 1993). *L. concolor* can cause significant levels of defoliation in years following periods of moist summer weather favorable for infection. Increment loss and mortality may occur after repeated attack, particularly in young trees (Hunt *et al.* 1987). Ring-width suppressions during *L. concolor* outbreaks may be similar to those of Dothistroma needle blight. Herbarium records from 1966 identified *L. concolor* in three distant locations in northwest British Columbia, but no record of infection level was provided. The FIDS reported three years of consecutive defoliation caused by *L. concolor* that started in 1992, with no other records of defoliation being recorded in the study area. In 1984 and 1992, low levels of needle discolouration caused by *L. montivaga* were identified in the study area. These records suggest that the fungal pathogens probably did not occur in outbreak proportions, but this remains an assumption of this study.

Approximately 23 insect defoliators utilize lodgepole pine trees as a host in British Columbia. The three major insect defoliators of lodgepole pine are *Zelleria haimbachi* Busck (Lepidoptera: Yponomeutidae), *Coleotechnites* spp. (Lepidoptera: Gelechiidae), and *Neodiprion nanulus contortae* Ross (Hymenoptera: Diprionidae). All are regarded as common colonial defoliators that occasionally reach epidemic levels causing significant defoliation. With successive years of defoliation infested trees will suffer increment loss and even mortality. Significant outbreaks have been recorded in many areas of southern British Columbia[2]. The FIDS records indicated light defoliation caused by *Z. haimbachi*

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[2] FIDS records maintained by the Canadian Forest Service. Date of outbreaks listed on the Conifer Defoliating Insect of British Columbia website: www.pfc.forestry.ca/entomology/defoliators/index_e.html

and *Coleotechnites* spp. east of our study area in 1981, 1982, and 1983, but no outbreaks were recorded. We assume, therefore, that outbreaks of these insect defoliators are not common disturbance agents of the forests in this study.

3.3.5 Tree selection

A total of 20 host and 20 spruce (non-host) increment cores were collected from each site (one core per tree). Trees were selected based on evidence of longevity and diameter (dbh >15cm). All trees were cored at 0.3m, unless the tree had substantial butt rot, in which case it was cored at 1.3m height. Where available, cross-sectional discs from standing fire-killed trees were sampled in order to extend the chronology back in time.

3.3.6 Non-host spruce

Natural introgressive hybridization between Engelmann, white, and Sitka spruce were present in the study area. The crosses have developed the Roche spruce (*Picea glauca* [Moench] Voss x *Picea sitchensis* [Bong.] Carr. x *Picea engelmannii* Parry ex Engelm.), hybrid spruce (*Picea glauca* [Moench] Voss x *Picea sitchensis* [Bong.] Carr.), and interior spruce (*Picea glauca* [Moench] Voss x *Picea engelmannii* Parry ex Engelm.) (Burns and Honkala 1990). Because it was difficult to distinguish between the crosses, the general term "spruce" will be used for the non-host in this study.

3.4 Laboratory Methods

3.4.1 Tree-ring analysis

All cores were mounted, and cores and discs were sanded with progressively finer sandpaper grits (180, 220, 320, and 400). This produced a well-polished surface on which the cellular structure of the wood could be observed (Stokes and Smiley 1968). Annual rings-widths were measured to the nearest 0.001mm using the Velmex "TA" System in conjunction with MeasureJ2X (1999-2004).

Calendar dates were then assigned to the cores and discs and verified visually using Yamaguchi plots (Douglass 1941) and statistically with the crossdating program COFECHA (Holmes 1983). COFECHA uses segmented cross correlation techniques to detect measurement and visual crossdating errors. Our time series were partitioned into 50-year segments with 25-year lags or 30-year segments with 15-year lags. Significance was determined at a 99% critical level of correlation of 0.320 or 0.423, respectively. Series that did not crossdate were deleted or corrected until a significant correlation was obtained for all series, including each stand chronology.

Crossdated series were then standardized with the program ARSTAN version 40 (Cook and Holmes 1984) to produce a master chronology for each species in each site. Standardization involves fitting the observed ring-width series to an estimated growth function and computes an index of the observed ring widths divided by the expected value. This procedure reduces the variance among cores and transforms the ring widths into dimensionless index values. A number of deterministic and stochastic methods of growth-trend estimations were compared. By choosing the flexible, stochastic methods, the strength of the observed high-frequency signal was maximized. The degree of curve flexibility was based on historical records and examination of ring-widths during known Dothistroma needle blight outbreak years. It was assumed that Dothistroma outbreaks lasted for wavelengths of less than 10 years. We chose a cubic smoothing spline with a 50% frequency response cutoff of 40-years as a method of standardizing our host and non-host ring-widths. This 40-year cubic function retained 100% of the signal at 12 years or less. The standardized master chronologies of the non-host were used for all outbreak analyses.

3.4.2 Signal development and inferred outbreaks

Similarity of climate response in the host and non-host species is necessary for identifying insect outbreaks in host trees (Ryerson *et al.* 2003). Preliminary comparison analyses included mean sensitivity and autocorrelation statistics, graphical plots, correlation coefficients, and response function analyses. Response function analysis, PRECONK version 5.17C (Fritts 1994), uses a multiple regression after extracting principal components to estimate the response of tree growth to climate variables (Cook and Kairiukstis 1992). The significance of these associations was tested using bootstrap methods (Guiot 1991). The climate variables we used were monthly mean and maximum 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 ANUSPLIN software provided by the Canadian Forest Service, Great Lakes Forestry Centre. Residual host and non-host chronologies for which autocorrelation had been removed were used to examine response functions from June in the year prior to the year of ring growth through July of the year of ring growth. This window of months is considered to include most of the climate variables in prior and current years that are important to radial growth of northern coniferous forests (Larocque and Smith 2005). The resulting regression coefficients from the individual monthly climate variables of the host and the corresponding non-host chronologies were directly compared. All comparisons were used to determine whether spruce was a suitable non-host species to use as a climate control for each of our study sites.

To verify the observed reduced growth as periods of disease outbreak, climate variation contained in the host index series was removed (or "corrected") through subtraction of the non-host index series. Without correcting for climate during analysis, a "false" (i.e. artifacts) interpretation of the outbreak periods may occur (Swetnam *et al.* 1985). The corrected series were calculated with the following equation:

$$\text{Corrected index} = I_{ht} - \left[\frac{SD_h}{SD_n} (I_{nt} - \bar{I}_n) \right]$$

where I_{ht} is 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 non-host composite chronology for the period common to both series, I_{nt} is the non-host index at year *t*, and $\bar{I}_n$ is the mean of the non-host index for the period common to both series (Swetnam *et al.* 1985, Ryerson *et al.* 2003). The software program OUTBREAK automates the correction procedure (Holmes and Swetnam 1996). In this study, each individual host index series was corrected separately using the corresponding non-host chronology, and then averaged to form a corrected host chronology for each site. The resulting corrected host chronology represents a record of host growth with little or no influence of climate. The corrected series in then normalized by subtracting the mean and dividing by the standard deviation.

Because little was known about outbreak patterns of Dothistroma, the development of criteria was necessary to identify pre-record growth reductions as Dothistroma outbreaks. Each of the five known Dothistroma needle blight records was compared with the timing and duration of the ring-width pattern in the wood samples and in the corresponding six corrected chronologies. A characteristic ring-width pattern of suppressed growth associated with Dothistroma needle blight defoliation was determined based on the timing, duration, and magnitude of the ring-width reductions in the stands. Growth reduction values from the initiation of the current outbreak were also quantified. These were set as initial characteristic criteria to calibrate the OUTBREAK program. OUTBREAK applies a set of user-defined criteria to identify outbreaks and quantify the amount of growth reduction in measured ring-width series (Ryerson *et al.* 2005). The program permits the user to specify and subsequently refine the parameters, or criteria, for outbreaks. To locate potential outbreaks, the program identifies all years in the normalized host series that are negative, that is, where growth is less than growth in the non-host chronology. Each of these periods is checked for compliance with the criteria and is eliminated as a possible outbreak if it does not attain the specified thresholds. The timing of the outbreak periods identified by OUTBREAK was verified by comparing them with the confirmed historical defoliation episodes from FIDS and CFS herbarium collection dates. If OUTBREAK did not identify the same historically observed period, the parameters were changed accordingly in an iterative process until OUTBREAK replicated the observed periods. The following criteria were modified from Speer *et al.* (2001) based on the timing, duration, and magnitude of the Dothistroma outbreaks and applied simultaneously to the normalized series: (1) a minimum of 1 year in the outbreak period must reach at least -1.20 standard deviation units. Normalized indices less than -1.20 standard deviation units delineates values in the smallest 10th percentile; (2) negative growth values in the normalized corrected series must last between 5 years and 10 years, which must be entirely consecutive; and (3) the beginning year of the outbreak must have a growth reduction of at least 70% that of the previous ring.

The percentage of trees affected by each of the identified outbreaks was calculated for each site and a ≥ 40% threshold was set to separate significant outbreaks from apparent smaller events. Both criteria (i.e., statistical and ≥ 40% threshold) were used to identify outbreaks of Dothistroma needle blight in the host chronology. The resulting criteria were applied simultaneously to identify probable pre-record outbreak periods at the 19 individual sites. All corrected host chronologies were truncated at ≥4 trees prior to analyses.

3.4.3 Analysis of outbreak characteristics and spatial patterns

The identified outbreak periods were directly compared between all the stands to determine if outbreaks were synchronous. A regional time series of outbreaks 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 numbers of trees included in the reconstruction decreased with increasing time before the present, so we standardized the time series by computing the percentage of trees recording an outbreak for each year. This time series was used to examine the periodicity of the recorded outbreaks. The spatial extent of the inferred outbreaks was also examined in comparison with the current Dothistroma needle blight outbreak. The individual outbreak periods were grouped into common outbreak periods and plotted using the location coordinates of the site. This enabled visualization of the apparent magnitude of the apparent outbreaks.

The duration and return intervals of the inferred Dothistroma needle blight outbreaks at the site level were calculated. Duration of the outbreaks was the number of years between the beginning and ending years of an identified outbreak. The beginning and end years were the first and last year, respectively, that the number of trees recording an outbreak exceeded the 40% threshold. The return interval was recorded as the time between the ending of an outbreak and the beginning of the next outbreak. 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 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 (Swetnam and Lynch 1989).

Sites were grouped by their respective variants (ICHmc1, ICHmc2, and SBSmc2) and compared. Correlation analyses of the outbreak reconstructions were used to examine whether outbreak patterns from sites close together within each variant were more correlated than those further apart. Correlations were also used to determine whether outbreak incidence differed between the variants. Two sites in the SBSmc2 were then used to represent remote areas largely absent of human influence. These sites were far from plantations and had no road access. We compared the outbreak reconstructions in these areas with a subset of three sites from the same variant that were located in heavily managed areas, some being adjacent to pine plantations. Because our two remote sites were located in the SBS zone we included only those heavily managed sites found in the same ecological zone. The percentage of trees recording outbreaks identified by the outbreak criteria was calculated to compare whether outbreak incidence varied between remote and managed areas.

3.5 Results

3.5.1 Host and non-host comparisons

A total of 815 cores and discs (421 host, 430 non-host) from 23 sites were successfully crossdated. Individual series not included in the analysis were removed during crossdating as a result of their low contribution to the overall series intercorrelation. Mean sensitivity describes the interannual variation in the ring width as a proportion of the local mean ring width. The mean sensitivity values for lodgepole pine chronologies were generally similar to that of spruce chronologies (Table 3.3). The values range between ~0.1 (being complacent) to ~0.3 (very sensitive) (Fritts 1976). Our values indicate low to moderate interannual variation in the tree-ring series. Prior to autoregressive modeling, the mean sensitivity values were slightly lower for the known outbreak sites (Table 3.4). The magnitude of the mean first-order autocorrelation coefficients for some sites varied between the host and non-host chronologies. This value describes the degree of relationship in ring-width between successive years within each chronology (Fritts 1976). Differences in the autocorrelation values may indicate that tree growth is not controlled by a common limiting factor or that the biological carry-over is not the same. Special attention was given to these sites during further comparisons.

Graphical comparisons indicate a general agreement in growth trends between the host and non-host chronologies during most years (Fig. 3.2). The graphical 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 non-host. Lodgepole pine from the Moricetown and Cedarvale sites, however, did not have a period of growth reduction in the increment core samples, and plots did not identify suppressions in the host chronology during the herbarium collection dates (Fig. 3.3). Pearson's correlation coefficients of the host and non-host chronologies are shown in Table 3.5. Except for three sites, correlation values were statistically significant ($p<0.05$) indicating the presence of a common high-frequency signal across the length of the series between the host and non-host chronologies. Significant correlation coefficients ranged from 0.185 to 0.581. Correlation values for Sediesh Creek, Poplar Park, and Campbell Road were not significant, indicating species or site-specific differences. These sites were removed from further analysis.

Response function analysis of the six known outbreak sites revealed that the host and non-host chronologies have a similar climate/tree-growth relationship. At each site, 53 years of meteorological data were used to calibrate the response functions (1950-2003). The variance accounted for by the maximum or mean monthly temperatures and total monthly precipitation from June in the previous year to July of the current year for lodgepole pine ranged from 0.51 and 0.70. For the non-host residual chronology, values ranged from 0.53 and 0.77 (Table 3.6). These associations were strong considering the sites were not characteristic of climate stressed sites. Both pine and spruce responded positively to greater amounts of precipitation in the spring/summer (May, June, and July) and in August preceding growth (Fig. 3.4a,b). The Rosswood site showed similar but a less pronounced response to precipitation. Negative growth responses to increases in maximum and 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 (mm) and poor growth to be associated with warmer summer temperatures (°C), 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.

3.5.2 Evidence of Dothistroma outbreaks in the tree-ring record

A total of five historically documented outbreaks from six sites were used to quantify the suppression signature and develop criteria to identify probable pre-record outbreaks in the host tree chronologies. Preliminary ring-width and earlywood/latewood ratios revealed a distinctive radial growth reduction pattern associated with most of the documented outbreak periods. The pattern included reduced early and latewood, with an overall pattern of reduced ring-width that lasted 5 to 10 years (Fig. 3.5).

The corrected known outbreak sites showed strongly demarcated negative growth responses during the known outbreak periods, except for the Moricetown and Cedarvale sites (Fig. 3.6). Because no clear signal was identified in these corrected chronologies and timing of these defoliation events were based only on herbarium collections, without indication of the severity of the foliar disease, these were removed from our criteria development. The 40% threshold applied to the four remaining known outbreak sites distinguished between periods of reduced growth attributable to the documented defoliation events and smaller events (or “noise”) expressed in the corrected host chronology (Fig. 3.7). The historical 1984 outbreak at Kisgegas Canyon had the highest percentage of host trees affected (reaching 100%) with the longest duration of 9 years. The peak of the outbreak occurred during the mid-1970s, with a gradual return to pre-outbreak levels by the early 1980s. The timing of the outbreak complements reports of observed mortality at the site. The development of the current outbreak was also identified at that site and exceeded the 40% threshold by 2001. At the Rosswood site, the timing of the current outbreak coincided with dates identified at Kisgegas. The previously mentioned 1957 outbreak was also evident but did not reach outbreak levels defined by our threshold. This minor peak does reflect a defoliation event that appeared in fewer than 40% of the host trees. An inferred outbreak was recorded at the Rosswood site, affecting 62.5% trees from 1939 to 1946. This coincides with herbarium samples collected in the area in 1941, which suggests that an outbreak occurred that was not described in the FIDS records. The 1964 outbreak near Cinema in the Prince George Forest District was identified in both the Cinema and Cottonwood River host chronologies. A recent inferred outbreak was also identified at both sites. The most recent outbreak was identified at the Cottonwood River site and occurred between 1994 and 2002, reaching 70.6% trees infected by 1997. A shorter outbreak was identified at the Cinema site between 1994 and 1998. High levels of Dothistroma infected needle samples were collected in 2005 from these sites, suggesting an outbreak could have occurred in the recent past. Host trees cored at these sites were dead as a result of the mountain pine beetle (*Dendroctonus ponderosae*) epidemic that currently plagues the central interior.

3.5.3 Outbreak dynamics

Inferred periods of Dothistroma needle blight defoliation based on the outbreak criteria were observed in host chronologies at 16 individual stands. A compilation of the outbreak history revealed little outbreak synchronicity among all sites (Fig. 3.8). Only the current outbreak seemed to cover most of the study area with the first year appearing as a cluster of dates rather than a single year. A number of individual outbreaks occurred between the 1960s-1980s. The exact starting and ending years of these outbreaks among the stands, however, did not usually coincide.

Over the 233-year record (A.D. 1771 to A.D. 2004), 10 outbreak periods were evident using a continuous time series of the percent trees recording an outbreak for all sites in the ICHmc1, ICHmc2, and SBSmc2. Each individual peak in the percentage time series was identified as one outbreak period. Our reconstructions revealed tree-ring evidence of an outbreak in the study area as early as 1831. Reduced sample depth (i.e. number of trees included in the record, Fig. 3.9c) explaining the trend of decreasing number of trees recording an outbreak further back in time (Fig. 3.9a) is not evident in the percent time series (Fig. 3.9b). Outbreaks identified after this 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. A period of increased frequency is evident during the 1960s, 1970s, and 1980s outbreaks compared to the previous outbreaks. These peaks correspond to documented records of Dothistroma needle blight incidence in the area during the 1960s and 1980s. Since the 1940s, there is no year in which an outbreak was not recorded until 1998. It is important to note that the number of years between each peak in the percentage of trees infected were represented by only a few sites (Fig. 3.10). The percentage of trees infected is greatest during the current outbreak. The higher percentage of trees affected during the current outbreak reflects the greater extent and synchronicity among the sites during this event. The distribution of sites recording an outbreak during each of the 10 identified outbreak periods showed an increasing frequency of stands experiencing an outbreak over time (Fig. 3.11). Although sample size was insufficient to allow a firm conclusion, the distribution of the outbreaks suggests a non-random pattern of disease outbreak (i.e., spatial clumping).

Dates of all inferred outbreaks, duration, and return intervals are listed in Table 3.7. 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 (Fig. 3.12). The interval between outbreaks ranged from 2 to 53, with a mean of 18.8 years (Fig. 3.13). Mean percent radial growth reduction during the outbreaks ranged from 1 to 45%, with a mean value of 16% (Fig. 3.14).

3.5.4 Outbreak characteristics between variants

Reconstructed outbreaks were grouped into their respective variants (ICHmc1, ICHmc2, and SBSmc2) and compared. More synchronicity in the timing of the outbreaks was observed within both of the ICH subzones, but was absent in the SBS subzone (Fig. 3.15). For example, all sites in the ICHmc1 recorded an outbreak between the 1960s and 1970s, with two sites actually recording a recovery period during a recent outbreak (i.e., early 1990s). Correlation analysis did not reveal any clear patterns of outbreak incidence (percent trees) among the sites (Table 3.8). Three of the four sites in the ICHmc2 also showed periods of outbreak synchronicity. Most apparent was the timing of the outbreak during the early 1980s. Significant correlations were found among three sites (NashY, Bulkley, and Suskwa) but not with the site located a greater distance away (Bretson Creek). For sites located in the SBSmc2, no clear pattern was found.

A continuous time series of the percent of trees recording outbreaks identified by the outbreak criteria was calculated for each variant. Outbreaks in the ICH subzones appear to affect more trees and last longer than those in the SBS subzone, with a notable increase in intensity after the 1960s for the ICH subzones (Fig. 3.16). Reconstructions of stands in the SBS show a high frequency of outbreaks but all being less intense than those in the ICH. The current outbreak is similar across all variants and represents the largest outbreak to date. The magnitude of the outbreaks was highly correlated between the ICH subzones, whereas only ICHmc1 was correlated with the SBS outbreaks (Table 3.9).

3.5.5 Outbreak incidence and forest management

Our outbreak reconstructions from remote sites showed an extended period of no detectable disease activity (Fig. 3.17). The period from 1940 to 1979 in these remote chronologies was a quiescent period, while outbreak chronologies from the managed areas identified four outbreaks. Because our two remote sites were located in the SBS zone we included only those heavily managed sites found in the same ecological zone. This becomes important when considering differences in outbreak incidence found in our correlation analyses between the three biogeoclimatic variants. The intensity of each outbreak was similar between the remote and managed sites. However, the extent of the current outbreak identified in the remote sites was greater than the current outbreak recorded in the managed sites.

3.6 Discussion

3.6.1 Quality and reliability of the Dothistroma needle blight signature

We found a distinct dendrochronological signature associated with Dothistroma needle blight defoliation. Examination of the annual ring-width structure from documented outbreaks revealed a sharp reduction in both early and latewood production, persisting for more than 5 years and a maximum of 10 years (Fig. 3.5). The formation of the earlywood in a ring is dependent primarily on older foliage, while the production 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 Dothistroma needle blight 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. This observed reduction in total annual growth during the outbreak periods support similar findings from New Zealand, of reduction of radial growth in young *Pinus radiata* trees infected with Dothistroma needle blight (Harris and McConchie 1978). The apparent lag between initial defoliation and reduced tree-ring growth is often attributed to stored photosynthates that permit cambial development to continue even after a tree is defoliated (Brubaker and Greene 1978, Alfaro *et al.* 1982, Speer *et al.* 2005). A lagged response at the beginning of an outbreak by one to several years has been found with a number of insect defoliators (Alfaro *et al.* 1982, Swetnam *et al.* 1995). Apparent lagged responses could also be due to insensitivity of tree-ring growth to initial low defoliation levels (Speer *et al.* 2001). Whyte (1968) found that a reduction in diameter increment is minimal during early stages of disease caused by Dothistroma needle blight, but increased when more than 25% of the foliage was attacked and the younger needle were involved. In another study, diameter increment was reduced by one half where 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 (Hoking and

Etheridge 1967). Although a lag response is likely, estimates of defoliation levels are unavailable or incomplete for outbreak periods in our study sites, so we cannot evaluate the relations of tree-rings and defoliation levels at the tree or site level.

It is unlikely that the outbreaks we identified and attributed to Dothistroma needle blight were a result of other disturbance agents. The observed reduction in total annual growth during Dothistroma needle blight events is unique in comparison to 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, the effects of defoliation in the first year of reduced growth manifests as only reduced latewood production (Jardon *et al.* 1994, Krause 1995, Muzika and Liebhold 1999). Differences in growth reduction patterns (i.e., duration and rates of growth reduction) can also be used to distinguish between defoliators with similar host preferences. Brubaker and Greene (1979) provided evidence that Douglas-fir tussock moth (*Orgia pseudotsugata* McDunnough) and western spruce budworm cause distinctive patterns to permit the discrimination of their effects on host chronologies of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) France) and grand fir (*Abies grandis* (Dougl.) Lindl.). A more rapid growth reduction due to tussock moth accurately reflected the tendency of tussock moth outbreaks to reach high densities more rapidly than spruce budworm. Growth reduction measurements identified during our criteria development suggests a unique tree-ring pattern associated with fungal defoliators. Numerous foliar pathogens defoliate lodgepole pine in British Columbia, but only three were considered common in the northwest: *Lophodermella concolor*, *Lophodermella montivaga,* and Dothistroma needle blight. Outbreaks of *L. concolor* and *L. montivaga* can be locally severe, where cool, moist environmental conditions persist. Although *Lophodermella* species can cause serious damage, *Dothistroma* has a greater potential due to its less restricted life cycle (Ying and Hunt 1987, Hunt 1995). For instance, *Dothistroma* can attack needles of all ages at any time temperatures are above 5°C and moisture is present (Sinclair *et al.* 1987). In contrast, *Lophodermella* species attack current year needles and are active only in the spring (Hunt 1995). No studies have characterized the tree-ring signature caused by the effects of defoliation of *L. concolor* or *L. montivaga* on lodgepole pine and, as a result, suppressions may be similar to those of Dothistroma needle blight. However, historical records suggest only a few *L. concolor* defoliation events have occurred, and the only *L. montivaga* infections documented from the sampling area were at low levels. We suggest that the characteristic sharp growth reduction (i.e., a growth reduction of 70%) during the first year of reduced growth eliminates defoliation events associated with weaker fungal pathogens. As a result, we are confident that the presence of this tree-ring signature provides reliable evidence of past Dothistroma needle blight outbreaks. The consistent recurrence of the Dothistroma-specific signature in association with the historically documented records enabled us to identify 10 Dothistroma needle blight peak outbreak periods in northwest British Columbia, extending back to A.D. 1831.

The most commonly used methods of outbreak reconstruction include a comparison of host and non-host tree species (Trotter *et al.* 2002). By comparing growth between the host and non-host species, variation due to shared factors such as climate can be removed, and periods of reduced growth observed only in the host species can be inferred as due to a host-specific biotic agent. The reliability of the "correction" procedure is based on two major assumptions: (1) the non-host species are unaffected by the agent causing the outbreak, and (2) the host and non-host species respond similarly to environmental influences (Swetnam *et al.* 1985). The verified Dothistroma needle blight outbreaks consistently appeared as periods with declining trends in the pine chronologies and relatively unchanging growth trends in the non-host spruce chronologies (Fig. 3.3). These graphical comparisons also reassured us that the observed periods of growth reduction in the host trees were not caused by a climate event. False (i.e, artifacts) interpretations of outbreak histories are introduced by systematic differences in climatic responsiveness or sensitivities of the host and non-host trees (Ryerson *et al.* 2003). However, our climate-tree growth response function analyses showed that the host and the non-host series were generally similar (Fig. 3.4a,b). 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 non-host species.

Inevitably there will be some species-related differences in response to climate or other environmental variations. Therefore, the corrected indices could retain varying 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 this is unlikely in our reconstructions. First, as previously mentioned, response function analyses showed a general agreement between climate-growth responses for both host and non-host species. Second, low-growth periods from our known outbreaks were verified as Dothistroma needle blight outbreaks by comparing the timing of the growth reductions in the corrected series to 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 record the outbreak helped to remove smaller events that could have been due to noise left over from the correction procedure.

Although the occurrence of the outbreaks was reliably detected, the precise timing of the recorded outbreaks in the tree-ring signature was difficult to determine. We have already speculated that our reconstructions of Dothistroma needle blight may contain a lagged response by identifying reduced earlywood during the first year of the identified signature. This suggests that the host tree may not record the defoliation of infected needles until years after the initial infection. However, the exact onset of each known outbreak was not included in the FIDS survey records and made it difficult to confirm or verify the presence of lags in response infection and defoliation. For instance, FIDS survey dates were often seen occurring years after the detection of the signature. These lags have important implications for evaluating outbreak initiation events (i.e., favourable climate). This kind of analysis, however, is beyond the scope of this paper, but there is clearly good potential to study such relations.

3.6.2 Extent and nature of inferred Dothistroma outbreaks

Our reconstructions demonstrate that Dothistroma needle blight outbreaks in northwest British Columbia have occurred periodically over the last 174 years. The results of our reconstructions indicate a change in outbreak incidence within our sampled stands. Since the early 1940s, there has been no year where the level of disease at a site fell below the 40% threshold used to identify an outbreak until 1998 (Fig. 3.9). During that time four outbreak peaks occurred (mid-1940s, mid-1960s, late-1970s, and late-1980s). The period between each of the identified outbreak peaks is represented by one or two sites that have more than 40% disease severity. This patchy distribution of Dothistroma needle blight is often considered as being due to the effects of topography on microclimate (Marks and Hepworth 1986). Even patches of severe infection within seemingly healthy stands have been observed (Kershaw *et al.* 1979), and local topography strongly influences their formation. Marks and Hepworth (1986) observed higher infection levels in shallow depressions or along low elevational gradients where heavy mist and cool air pools. It is possible that these "hot spots" are present at some of our sites and maintained background levels (or low levels) of infection between the observed outbreak peaks. The eventual spread from these areas may be a result of some environmental trigger that acts over a wide geographical area, such as favourable climate fluctuations. Spore dispersal from these "hot spots" to distant stands, however, does not totally explain the sudden peak in the outbreak levels. These outbreak peaks occurred among spatially dispersed sites during the 1940s, 60s, 70s, and 80s (Fig. 3.11). We are limited in making firm conclusions about the spatial patterns of the disease, but it is likely that background levels were already present in some of these sites. Either infection levels were too low to be detected in the tree-ring record or infected trees were not sampled. These problems of spatial variability and sampling encountered in this study are common among dendroecological studies (Speer *et al.* 2005).

Our outbreak reconstructions indicate an increase in the extent and severity of the outbreaks since the 1940s. For instance, 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 (i.e., covers more sites) 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 *et al.* 2003). Our reconstructions also support claims of short-term directional climate changes as a factor causing disease spread. Since the 1970s, warm rain events have been increasing in northwest British Columbia. Woods *et al.* (2005) found that spikes in these weather events corresponded to the timing of the first published record of Dothistroma needle blight and the 1984 Dothistroma needle blight outbreak identified by the FIDS. The 1960s, 70s, and 80s outbreak peaks in our reconstructions coincide with the timing of the documented records and suggest that these increases in past warm rain events had a larger influence on outbreak incidence over the study area than previously thought. The gradual recovery to pre-outbreak levels after the late-1980s peak in our reconstructions coincides with the identified reductions in precipitation levels during this time. The current, much more severe Dothistroma needle blight epidemic is also thought to be a result of an increased frequency of warm rain events observed during the mid-to-late 1990s. 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. These precipitation events have increased markedly from earlier decades and appear to be a part of directional climate change, rather than a result of the influence of the Pacific Decadal Oscillation (Woods *et al.* 2005).

The most distinct change observed in the outbreak history was the greater synchronicity among sampled sites during the current outbreak (Fig. 3.8). Spatial synchrony refers to changes in abundance that is coincident among geographically distant populations (Liebhold *et al.* 2004). While synchrony is easily detected, the causes can be elusive. 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). As previously discussed, outbreak events of Dothistroma needle blight in the study area coincide with increases in warm rain. These weather events may be a common trigger called the Moran effect that acts sporadically to synchronize populations of the disease that are oscillating at different densities over the landscape (Myers 1998). Evidence of an environmental trigger is provided by literature examining the direct influence of these factors (i.e., temperature and precipitation) on the development of the disease. For instance, Peterson (1973) found that the majority of Dothistroma spores were released during periods of warm rain or heavy mist. Longer wetness periods were also shown to be related to an increase in the severity of infection (Gadgil 1977). Therefore, it is likely that recent increases in summer precipitation and, more specifically, warm rain events over large geographic distances represent an environmental trigger that was required to synchronize the current outbreak.

Differences in outbreak pattern and impact among ecological variants could be explained by environmental heterogeneity that leads to varying suitability for disease. The climate condition of 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 the SBSmc2, which may explain the similarity in outbreak pattern observed between the ICHmc1 and SBSmc2. The warmer and wetter climatic conditions of the ICH may explain the observed increases in the severity and spread in that zone as compared to those outbreaks recorded from sites in the SBS zone. Greater synchrony among sites from both the ICHmc1 and ICHmc2 were also observed. The notable increase in disease severity and spread after the 1960s in the ICH zone corresponds to the implementation of industrial forest management practices in the area. Forest management practices over the past 30 years have demonstrably increased host abundance in the ICH. These lodgepole pine-dominated stands represent approximately 40% of the managed stands, compared with a historical level of 10% before active forest management began (Woods 2003, Woods *et al.* 2005). The increase in available hosts on the landscape could cause a build-up of inoculum that may explain the observed increase in severity and spread over time of Dothistroma needle blight in the ICH. The build-up of inoculum may have also contributed to severity levels of the current epidemic. Although we observed differences in outbreak incidence and spread among sites from highly managed areas and those largely absent of human impact, few stands were used for the comparisons and chronology lengths of the remote sites were short. Further research is needed to examine how forest management has increased the risk of Dothistroma needle blight in the area.

Our reconstructions of Dothistroma needle blight dynamics indicate that outbreak duration, severity, and frequency has varied over the past two centuries. Because the current outbreak is still ongoing, outbreak dynamics between the historical and current outbreaks were not compared. However, it is clear that the current outbreak is much more severe than those outbreaks observed in the documented and reconstructed past. The wide range in outbreak dynamics may reflect the patchy distribution of the disease as a result of microclimate. We suggest that more research is needed to understand the role stand-level factors (i.e., topography) play in influencing disease spread and severity. Changes in weather conditions towards more frequent events of warm rains has been shown to be a principal cause of the current disease event (Woods *et al.* 2005). More detailed analyses on the relationship between climate and our 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.

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Table 3.1. Site names and descriptive characteristics of the six sites with known outbreaks.

Site Name	**Designation**	**Zone**	**Easting**	**Northing**	**Elevation**	**Variant**
Moricetown	MT	9	606245	6096584	222.6	ICHmc2
Cedarvale	CV	9	555498	6106703	285.3	ICHmc1
Kisgegas Canyon	KG	9	588364	6173940	418.5	ICHmc1
Rosswood	RW	9	515011	6073820	186	CWHws1
Cinema	CM	10	532154	5887995	705.3	SBSmh
Cottonwood River	CR	10	534032	5891419	736	SBSmh

Table 3.2. Site names and descriptive characteristics for the 19 individual sites.

Site Name	**Designation**	**Zone**	**Easting**	**Northing**	**Elevation**	**Variant**
Brown Bear	BB	9	511382	6189218	465.3	ICHmc1
Orendo	OR	9	497725	6197338	252.3	ICHmc1
Sanyam	SY	9	515204	6230174	355.5	ICHmc1
Kinscuch	KN	9	502718	6152541	230.4	ICHmc1
Kuldo	KL	9	563541	6168491	551.1	ICHmc1
Gail Creek	GC	9	606101	6160263	805.5	ICHmc1
McDonell Lake	MD	9	580567	6075257	834.6	ICHmc1
Suskwa	SK	9	604295	6125590	501.4	ICHmc2
Bretson Creek	BC	9	580749	6157910	412.7	ICHmc2
Bulkley Canyon	BU	9	597373	6123552	369.6	ICHmc2
NashY	NY	9	571908	6105574	225.6	ICHmc2
Poplar Park	PP	9	578928	6147534	294.1	ICHmc2
Campbell Road	CB	9	607580	6101218	396.2	ICHmc2
Sediesh Creek	SC	9	585246	6151147	440.4	ICHmc2
Mosque River	MQ	9	588016	6266314	900	SBSmc2
Squingula River	SQ	9	613647	6231737	900	SBSmc2
Upper Fulton	UF	9	646321	6090939	875.1	SBSmc2
Telkwa	TK	9	607711	6053305	674.7	SBSmc2
Ganokwa	GA	9	632006	6074744	814.1	SBSmc2

Table 3.3. Chronology statistics and length of master chronologies for lodgepole pine (PL) and spruce (SX) for the 16 sites used to study outbreak patterns of Dothistroma needle blight.

Site[a]	**Species**	**No. of tree cores**	**Series Intercorr.**	**Mean Sens.**	**AC(1)**[b]	**Stand dev.**	**start**	**end**
BB	PL	16	0.480	0.134	0.440	0.157	1624	2004
	SX	19	0.527	0.152	0.354	0.172	1719	2004
OR	PL	16	0.524	0.134	0.404	0.156	1899	2004
	SX	19	0.516	0.128	0.336	0.392	1903	2004
SY	PL	16	0.521	0.164	0.056	0.152	1913	2005
	SX	19	0.578	0.220	0.410	0.244	1897	2005
KN	PL	15	0.438	0.119	0.342	0.126	1898	2004
	SX	18	0.579	0.136	0.085	0.123	1900	2004
KL	PL	17	0.522	0.116	0.372	0.129	1923	2004
	SX	14	0.465	0.114	0.345	0.131	1894	2004
GC	PL	20	0.527	0.117	0.400	0.125	1872	2004
	SX	18	0.455	0.118	0.398	0.134	1874	2004
MD	PL	16	0.466	0.107	0.379	0.118	1811	2004
	SX	17	0.451	0.098	0.380	0.112	1849	2005
SK	PL	19	0.476	0.124	0.310	0.122	1918	2004
	SX	16	0.493	0.111	0.380	0.128	1919	2004
BC	PL	16	0.506	0.164	0.219	0.159	1936	2004
	SX	18	0.577	0.117	0.187	0.117	1922	2005
BU	PL	17	0.575	0.132	0.577	0.184	1900	2004
	SX	16	0.493	0.096	0.404	0.112	1919	2004
NY	PL	20	0.531	0.167	0.241	0.172	1918	2004
	SX	14	0.490	0.103	0.301	0.110	1891	2004
MQ	PL	17	0.533	0.174	0.421	0.204	1926	2004
	SX	15	0.538	0.137	0.070	0.134	1933	2004
SQ	PL	14	0.516	0.137	0.573	0.187	1937	2004
	SX	13	0.423	0.105	0.120	0.113	1950	2004
UF	PL	13	0.460	0.119	0.370	0.103	1788	2003
	SX	18	0.507	0.117	0.569	0.158	1820	2004
TK	PL	16	0.541	0.141	0.280	0.155	1883	2004
	SX	15	0.417	0.099	0.409	0.110	1882	2004
GA	PL	13	0.461	0.120	0.351	0.128	1806	2003
	SX	16	0.440	0.107	0.407	0.119	1787	2004
SC	PL	14	0.509	0.211	0.425	0.260	1907	2005
	SX	18	0.577	0.111	0.443	0.128	1919	2004
PP	PL	17	0.714	0.215	0.425	0.235	1935	2004
	SX	13	0.362	0.120	0.417	0.155	1782	2004
CB	PL	18	0.523	0.161	0.314	0.201	1905	2004
	SX	19	0.635	0.163	0.246	0.174	1944	2004

[a] For site names and locations see Table 1.

[b] 1st order autocorrelation.

Table 3.4. Chronology statistics and length of master chronologies for lodgepole pine and spruce for the six known outbreak sites.

Site[a]	Species	No. of tree cores	Series Intercorr	Mean Sens.	MS(res)[b]	AC(1)[c]	Stand dev.	start	end
KG	PL	15	0.492	0.197	0.218	0.603	0.280	1879	2004
	SX	19	0.677	0.175	0.205	0.308	0.176	1926	2004
MT	PL	17	0.517	0.152	0.171	0.435	0.173	1932	2004
	SX	19	0.635	0.163	0.178	0.246	0.174	1944	2004
CV	PL	24	0.649	0.179	0.205	0.219	0.186	1921	2004
	SX	17	0.530	0.118	0.142	0.386	0.134	1868	2004
RW	PL	20	0.542	0.173	0.193	0.472	0.219	1905	2004
	SX	20	0.605	0.144	0.172	0.214	0.138	1930	2004
CM	PL	16	0.595	0.137	0.161	0.273	0.139	1949	2004
	SX	20	0.543	0.140	0.174	0.569	0.211	1927	2004
CR	PL	19	0.626	0.221	0.241	0.448	0.260	1918	2004
	SX	20	0.543	0.140	0.174	0.569	0.211	1927	2004

[a] For site names and locations see Table 1.

[b] Mean sensitivity after autoregressive modeling.

[c] 1st order autocorrelation.

Table 3.5. Pearson's correlation coefficients of chronologies between lodgepole pine and the non-host spruce. Sites shaded grey indicate sites with known outbreaks.

Site Name	Correlation	P-value
Kisgegas	0.248	0.039
Rosswood	0.518	0.000
Cinema	0.409	0.000
Cottonwood River	0.288	0.014
Moricetwon	0.345	0.006
Cedarvale	0.361	0.001
Brown Bear	0.350	0.000
Orendo	0.473	0.000
Sanyam	0.362	0.000
Kinscuch	0.420	0.000
Kuldo	0.581	0.000
Gail Creek	0.292	0.001
McDonell Lake	0.408	0.000
Suskwa	0.484	0.000
Bretson Creek	0.572	0.000
Bulkley Canyon	0.225	0.037
NashY	0.226	0.037
Mosque River	0.361	0.002
Squingula River	0.374	0.005
Upper Fulton	0.302	0.000
Telkwa	0.252	0.033
Ganokwa	0.185	0.009
Sediesh Creek	0.065	0.555
Poplar Park	0.119	0.326
Campbell	0.209	0.106

Table 3.6. Response function coefficients showing the variance explained by climate (i.e., previous year June to current year July).

Site	Pl	SX
Maximum Temperature and Precipitation		
KG	0.58	0.60
RW	0.63	0.77
MT	0.70	0.55
CV	0.67	0.58
CM	0.51	0.71
CR	0.57	0.70
Mean Temperature and Precipitation		
KG	0.61	0.53
RW	0.66	0.71
MT	0.70	0.67
CV	0.70	0.59
CM	0.53	0.71
CR	0.42	0.66

Table 3.7. 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 (See Table 1 and 2 for site names).

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
KG	**1971-1979**	**9**	
	1996-2004	**9**	**17**
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
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**

Table 3.8a. Correlations coefficients between corrected chronologies from all sites in the ICHmc1. Significant coefficients are in bold (p ≤0.05).

	BB	OR	SY	KN	KL	GC	MD
BB	1						
OR	0.106	1					
SY	-0.033	**0.452**	1				
KN	-0.024	**0.222**	**0.283**	1			
KL	0.138	**0.428**	**0.239**	**0.232**	1		
GC	**0.431**	**0.421**	0.076	0.098	**0.314**	1	
MD	**0.422**	0.087	-0.042	-0.105	0.042	**0.405**	1

Table 3.8b. Correlations coefficients between corrected chronologies from all sites in the ICHmc2. Significant coefficients are in bold (p ≤0.05).

	SK	BC	NY	BU
SK	1			
BC	0.00	1		
NY	**0.542**	0.000	1	
BU	**0.669**	-0.035	**0.759**	1

Table 3.8c. Correlations coefficients between corrected chronologies from all sites in the SBSmc2. Significant coefficients are in bold (p ≤0.05).

	MQ	SQ	UF	TK	GA
MQ	1				
SQ	0.108	1			
UF	**0.262**	**0.367**	1		
TK	0.033	**0.645**	0.197	1	
GA	0.150	0.265	**0.227**	-0.009	1

Table 3.9. Correlation coefficients between the percent of trees recording an outbreak, as defined by the OUTBREAK criteria and the 40% threshold, separated into their respective biogeoclimatic variants. Significant coefficients are in bold (p ≤0.05).

	ICHmc1	ICHmc2	SBSmc2
ICHmc1	1		
ICHmc2	**0.481**	1	
SBSmc2	**0.239**	0.211	1

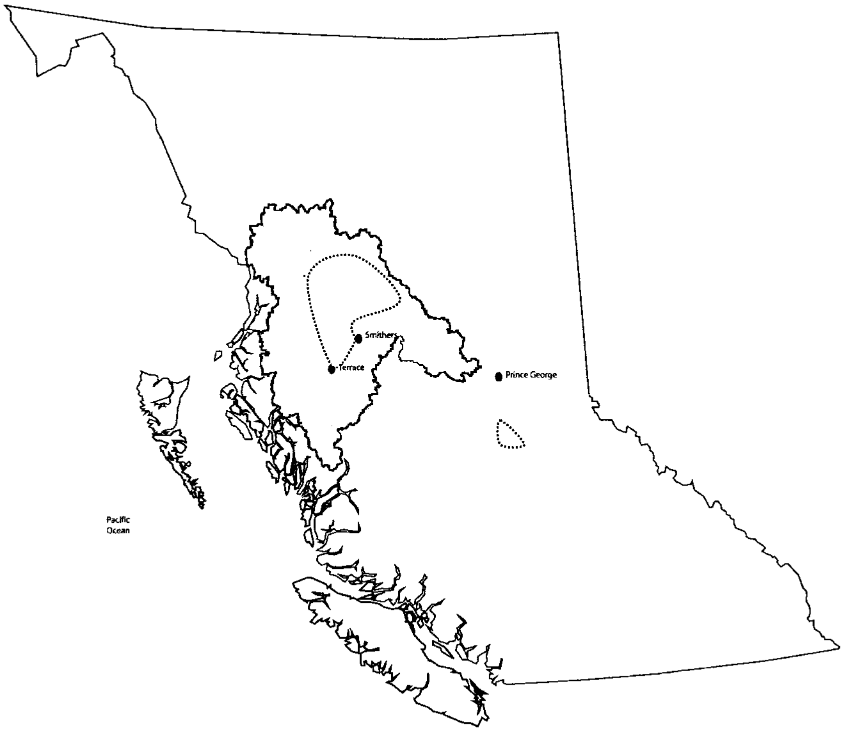
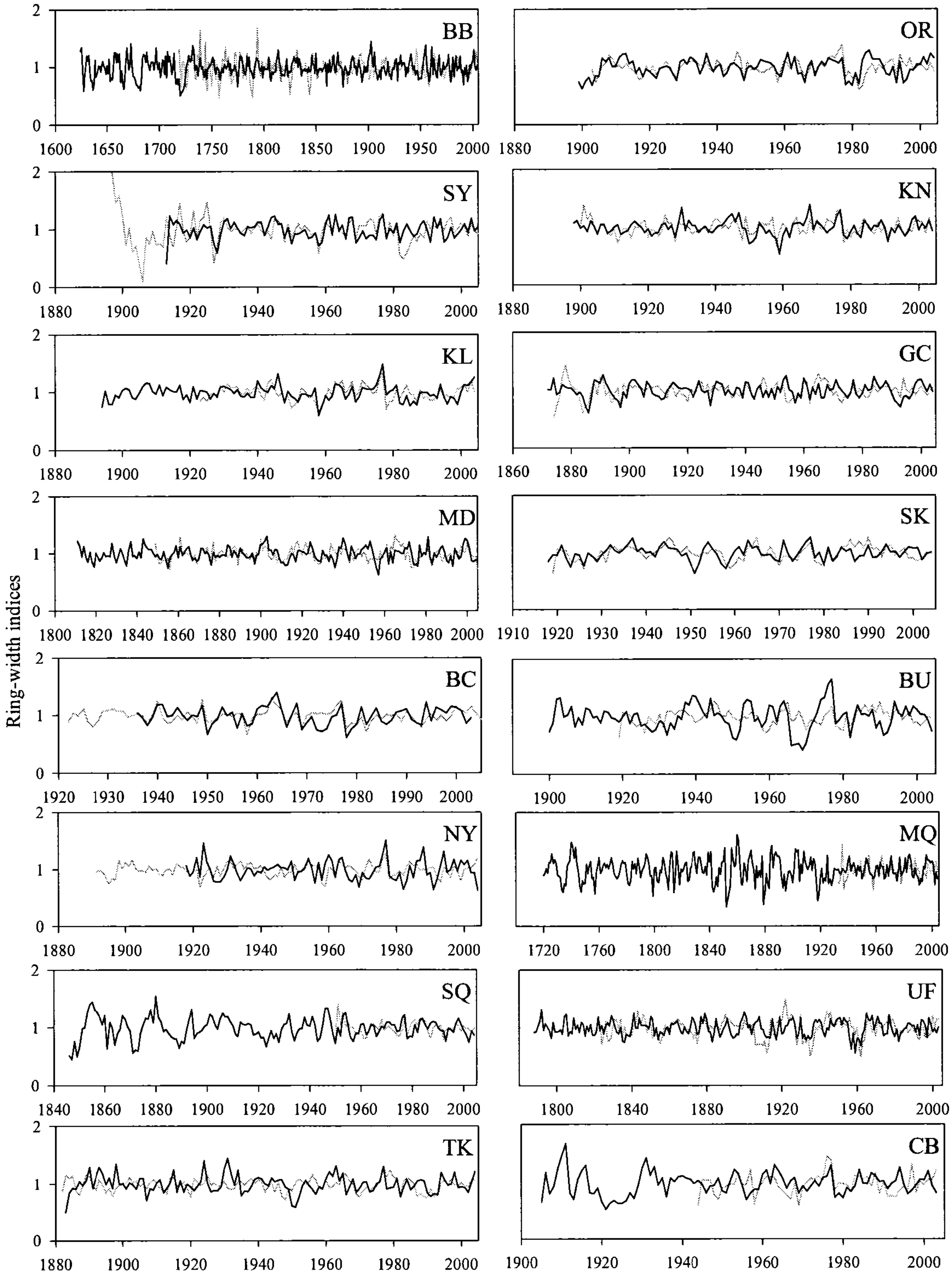


Figure 3.1. Map of British Columbia, Canada, showing sampling area. The solid line represents the area covered by the four Forest Districts. The dotted line indicates the general sampling area within the northwest and central interior.


Ring-width indices
BB
0
1
2
1600 1650 1700 1750 1800 1850 1900 1950 2000
OR
1880 1900 1920 1940 1960 1980 2000
SY
1880 1900 1920 1940 1960 1980 2000
KN
1880 1900 1920 1940 1960 1980 2000
KL
1880 1900 1920 1940 1960 1980 2000
GC
1860 1880 1900 1920 1940 1960 1980 2000
MD
1800 1820 1840 1860 1880 1900 1920 1940 1960 1980 2000
SK
1910 1920 1930 1940 1950 1960 1970 1980 1990 2000
BC
1920 1930 1940 1950 1960 1970 1980 1990 2000
BU
1900 1920 1940 1960 1980 2000
NY
1880 1900 1920 1940 1960 1980 2000
MQ
1720 1760 1800 1840 1880 1920 1960 2000
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UF
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TK
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CB
1900 1920 1940 1960 1980 2000

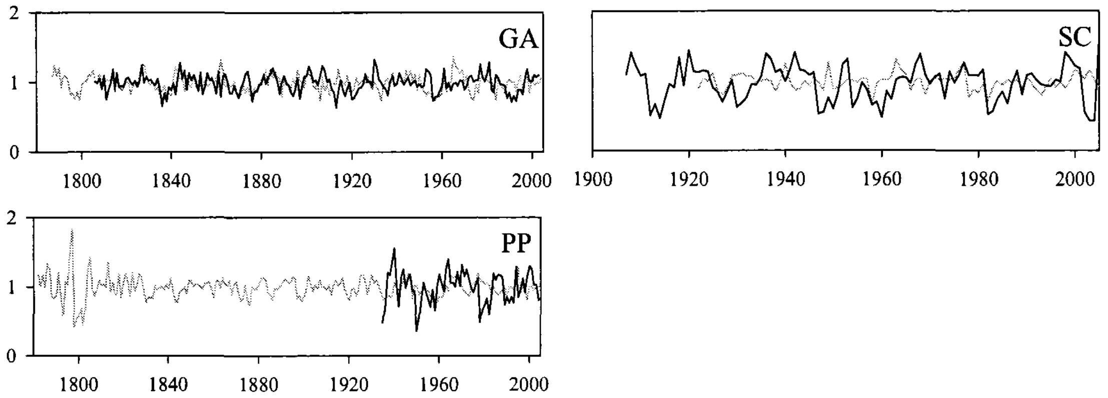

Figure 3.2. Standardized ring-width indices of all 19 host chronologies with corresponding non-host species. The darker line represents the pine host chronology and the grey line represents the non-host spruce chronology. Site designations are located on the top, right corner of each graph (see Table 2 for site names).

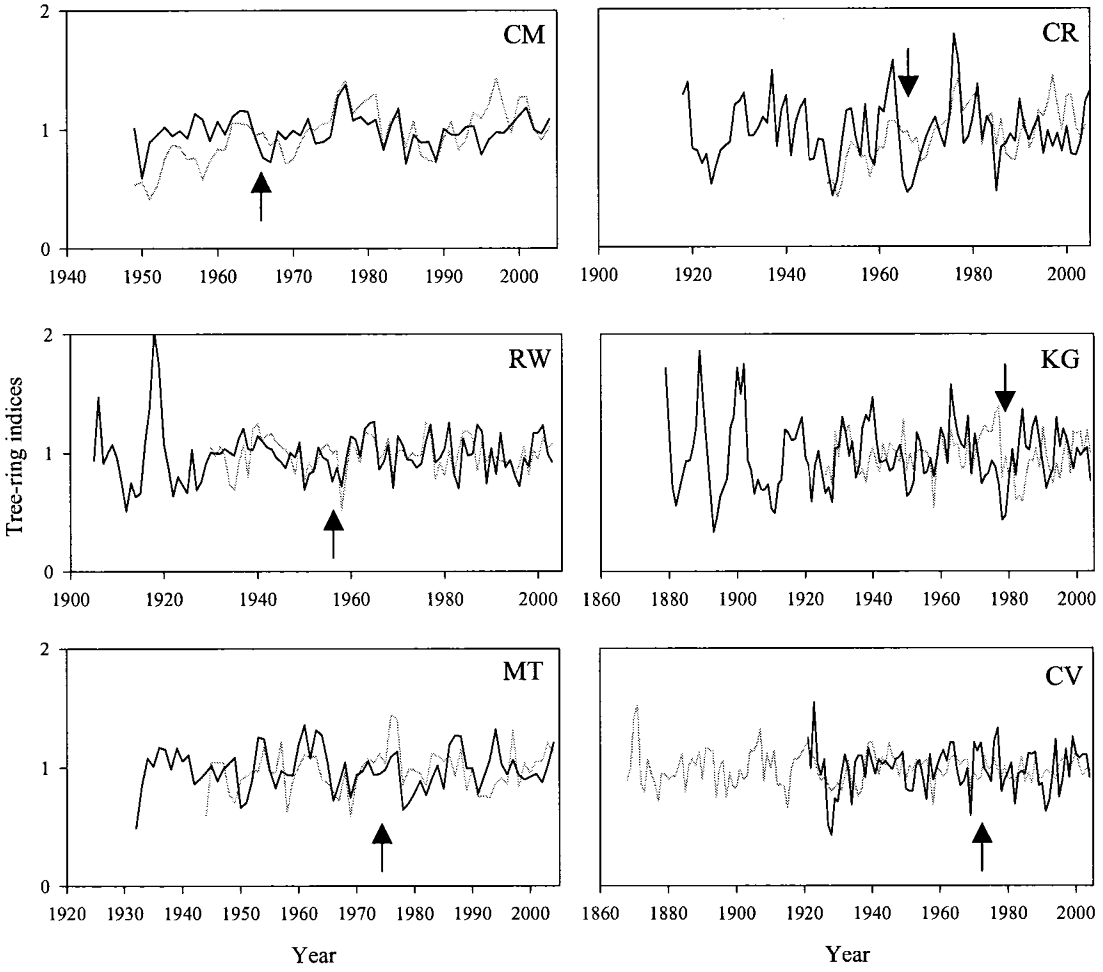

Figure 3.3. Standardized ring-with indices of the six known outbreak sites. The darker line represents the pine host chronology and the grey line represents the non-host spruce chronology. Arrows indicate years of the documented outbreaks. Both MT and CV dates were identified from herbarium collections. Site designations are located on the top, right corner of each graph (see Table 1 for site names).

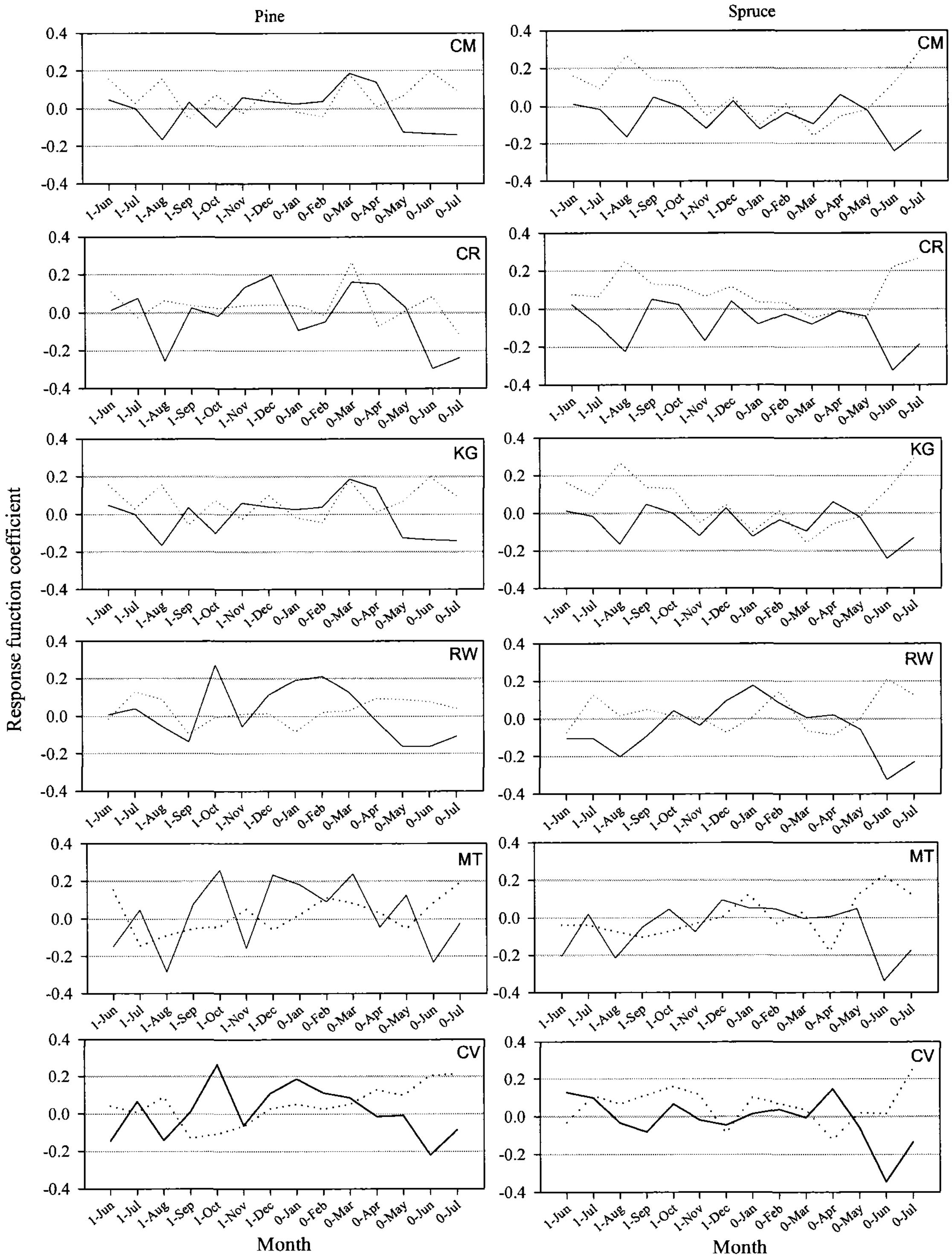

Figure 3.4a) Response function coefficients for maximum temperature and precipitation for lodgepole pine and non-host spruce over the chosen 14 month window. The coefficients (or weights) describe the nature of the relationship of ring width growth with variables of climate. Months associated with "1" indicate previous year, with "0" current year. Solid line represents the maximum temperature variable and dotted line represents precipitation. Site designations are located on the top, right corner of each graph (see Table 1 for site names).

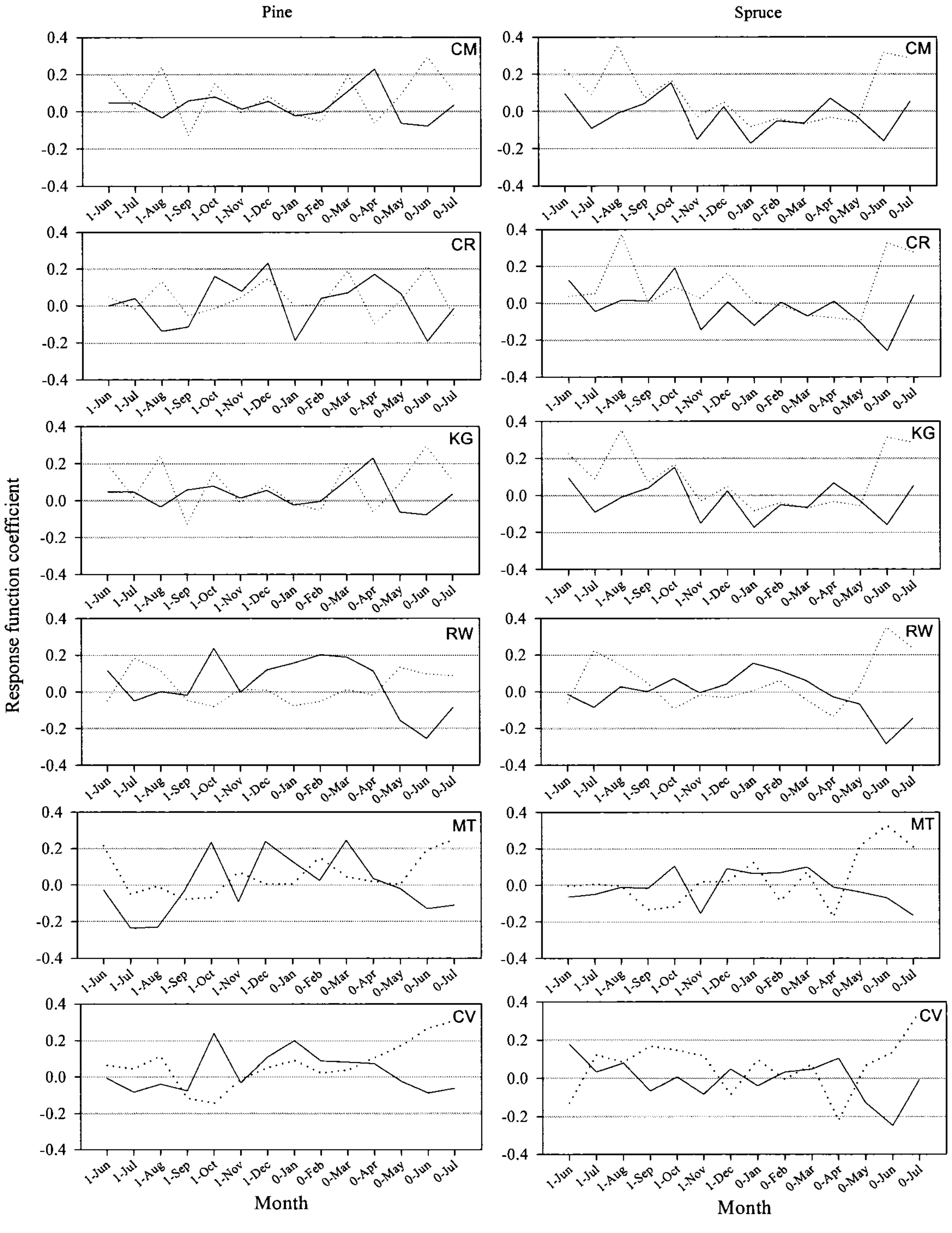

Figure 3.4b) Response function coefficients for mean temperature and precipitation for lodgepole pine and non-host spruce over the chosen 14 month window. The coefficients (or weights) describe the nature of the relationship of ring width growth with variables of monthly climate. Months associated with "1" indicate previous year, with "0" current year. Solid line represents the mean temperature variable and dotted line represents precipitation. Site designations are located on the top, right corner of each graph (see Table 1 for site names).

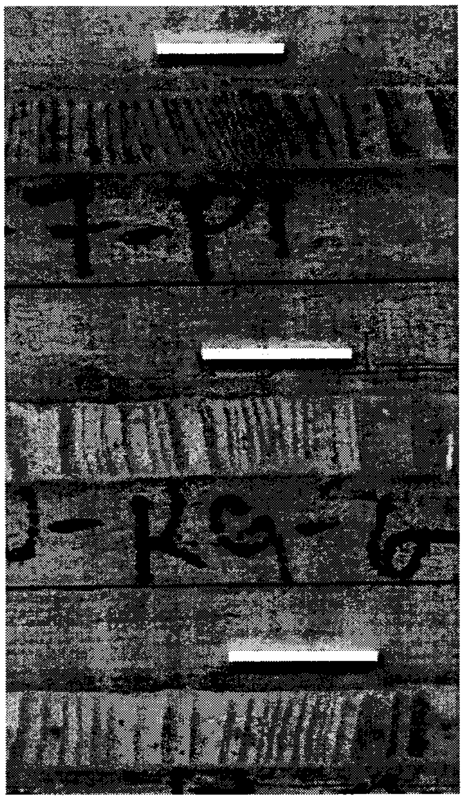

Figure 3.5. Dothistroma needle blight impacts on ring characteristics for three trees from the same site during the 1984 documented outbreak. White bars show the outbreak period. The signature starts with a sharp reduction in early and latewood, and lasts up to 10 years.

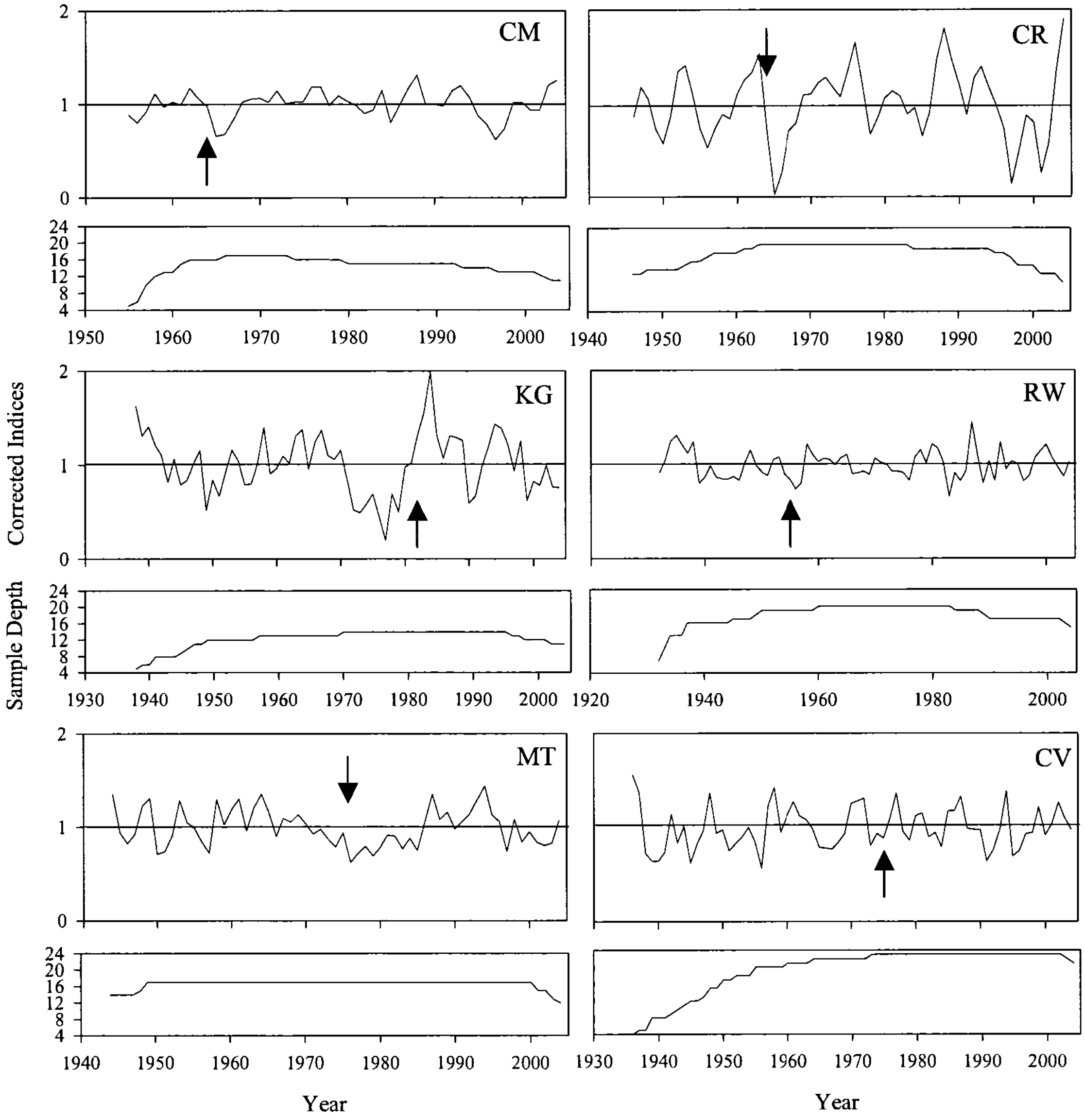

Figure 3.6. The corrected host indices showing negative growth responses during known outbreak years. Note that MT and CV do not show the characteristic growth reductions as seen with the other sites during the known outbreak events. Arrows indicate documented outbreak years. Site designations are located on the top, right corner of each graph (see Table 1 for site names). Plots below each bar graph indicates the number of trees (or sample depth) included in the corrected indices for each year.

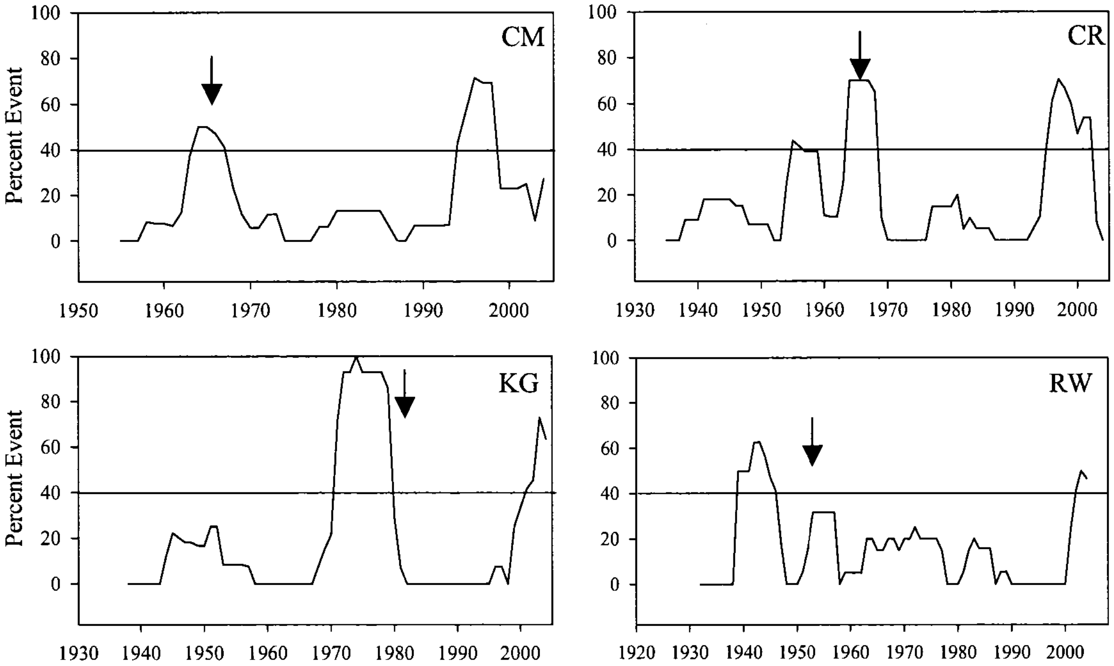

Figure 3.7. Percent trees showing growth reduction possibly due to defoliation by Dothistroma needle blight at four known outbreak sites in the northwest of British Columbia, Canada. The straight line represents a threshold of 40% that was chosen as a criterion for possible outbreaks. Site designations are located on the top, right corner of each graph (see Table 1 for site names). Arrows indicate documented outbreak years.

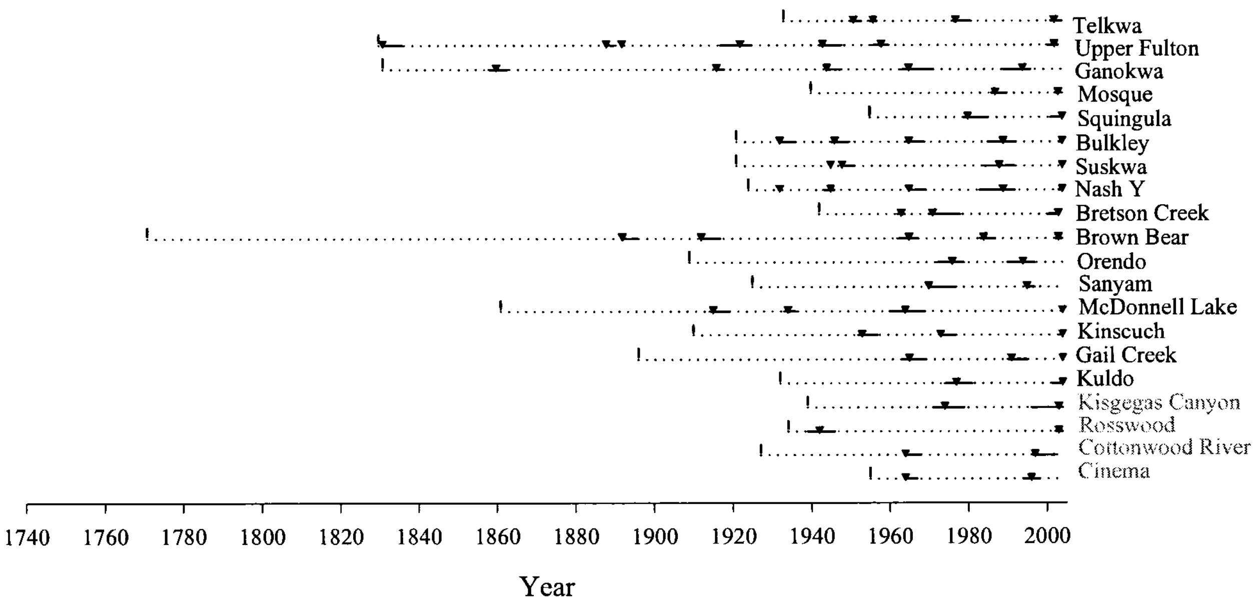

Figure 3.8. Composite chronology of Dothistroma needle blight outbreaks in 20 lodgepole pine stands. The arrowheads indicate the peak percentage of trees recording an outbreak. The vertical line indicates the innermost ring year. The solid line indicates the duration of each outbreak that met the 40% threshold. The dotted line indicates the length of the corrected chronology.

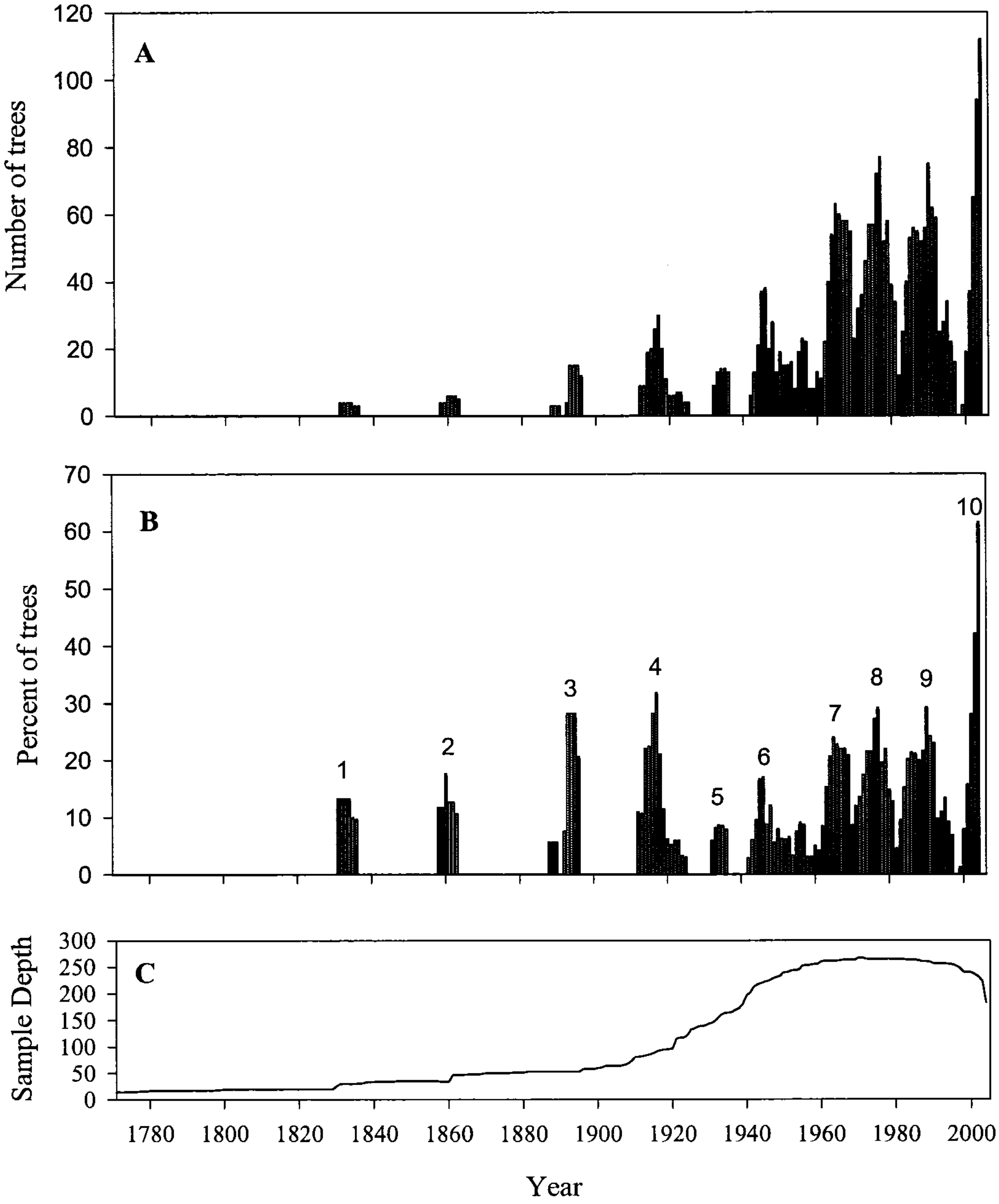

Figure 3.9a) Time series of the number of trees from sites recording outbreaks identified by the outbreak criteria (i.e., statistical criteria and 40% threshold). b) Percent trees from sites recording an outbreak identified by the outbreak criteria. Numbers indicate 10 outbreak periods. c) sample depth curve (or the number of trees included in the regional outbreak reconstruction for each year).

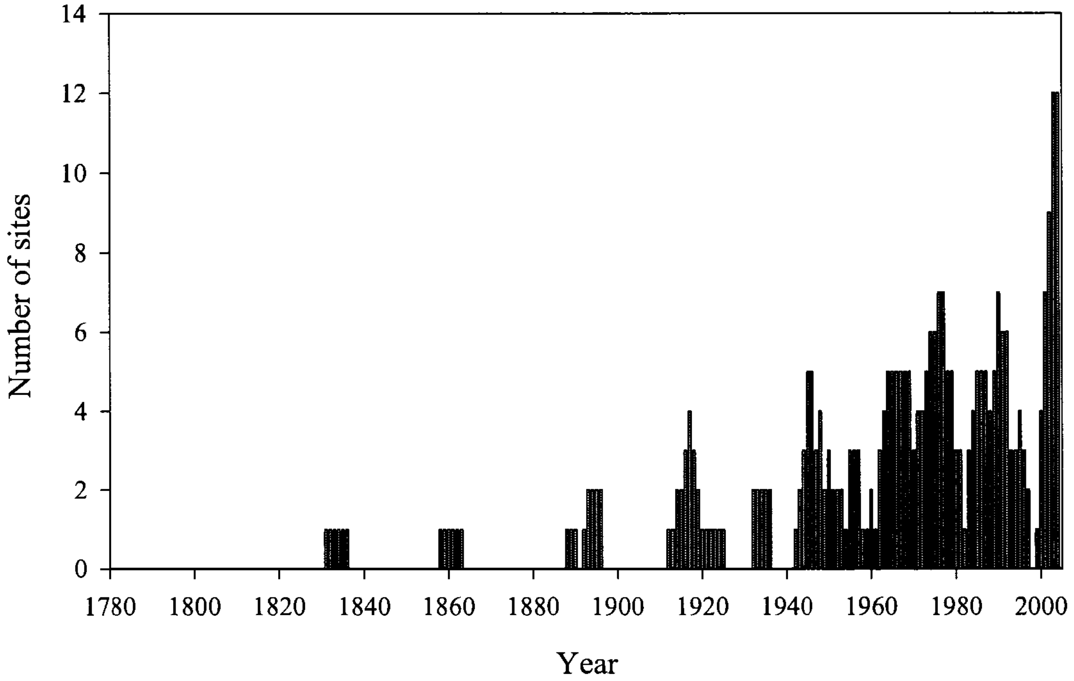

Figure 3.10. Number of sites representing each outbreak period.

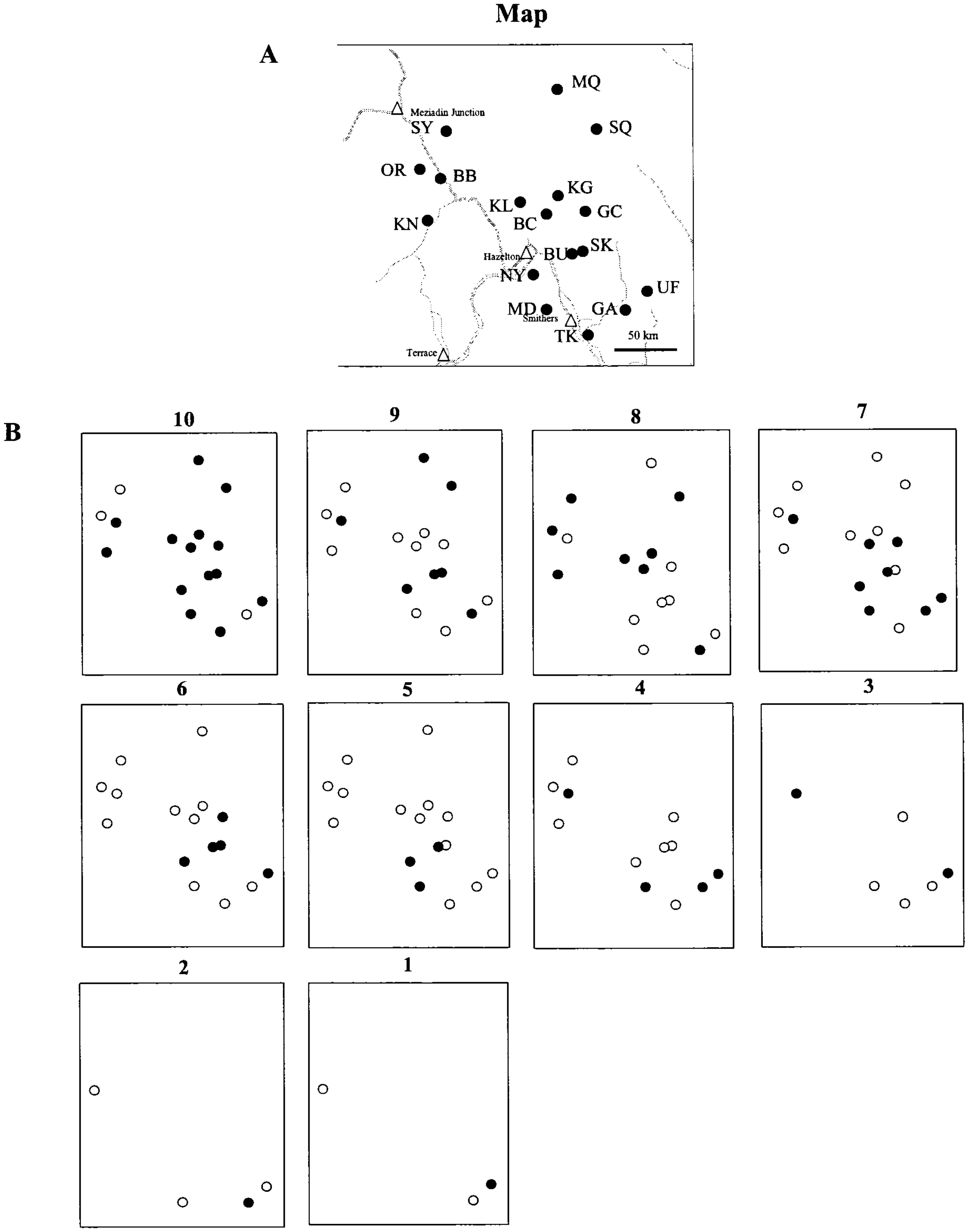

Figure 3.11a) Map of study area with UTM coordinates of sample sites. Black dots represent sampled sites, blank triangles represent towns/cities, and lines indicate highways/roads. See Table 1 and 2 for site names. b) Distribution of Dothistroma needle blight outbreaks for each of the 10 identified outbreak periods for the entire tree ring chronology (refer to Fig. 3.9b). Sites are plotted based on UTM coordinates. Filled dots represent outbreak events and blank dots represent unaffected sites.

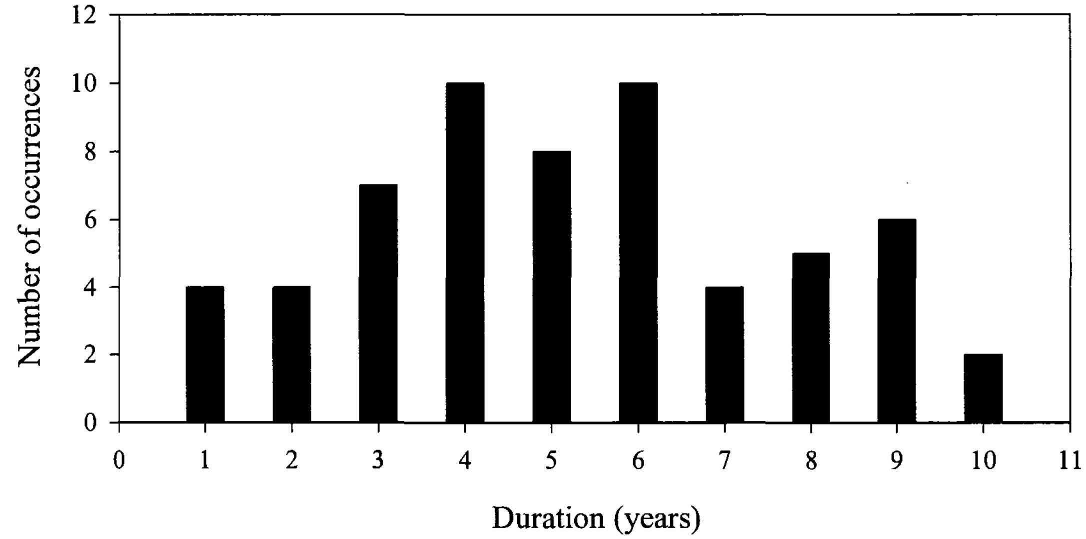

Figure 3.12. Frequency distribution of the duration of outbreaks.

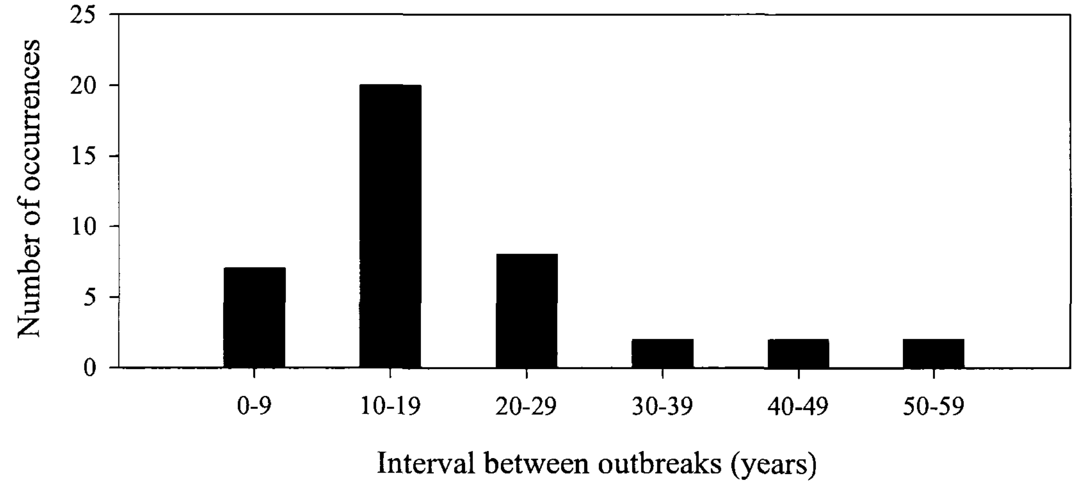

Figure 3.13. The frequency of the intervals between outbreaks. Values are binned into 10 year groups, with the first bar representing intervals 0-9. The mean is 5.2 years.

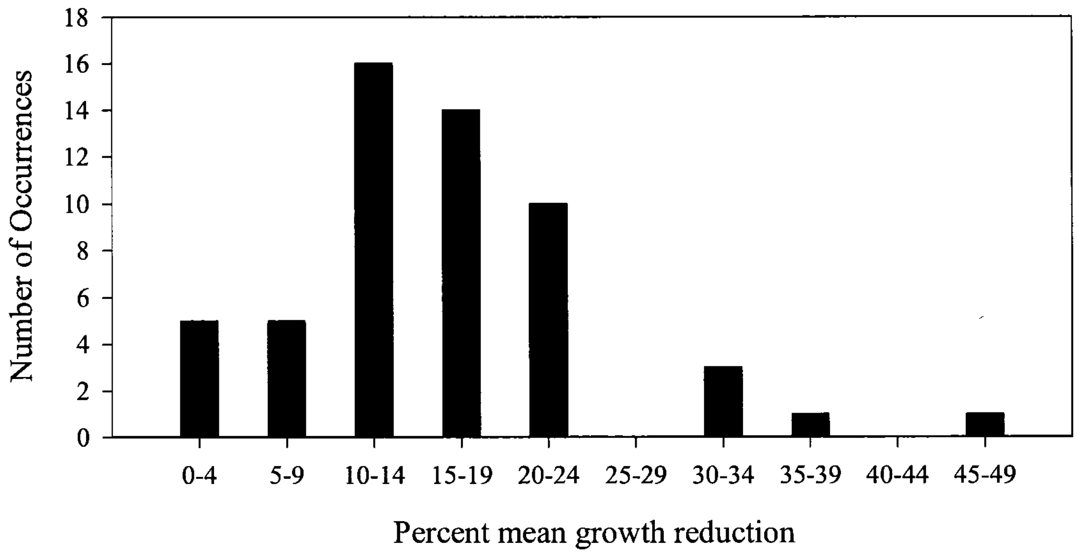

Figure 3.14. Frequency distribution of the percent mean growth reduction. This is a measure of the amount of growth reduction due to Dothistroma needle blight. Each bar represents a binned value of 5%, with the first bar indicating the value 0-4. The mean value is 16% and the standard deviation is 9%.

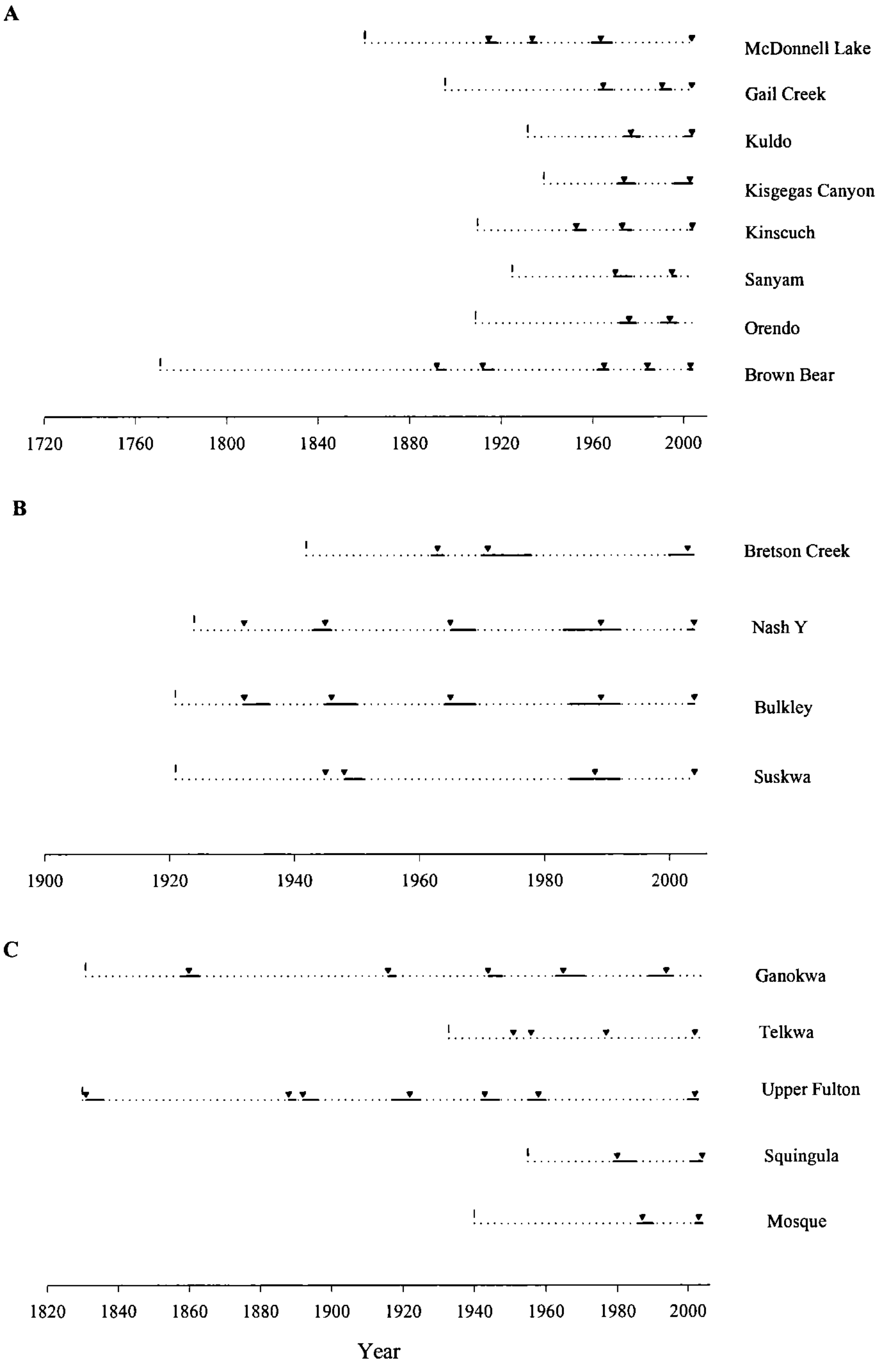

Figure 3.15. Composite chronology of Dothistroma needle blight outbreaks for sites from the a) ICHmc1, b) ICHmc2, c) SBSmc2. The arrowheads indicate the peak percentage of trees recording an outbreak. The vertical line indicates the innermost ring year. The solid line indicates the duration of each outbreak. The dotted line indicates the length of the corrected chronology.

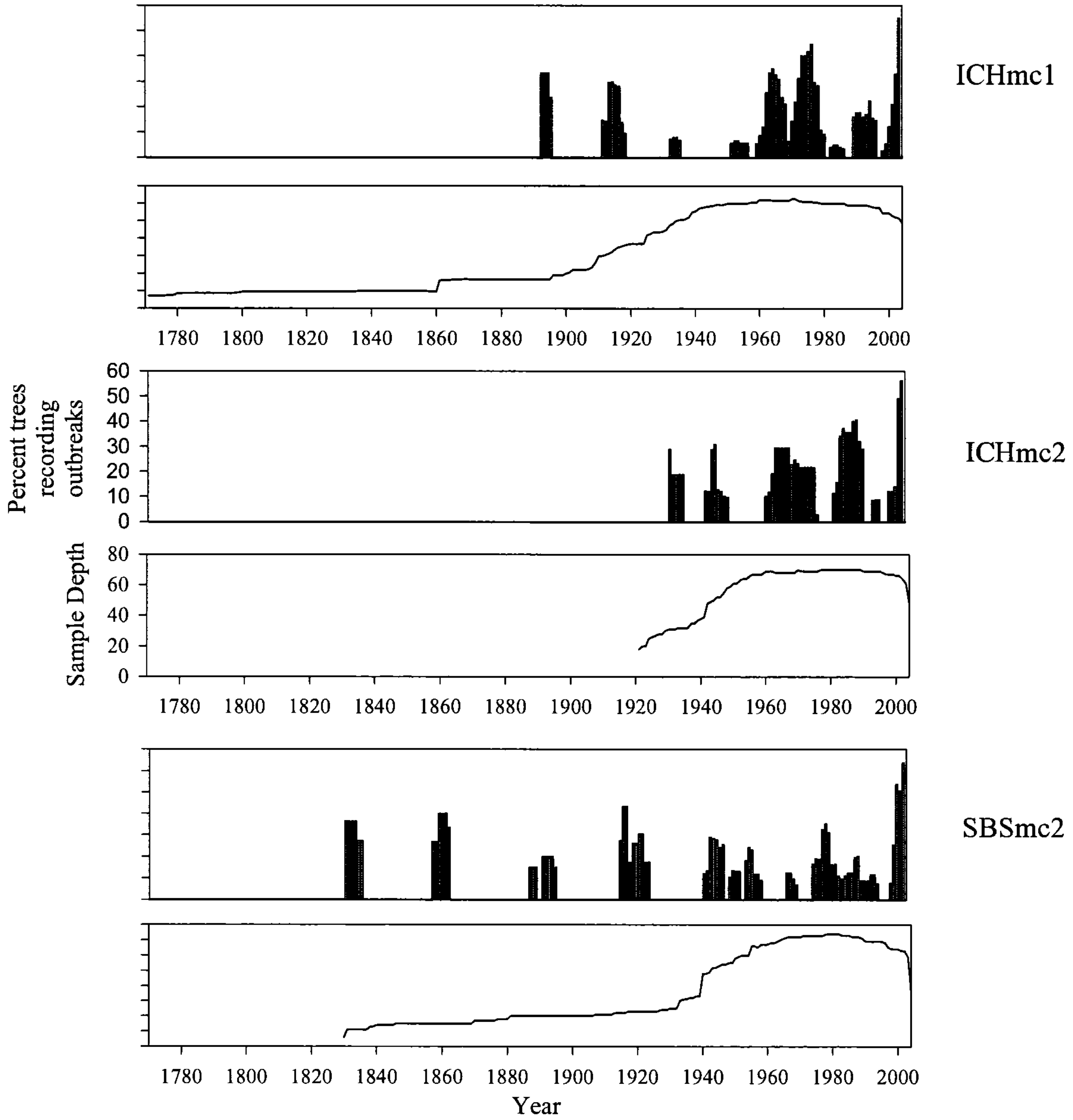

Figure 3.16. Percent trees recording an outbreak for each variant (ICHmc1, ICHmc2, and SBSmc2). Plots below each bar graph indicates the number of trees (or sample depth) included in the reconstruction for each year.

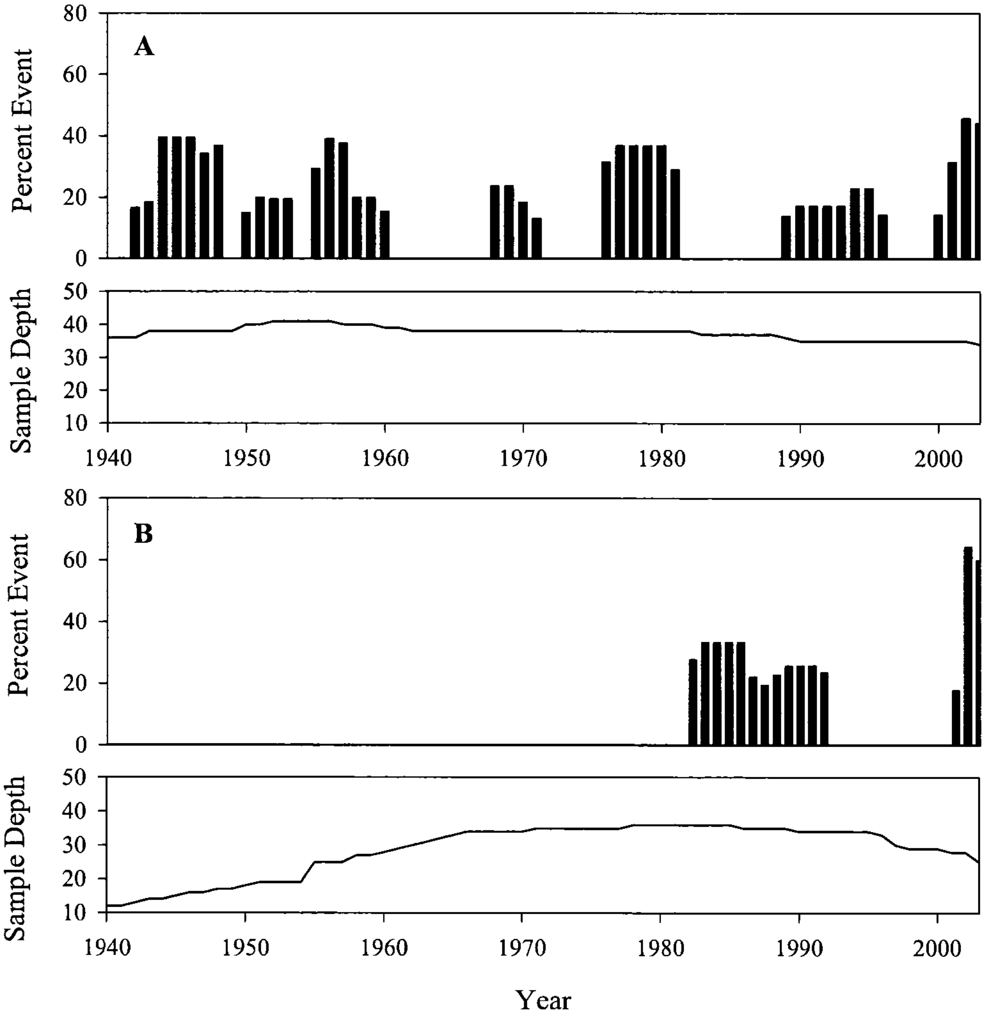

Figure 3.17a) Sites from highly managed areas and, b) areas largely absent from human influence (remote sites). All sites were selected from SBSmc2 variant. A total of three sites represent the managed areas and two sites for the remote areas. Plots below each bar graph indicates the number of trees (or sample depth) included in the reconstruction for each year.

CHAPTER 4

DETERMINING THE LONGEST AND MOST SPATIALLY REPRESENTATIVE RECORD OF CLIMATE FOR EXAMINING THE RELATIONSHIP BETWEEN CLIMATE AND OUTBREAK HISTORY OF DOTHISTROMA NEEDLE BLIGHT

4.1 Abstract

To determine the relationship between climate and the outbreak history of Dothistroma needle blight (*Dothistroma septosporum* (Dorog.) Morlet) in northwest British Columbia it was important to use the longest and most spatially representative climate information available. Because the climate sensitivity of long-lived tree species offers an opportunity to develop histories of past climate, we examine the possibility of using dendrochronology to reconstruct local climate unique to the study area. Tree rings of lodgepole pine (*Pinus contorta* var. *latifolia* Dougl. Ex Loud.) from six distant sites were calibrated using interpolated climate data. The accuracy of each statistical model was measured by calculating a number of verification statistics. Precipitation reconstructions were complicated by a shift in weather conditions that occurred in the late-1970s. Transfer function models were then used to reconstruct a record of the temperature and precipitation variables prior to the period of instrumental climate data. Comparisons with distant, long-term weather station data were used to determine whether the climate reconstructions represented climate variability differently from more regional patterns. It is apparent that our climate reconstructions did not represent local climate variability, but rather a reconstruction of larger regional climatic processes. As a result, we found that climate data from the long-term weather stations were equally representative of climate variability in the study area. Climate records from the Fort St.

James weather station were most representative of climate variability in our reconstructions, and were the longest documented record of climate in central British Columbia. Therefore, we chose the Fort St. James weather records for further analysis with our Dothistroma needle blight outbreak reconstructions.

4.2 Introduction[1]

Establishing a causal relationship between climate and long histories of Dothistroma needle blight outbreaks requires high-resolution archives of past climate fluctuations. Because yearly differences in weather are known to result in considerable annual variations in the amount of infection by Dothistroma needle blight (Peterson 1973), it was important to focus on the impacts of local climate variability on disease incidence. In northwest British Columbia, the required temporal and spatial coverage of meteorological data is limited for such a study. In addition, homogeneity problems caused by station relocation, changes to instrumentation and observation practices compromise the quality and continuity of weather data. However, the climate sensitivity of long-lived tree species offers an opportunity to develop histories of past climate fluctuations that are preserved in the tree-ring record.

The purpose of this study was to identify the longest and most spatially representative climate records available for use in a later study to determine the relationship between climate and the outbreak history of Dothistroma needle blight. Comparisons of climate reconstructed from tree rings of lodgepole pine and distant, long-term weather station data were used to determine whether our climate reconstructions

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[1] A version of this document will be submitted for publication under multiple authors. All data used in this study were collected by C. Welsh and a number of field and lab assistants. In this thesis I use 'we' and 'our' to reflect the involvement of others in various aspects of this work.

represent climate variability differently than more regional climatic patterns. We anticipated that our climate reconstructions would differ between sites, and from regional weather station data, because of differences in the tree's response to local climatic patterns. A goal of our climate reconstructions was to reconstruct a climate variable that could be related to the occurrence of Dothistroma needle blight outbreaks. However, these climate variables must also be reflected as growth-controlling factors in the tree rings, which posed a possible limitation to the study.

4.3 Site Methods

4.3.1 Study area description

Four climate reconstruction sites were located within three biogeoclimatic variants in northwest British Columbia: 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). Two sites were identified within the SBSmc2 in the Fort St. James Forest District to expand the range of the variant. The site locations were selected to cover areas sampled for the reconstruction of Dothistroma needle blight outbreak history in a previous study (see Chapter 3). Additional sites were established in the southern portion of the Kalum Forest District and the Prince George Forest District to correspond to two other known Dothistroma needle blight outbreaks that occurred outside the general sampling area (Table 4.1).

4.3.2 Biogeoclimatic zones

Climatic conditions within the ICH zones are intermediate, characterized by warm, moist summers, wet falls and cold winters. Average annual precipitation ranges from 500 to 1200 mm (Banner *et al.* 1993). The ICHmc1 includes the mid-to-low elevation northern temperate forests and has a mild, humid climate that largely escapes fire, permitting growth of coastal tree species. The ICHmc2 occupies the low-elevation forests and has a warmer and drier climate. The climax forests of the ICH are dominated by western hemlock (*Tsuga heterophylla* [Raf.] Sarg.). Lodgepole pine is typically a seral component of these forests, which co-occurs with subalpine fir (*Abies lasicocarpa* [Hook.] Nutt.); western redcedar (*Thuja plicata* Donn ex D. Don); hybrid spruce, a cross of white spruce (*Picea glauca* [Moench] Voss) and Sitka spruce (*Picea sitchensis* [Bong.] Carr.); paper birch (*Betula paprrifera* Marsh.); trembling aspen (*Populus tremuloides* Michx); and black cottonwood (*Populus balsamifera* ssp. *Trichocarpa* Torr. & Gray).

The SBS zone covers most of the interior lowland forest to the east of the ICH. The climate of the SBS zone is continental, characterized by long, cold winters and relatively short warm and moist summers. Annual precipitation is roughly 440-650 mm; less than half falls as snow. The SBSmc includes the higher elevation forests and has a wetter climate than other SBS subzones. The SBSmc is represented by a single variant in our study area, the SBSmc2. Upland coniferous forests dominate the SBS landscape. Hybrid spruce and subalpine fir are the major climax tree species in the SBS zone. Lodgepole pine and trembling aspen pioneer extensive seral stands. Lodgepole pine is common in mature forests in the drier parts of the zone (Banner *et al.* 1993).

4.3.3 Site selection and field collections

Areas sensitive to climate fluctuations, such as rocky outcrops and exposed valley slopes, and are less likely to be affected by Dothistroma needle blight due to dry conditions (*unpublished*, K. Lewis[2] and *unpublished*, A. Woods[3]) were selected as sites for our climate reconstructions. These more extreme environments assure that tree growth is sufficiently limited by climatic factors (Fritts and Shatz 1975). Lodgepole pine was chosen for climate reconstruction because of its extensive occurrence and availability in the area affected by a pine-specific forest pathogen, the focus of the study. Two increment cores were extracted at 0.3m from 20 lodgepole pine trees at each of the six sites. Where available, discs from standing fire-killed trees were sampled in order to extend the chronology back in time.

4.4 Laboratory Methods

4.4.1 Tree-ring analysis

All cores were mounted, and cores and discs were sanded with progressively finer sandpaper grits (180, 220, 320, and 400). This produced a well-polished surface on which the cellular structure of the wood could be observed (Stokes and Smiley 1968). Annual rings-widths were measured to the nearest 0.001mm using the Velmex "TA" System in conjunction with MeasureJ2X (1999-2004).

Calendar dates were then assigned to the cores and discs and verified visually using Yamaguchi plots (Douglass 1941) and statistically with the crossdating program COFECHA (Holmes 1983). COFECHA uses segmented cross correlation techniques to detect measurement and visual cross-dating errors. Verification was based on 50-year dated segments with 25-year lags, significant at the 99% critical level of correlation of

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0.328. Segments that were not significantly correlated were visually inspected for dating errors or re-measured to ensure the original measurements were accurate.

Crossdated series were then standardized with the program ARSTAN version 40 (Cook and Holmes 1984) to produce a master chronology for each site. Standardization of the tree-ring series was necessary to remove age-related trends in growth so that other factors causing growth variation could be evaluated separately. A number of deterministic and stochastic methods of growth-trend estimations were compared. The signal-to-noise ratio (SNR) was examined between each standardization method to help select an optimal frequency response for our climate analysis. The SNR is an expression of the strength of the observed common signal among the trees (Cook and Kairiukstis 1990). By choosing the stochastic cubic smoothing spline, the strength of the observed signal was maximized. To ensure that little high-frequency variance was lost in estimating and removing the growth trend, the degree of curve flexibility was set at a common level of 67% frequency-response cutoff (Cook and Kairiukstis 1990). The standardized ring-width series were then prewhitened with autoregressive modeling to remove temporal autocorrelation. Autoregressive modeling, therefore, makes observations independent to meet the condition of most statistical analyses. Furthermore, autoregressive modeling removes low-frequency variation and enhances the common growth signal, which is usually best correlated with yearly climatic fluctuations (Linderholm *et al.* 2003, Chinn *et al.* 2004).

4.4.2 Climate reconstruction

The determination of relationships between climatic variation and tree growth in northwest British Columbia is not simple given the complexity of mountain climates.

Over relatively short distances, ecologically significant climatic differences may result from variations in elevation, aspect, and topographic position. Thus, the record of a single station may have limited spatial applicability in this type of study. Therefore, weather station data were statistically interpolated as functions of elevation and geographic co-ordinates using the ANUSPLIN computer program (Hutchinson 1995). Limitations of this climate model are critically assessed in literature (Semenov and Brooks 1999, Daly 2006), but are beyond the scope of this paper. All climate data generated by ANUSPLIN was provided by the Canadian Forest Service, Great Lakes Forestry Centre for the period 1950-2003.

Climate-growth relationships were investigated using Pearson's correlation analysis and a more conservative response function analysis (Fritts 1976). The purpose of these preliminary analyses was to filter out spurious relationships, thus allowing one to concentrate on examining relationships that are reasonable and likely to exist (Cook and Kairiukstis 1990). Response function analysis was performed with the program PRECONK (version 5.17C; Fritts 1994) to identify monthly climate variables that had significant associations with annual radial growth of lodgepole pine. The method recalculates matrices of climatic data using principal component analysis to form new variables that maximize the variance in the factors influencing tree growth (Laroque and Smith 1999, Gedalof and Smith 2001). These variables are then graphically represented as response functions to establish which climate variables represent the most important limiting factor of growth. The significance of these associations was tested using 999 bootstrap iterations (Guiot 1991). The climate variables used were monthly mean, minimum, and maximum temperature (°C) and monthly total precipitation (mm) for the period 1950-2003. Response functions were calculated for monthly precipitation in combination with each temperature variable extending over two growing seasons from June of the previous year (t-1) to September of the current year (t). For the correlation analysis, climate-growth relationships were examined over two years from January of the previous year to December of the current year. As the climate variables may have cumulative or long-term effects, the relationship between seasonal and annualized periods were examined using Pearson's correlation analysis. The common significant variables of the response function and correlation analysis ($p \leq 0.01$) were then used in our calibration procedure.

Transfer function models[4] predicting climate from the residual chronologies were calibrated using linear regression. The objective of the calibration procedure was to establish the appropriate statistical growth-climate relationship (Cook and Kairiukstis 1990). In this study, the calibration period was chosen as the last half of the historical climate series (i.e., 1977-2003). The estimated climate values were computed by applying the predictor data (ring-widths) to the model coefficients. The resulting values were graphically compared with those of the actual climate data over the entire instrumental period. We examined scatter plots to confirm whether the estimated values followed a general straight-line relationship. If the agreement between the estimates and the actual values were insufficient, the calibration was rejected and the statistical model was reexamined.

The modeled relationships were confirmed using various statistical verification techniques. A verification scheme is often used to test for "prediction bias" of a

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[4] The term transfer function refers to a set of weights or coefficients used to estimate climate from ring-width values (Fritts 1976).

regression model by observing the predictive power of the model against a set of the dependent data (climate data) held back from the calibration process (Cropper 1982). Verification is established when estimates derived from the original calibration resemble those from the predictor data. This procedure is essentially a method of statistical proof that a particular relationship is not the result of pure chance and that the reconstructions do in fact represent conditions that actually did exist (Fritts 1976). Therefore, a successful reconstruction must not only have significant calibration statistics, but also have significant verification statistics (Cook and Kairiukstis 1990). In this study, relationships were verified using the first half of the observed climate data (1950-1976). Standard verification statistics were computed to test the prediction ability of the model. The statistics used included the Reduction in Error (RE) and the Coefficient of Efficiency (CE) statistic. The RE statistic was first introduced by Lorenz (1956) to meteorological data as a measure of forecast skill, and now is extensively used in dendroclimatology to verify reconstructions of climate from tree-rings (Fritts 1976). The RE statistic was calculated with the following equation:

$$\mathrm{RE} = 1.0 - \left[\frac{\sum (x_i - \hat{x}_i)^2}{\sum (x_i - \bar{x}_c)^2} \right]$$

where x_i and $\hat{x}_i$ are the actual and estimated data in year i of the verification period and $\bar{x}_c$ is the mean of the actual data in the calibration period (Cook *et al.* 1999). RE has a theoretical range of $-\infty$ to $+1$. An $\mathrm{RE} > 0$ indicates the reconstruction skill is in excess of the actual calibrated data (i.e., $\bar{x}_c$); an $\mathrm{RE} < 0$ indicates less skill than actual data. That is, if the reconstruction does a better job at estimating the independent data than the average of the dependent period, then the total error of the regression estimates would be less, the ratio would be less than one, and the RE statistic would be positive (Cook and Kairiukstis 1990). Among the verification statistics used in this study the CE is the most rigorous. The CE statistic is calculated by the following equation:

$$\mathrm{CE} = 1.0 - \left[\frac{\sum (x_i - \hat{x}_i)^2}{\sum (x_i - \bar{x}_v)^2} \right]$$

where x_i and $\hat{x}_i$ are the actual and estimated data in year i of the verification period and $\bar{x}_v$ is the mean of the actual data in the verification period (Cook *et al.* 1999). The only difference between the RE and CE lies in the denominator term. However, this difference makes the CE more difficult to pass (i.e., CE > 0). When $\bar{x}_v = \bar{x}_c$, CE = RE. But when $\bar{x}_v \neq \bar{x}_c$, RE will be greater than the CE by a factor related to that difference. A major disadvantage of these statistics is their high sensitivity to even a single poor estimate, suggesting that any value greater than zero is encouraging (Fritts 1976). When the model passed both verification tests, we considered the transfer function estimates of the climate variable stable. The transfer function equations were then used to reconstruct a record of some climate variable prior to the period of instrumental data.

To reduce the effect of changing sample size on the variance of the tree-ring chronologies, a process of variance stabilization was conducted (Cook *et al.* 1999). The subsample signal strength (SSS) provides a statistical tool useful for determining the number of sample replications needed to capture the theoretical population signal of tree-ring variation. The number of samples required to reach a SSS threshold of 0.85 was used to identify a cutoff year in the chronologies, above which there was sufficient sample robustness to reconstruct a reliable time series. This threshold has been tentatively suggested as desirable for climate reconstruction work (Wigley *et al.* 1984, Cook and

Kairiukstis 1990). This process removed potential artifacts from the data that are unlikely to be related to changes in climate variability.

4.4.3 Comparisons of local climate variability of reconstructions

Correlation analyses were used to determine whether each reconstructed variable revealed regional or local climate variability. Each climate reconstruction was also compared to meteorological data extracted from individual weather stations at Fort St. James and Terrace, British Columbia (Environment Canada 2006). Graphical comparisons were used to determine whether our climate reconstructions recorded climate variability that was locally unique. These results were used to determine the best available record of climate variability for our study area. No statistical comparisons were made between the individual weather stations, reconstructions, and interpolated ANUPSLIN weather data used in the calibration procedure. Because the single station data were used in the interpolation of the ANUSLPIN data, comparisons of this data violate assumptions of many statistical analyses (i.e., multicollinearity).

4.5 Results

4.5.1 Dendrochronological characteristics

A total of 218 radial series from 106 trees were used in our analysis. Comparative statistics for six chronologies are given in Table 4.2. Mean series intercorrelation describes the strength of a chronology by averaging the internal correlation of all of the cores in a chronology (Holmes *et al.* 1986). The mean series intercorrelations recorded for lodgepole pine ranged from 0.461 to 0.626 and indicate that all six chronologies contain a common signal significant at the 95% confidence interval when using 50-year chronology segments. Mean sensitivity, which describes the interannual variation in the ring width as a proportion of the local mean ring width (Fritts 1976), was moderately sensitive (0.137 to 0.214). Standard deviation values were also indicative of good dendroclimatic quality. All chronologies retained adequate signal strength (EPS ≥ 0.85) back approximately 90 years, with the longest chronology coming from the central interior study site, located in Cinema (AD 1901-2005, 104 years).

4.5.2 Dendroclimatological relationships

Four similar radial growth-climate associations were observed in the response functions of lodgepole pine chronologies at the six sites: (1) a negative response to warmer temperatures in the early summer of the current growing year; (2) a negative response to warmer late summer temperatures in the year preceding ring formation; (3) a positive response to greater precipitation in the early summer; and (4) a positive response to greater precipitation in the summer preceding growth (Fig. 4.1). These consistent relationships suggest the tendency for good growth to correspond to above-average summer precipitation (mm) and poor growth to be associated with warmer summer temperatures (°C), especially above-average summer temperatures in the following year. In addition, response function analysis indicated that the combination of maximum temperature and precipitation explained most of the variance in radial growth at all sites (Table 4.3).

Although few differences in growth response patterns were detected between minimum, maximum, and mean air temperatures, we still considered the impact of these variables in our correlation analysis. Correlation analysis showed that radial growth of lodgepole pine for all sites was significantly negatively correlated with current year maximum June temperatures ($p \leq 0.01$) (Fig. 4.2). Previous August maximum temperatures (t-1) were also shown to be significant among most of the climate sites ($p \leq 0.01$). Although not as distinct, relationships between radial growth and mean temperature were generally similar to maximum temperature results (Fig. 4.3). In contrast, few significant correlation coefficients were found between radial growth and minimum temperatures among the sites (Fig. 4.4). For the analysis of total precipitation, late-spring and early-summer precipitation (mm) of the current year were found to be positively associated with radial growth for most sites (Fig. 4.5). The relationship between climatic annualized and seasonal periods of precipitation and radial growth showed that current year spring total precipitation (March, April, May) had a significant, positive effect on radial growth for all sites in the analysis ($p \leq 0.05$) (Table 4.4). As a result, we examined different combinations of spring and summer months and identified a significant response in radial growth to May-June and May-July mean total precipitation. For the annualized and seasonal periods of mean, minimum and maximum temperatures, winter temperatures showed a significant, positive effect on growth for all sites. However, winter temperatures were not considered candidate variables for our climate reconstructions.

4.5.3 Dendroclimatic reconstructions

All correlation and response functions were carefully examined and used to identify statistically significant regression functions performed on the second half of the data set (1977-2003). The calibration statistics for all significant regressions are given in Table 4.5. A significant relationship was found between radial growth of lodgepole pine and mean June maximum temperature for all sites, except at the Rosswood (RWC) site. August maximum temperature of the previous year showed statistically significant regression functions for all sites, except at the Cinema (CRC) site. Models predicting spring precipitation, May-June, and May-July total precipitation also calibrated well for most sites. The variation in radial growth explained by temperature variables ranged between 8% and 36%, while precipitation variables explained between 19% and 50% of measured variation. When transfer functions from these preliminary models were applied to the predictor data (ring-widths), and compared with the instrumental climate data (1950-2003), many of the estimated values of the temperature and precipitation variables demonstrate straight-line relationships (Fig. 4.6a,b,c,d,e). Some reconstructions indicate less variability (or sensitivity) compared to the instrumental climate data, but were considered sufficient for further analysis.

The accuracy of each statistical model was measured by calculating a number of verification statistics. The positive RE and CE values for the mean June maximum temperature indicate that all calibrated sites passed the verification tests, and that the transfer function estimates may be considered stable (Table 4.6). For the model predicting previous year August maximum temperatures all sites passed the verification procedure, except for Nilkitkwa (NLC). Transfer function estimates for both precipitation variables indicated weak areas in the reconstruction, with RE and CE both close to or <0. Since these variables calibrated reasonably well, we suspected a shift in climatic conditions between the verification and calibration period. Scatter plots of the entire instrumental period (1950-2003) for each precipitation variable at each site indicated a shift towards an increase in total precipitation during the mid-to-late 1970s (Fig. 4.7a,b,c). The shift was less pronounced in meteorological data from the central interior (Cottonwood). To remove bias introduced by the different climatic condition, our calibration/verification procedure for the two precipitation variables was instead performed on odd/even years of the instrumental climate data, excluding the site from the central interior. As a result, fewer site chronologies were found significant when calibrated with odd years of each precipitation variable (Table 4.7). The performance of these new transfer function models was tested with even years of the data. Few improvements were found using even years as the verification period compared to the previous modeling strategy. Because this procedure did not greatly improve results, the previous models were used. Temperature and precipitation models derived from these relationships are presented in Figure 4.8a,b,c,d,e. In all cases, the reconstructed series exhibited reduced variance over the observed series, suggesting that the tree-ring record gave a conservative estimate of the year-to-year variability in the climate variables. The reconstructions of temperature and precipitation variables are presented in Figure 4.9a,b,c,d,e. These proxy records provide perspectives on climate for the last ~90-100 years.

4.5.4 Climate comparisons between reconstructions

Correlation analyses revealed that sites reconstructed for June maximum temperature were significantly correlated, although coefficients were lower for the central interior site (Table 4.8a,b). The Kwinageese (KWC) reconstructions of mean June maximum temperature and previous year August maximum temperature provided the highest predictive results during calibration, and were used in comparison with the long-term weather data (see section 4.5.5).

Correlation analyses between the northwest and central interior reconstructions of May-June total precipitation were significant, but low (Table 4.9a). In contrast, the northwest sites used to reconstruct May-July total precipitation were highly related (Table 4.9b). Both reconstructions of May-July total precipitation showed the same increasing trend since the late 1970s (see Fig. 4.9e). This increase was not observed in the May-June total precipitation reconstruction from the central interior (see Fig. 4.9c). The Rosswood (RWC) reconstruction of May-July total precipitation and the Kwinageese (KWC) reconstruction of May-June total precipitation provided the highest predictive results during calibration, and were used in comparison with the long-term weather data (see section 4.5.5). The reconstruction of May-July total precipitation for the central interior site (CRC) was also examined separately. Because only a single site (KWC) was used to reconstruct total spring precipitation, no correlation analysis was conducted.

4.5.5 Climate comparisons between weather stations

Graphical comparisons between each of the climate reconstructions for the northwest and the Fort St. James and Terrace weather data indicate that the year-to-year variability in the temperature and precipitation variables did not contain any explicit spatial differences (Fig. 4.10). Although the reconstructions revealed less year-to-year variability, the comparisons indicated general agreement between the long-term weather station data and the reconstructed periods. Climate variability at the Fort St. James weather station was most similar to the reconstructed variables.

Weather records from the Quesnel station were used to examine if these reconstructions represented regional or site-specific responses to climate variability in the central interior reconstructions. Reconstructions were generally less variable, but had a general agreement between most years (Fig. 4.11).

4.6 Discussion

4.6.1 Quality and reliability of the climate reconstructions

Successful extraction of a climatic signal from a tree ring record depends on the quantification of the influence of climatic variables on radial tree growth (Villalba *et al.* 1994). The first consideration should be the development of a calibration model that matches current understanding of the biological and physical processes that link the climate-growth relationship (Cook and Kairiukstis 1990). In this study, the modeled relationships indicated that maximum air temperatures during August of the previous year and June of the current year strongly influenced lodgepole pine growth. Radial growth of conifers is especially sensitive to variations in growing season temperature (Kozlowski *et al.* 1991, Coleman *et al.* 1992), which probably reflects the importance of temperature in regulating metabolic activity, as well as respiration and photosynthesis. The negative response to previous year August maximum temperature suggests that high maximum temperatures during this period are a limiting factor of current year radial growth. Several physiological factors could be responsible for this lag between prior year's climate and growth. For instance, warm temperatures in previous years may increase evapotranspiration demands and lead to an increased rate of respiration, thus depleting food reserves for the following year (Kozlowski *et al.* 1991).

The relationship established between radial growth and current year June maximum temperatures indicate that hot early summer conditions limit radial growth possibly through a decrease in photosynthesis as a result of increased photorespiration (Rundel and Yoder 1998). Elevated leaf temperatures increase rates of photorespiration and dark respiration, reducing net photosynthesis. Reduced radial growth during warm conditions in the early summer may also suggest that radial growth of lodgepole pine is responding to a decrease in soil water availability, possibly due to rapid snowmelt. Spring and summer conditions in northwest British Columbia are generally considered cool and moist compared to the interior plateau, however, minor to severe summer droughts are not uncommon (Banner *et al.* 1993). Decreased soil water availability and atmospheric water deficits reduce photosynthetic rates as a result of stomatal closure and the inhibitory effects of CO_2 fixation (Rundel and Yoder 1998). The tendency of warm summer temperatures to be associated with lowered growth in lodgepole pine is consistent with previous studies conducted in the central interior of British Columbia (Anonymous 1998), the Colorado Front Range (Villalba *et al.* 1994), and Mammoth Mountain, California (Biondi and Fessenden 1999).

All of our study sites showed high correlation and response coefficients to spring/summer precipitation during the current year. This response to precipitation exemplifies the strong effect moisture stress has on growth of lodgepole pine in the study area. In northern British Columbia, snowmelt begins in late spring and often extends into summer months with cooler temperatures (Schwab and Septer 1995). Therefore, hot spring/early summer temperatures may cause rapid snowmelt and subsequent drought stress. Although the study area is not considered moisture-limited, dry conditions are recorded regularly (Banner *et al.* 1993). As a result, soil moisture in the upper horizons may dry out quickly and water in deeper horizons may still be frozen or cool soil temperatures may impede water uptake (Splechtna *et al.* 2000). In this study, lodgepole pine growing at low-elevation mountain slopes and rocky valley floors are likely responding more to changes in moisture availability in the form of snowmelt and rainfall as a result of warm temperatures. However, this relationship with total precipitation variables was only significant for few of the sites located in northwest British Columbia, which will be discussed later. These climate-growth relationships are similar to those reported for lodgepole pine in the more continental climate of the central interior; there, spring and summer temperature and, in most cases, summer precipitation are the primary factors associated with annual growth variability (Anonomous 1998).

Because of the empirical nature of the climate-ring width links established here, the need to verify calibrated models is fundamental (Fritts 1976, Briffa *et al.* 1983). In this study, all significant calibration models were tested against an independent period for which actual climate data exists. Significant verification statistics are essential if quantitative climatic reconstructions are to be reliable (Cook and Kairiukstis 1990). A disadvantage of the Reduction in Error (RE) and Coefficient in Efficiency (CE) statistics is that one extremely poor estimate can offset the effect of several good estimates (Fritts 1976). Therefore, it is possible that RE and CE are underestimating the true skill of the tree-ring models, and may explain why many of our models did not pass verification. However, to ensure the reliability of a particular statistical model the accuracy needs to be measured to provide the proper perspective with which to view the climate reconstructions (Cook and Kairiukstis 1990). The more rigorous the verification, the more likely a reconstructed climate variable expresses a universal property relating the predictors and the predictands.

The method of cross validation is intended to avoid bias that might be introduced by the arbitrary division of a time-series into segments (Cook and Kairiukstis 1990). In this study, the precipitation data for our calibration period indicated that a climatic shift occurred that differs from conditions of the verification period. More specifically, an observed shift towards an increase in total spring and summer precipitation levels since the late-1970s. Climate variability in British Columbia is thought to be driven by cyclic changes in ocean surface temperatures, specifically those related to the El Niño Southern Oscillation (ENSO) and the Pacific Decadal Oscillation (PDO) (Stahl *et al.* 2006). The PDO is distinct from ENSO in that it does not appear to be truly oscillatory, but rather may shift abruptly between relatively warmer and cooler states (Gedalof and Smith 2001). Mantua and Hare (2002) speculated that the cool phase is associated with wet conditions in British Columbia and the warm phase with dry conditions. Shifts to cool phases were recorded in 1890-1924 and 1947-1976 and alternated with warm phases during 1924-1946 and 1977-present (Mantua *et al.* 1997), suggesting climate in our study area is in a warm, dry phase. However, in northwest British Columbia meteorological data of precipitation levels show the opposite of the trend suggested by Mantua and Hare (2002), where dry conditions are associated with cool phases and wet conditions during the warm phases (Egginton 2005). On the other hand, more inland and areas in northeastern British Columbia still follow the typical PDO patterns (Egginton 2005). This is supported by our data when comparing precipitation data from the northwest sites to precipitation data from the central interior; the current phase of increased precipitation is not apparent in meteorological data from the interior (Fig. 4.9c). Therefore, this shift in spring and summer precipitation during the late-1970s was likely influenced by the PDO. Because the calibrated model optimizes coefficients for the current warm and wet phase, the predictive power of the regression model decreases when applied to the independent data. Although a gradual increase in precipitation has occurred since the late-1970s, it is important to note that the PDO may not be dominating precipitation trends in the northwest. No relationship between the PDO and the current increase in precipitation during the mid-1990s has been found, suggesting the trend is more likely a part of a directional global change pattern (Woods *et al.* 2005).

4.6.2 Climate variability between sites and weather stations

Although it is apparent that each of our climate reconstructions is statistically robust, the purpose of the study was to determine whether the reconstructions represent local climate variability. British Columbia is a region of complex terrain that modulates the spatial patterns of climate, due to sharp variations in elevation and terrain-induced climate transitions (i.e., rain shadows) (Daly 2006, Stahl *et al.* 2006). Because yearly differences in weather are known to result in considerable yearly variations in the amount of infection by Dothistroma needle blight (Peterson 1973), it was important to focus on the impacts of local climate variability on disease incidence. However, it is apparent that our climate reconstructions did not represent local climate variability, but rather a reconstruction of larger regional climatic processes. For instance, it was found that the radial growth of lodgepole pine in this region was controlled primarily by the same climate variables. In addition, the significant correlations among the reconstructions between all the sites indicate that tree rings of lodgepole pine in the study area are only able to provide common regional climate information for sites in the northwest. This finding was further exemplified when selected climate reconstructions appeared climatically similar to the two geographically distant weather stations.

Lodgepole pine is generally considered less climatically sensitive than many other species. For instance, Villalba *et al.* (1994) compared the climatic response of lodgepole pine, Engelmann spruce (*Picea engelmannii* [Parry] Engelm.), and subalpine fir (*Abies lasiocarpa* [Hook.] Nutt) in subalpine forests of the Colorado Front Range. In that study, lodgepole pine had lowest mean sensitivity and standard deviation values, suggesting that the species had the lowest dendroclimatological quality. In another study, the strength and nature of the climate signal in lodgepole pine and Douglas-fir (*Pseudotsuga manziesii* (Mirb.) Franco) were compared among different sites in the Cariboo region of British Columbia (Daniels and Watson 2003). Although similar response patterns to precipitation were seen between the chronologies, correlations were higher for the co-located Douglas-fir chronologies. Lodgepole pine at Mammoth Mountain, California, was characterized by "complacent" ring patterns, with little year-to-year variability and a relatively small amount of common variance (Biondi and Fessenden 1999). As a result, climate signals were considered weak, even when separate tree-ring chronologies were developed for live, stressed, and dead pines. It was suggested that stand dynamics (i.e., competition) played a more important role than climate in forcing tree growth (Biondi and Fessenden 1999). Until now, the dendroclimatic utility of lodgepole pine has not been investigated in northwest British Columbia. As already discussed, lodgepole pine growth is largely limited by spring/summer precipitation and temperature during June and August of the previous year. Based on the chronology statistics and response to climate variations, it is apparent from this study that lodgepole pine does have significant dendroclimatological utility for reconstructions of regional climate in our study area.

Relatively minor changes in site condition are important in determining the nature of a tree's response to climatic variation (Villalba *et al.* 1994). Villalba *et al.* (1994) examined the significance of interhabitat differences (i.e., xeric vs mesic sites) in tree growth responses to climate variation. Differences in growth responses were evident among the sites for Engelmann spruce and subalpine fir, but absent for lodgepole pine (Villalba *et al.* 1994). That is, at all sites the growth of lodgepole pine was favoured by high temperature and depressed by high precipitation in fall months. We found similar results in that lodgepole pine chronologies from distant biogeoclimatic sites exhibited generally similar growth responses to climate variations. Lodgepole pine is considered a species of wide ecological amplitude (Burns and Honkala 1990) that is ecologically dominant at middle elevations in open, early-successional conditions throughout its range (Rundel and Yoder 1998). Near the center of its geographical distribution, climate factors may rarely be limiting to growth except in years of most extreme weather (Fritts 1976). It is possible, therefore that hereditary factors of lodgepole pine explain why the climate reconstructions were more representative of regional climate than local climatic conditions.

It is not totally clear why our climate reconstructions were not more representative of local climatic variability. Two possible explanations are that (1) the meteorological data used in the calibration analyses are not representative of the sample sites, and (2) hereditary factors of lodgepole pine limited the spatial scale of the reconstruction, as already discussed. Due to the high spatial variability of topography in the area, meteorological data may not have provided representative data for local climate reconstructions. Although a number of climate records were statistically interpolated, the spatial variability introduced by local climate conditions may not have been fully expressed in the meteorological records. As a result, only regional climate conditions were reconstructed. Unrepresentative meteorological data could substantially decrease the statistical strength of the model, which may also explain why so many reconstructions did not pass the verification procedure.

As only larger regional climatic processes were reconstructed in this study, we found that climate data from the long-term weather stations were equally representative of climate variability. Our reconstructions revealed generally less year-to-year variability than records from the weather stations. This difference was considered a result of the predictive power of the models rather than differences due to spatial variability. The Fort St. James weather data covered a longer period and was more similar to the climate variability recorded in our reconstructions than the Terrace weather station data. Therefore, we consider the Fort St. James weather records the best spatially representative climate record to determine the relationship between climate and outbreak history of Dothistroma needle blight. Using meteorological data rather than climate reconstructions will also allow greater flexibility to examine a number of climate variables in relation to the incidence of historical Dothistroma needle blight outbreaks.

4.7 Literature cited

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Table 4.1. Site names and descriptive characteristics.

Site Name	Designation	Zone	Easting	Northing	Elevation	District	Variant
Kwinegeese	KWC	9	513773	6226074	659.9	North Kalum	ICHmc1
Suskwa	SKC	9	606969	6126283	516.6	Skeena-Stikine	ICHmc2
Nilkitkwa	NLC	9	639206	617276	606.0	Fort St. James	SBSmc2
Sustut	STC	9	598444	6237882	615.7	Fort St. James	SBSmc2
Rosswood	RWC	9	515174	6072542	167.6	South Kalum	CWHws1
Cottonwood River	CRC	10	534937	5889496	641.0	Prince George	SBSmh

Table 4.2. Chronology statistics and length of master chronologies for lodgepole pine for the six sites used to reconstruct climate.

Site[a]	No. of tree cores	Series Intercorr.	Mean Sens.	AC(1)[b]	Stand dev.	Mean rbt[c]	SSS[d]	Start	Start2[e]	End
NLC	36	0.461	0.137	0.569	0.127	0.256	16	1853	1904	2005
SKC	32	0.502	0.137	0.438	0.123	0.306	13	1917	1923	2005
KWC	48	0.626	0.186	0.398	0.157	0.421	8	1911	1913	2005
STC	39	0.605	0.169	0.377	0.143	0.421	8	1915	1917	2005
RWC	37	0.601	0.180	0.258	0.169	0.420	8	1910	1914	2005
CRC	26	0.595	0.214	0.563	0.228	0.372	10	1884	1901	2005

[a] For site names and locations see Table 1.

[b] 1st order autocorrelation.

[c] Interseries correlation between indexed series.

[d] Subsample signal strength.

[e] Start date with the effects of changing sample size removed.

Table 4.3. Percentage of tree-ring variance explained by monthly climate from June (*t*-1) to September (*t*).

Site	Percentage
1. Mean Temperature and Precipitation	
NLC	58.7
SKC	64.7
KWC	67.3
STC	66.5
RWC	75.5
CRC	67.1
2. Minimum Temperature and Precipitation	
NLC	49.6
SKC	59.9
KWC	64.2
STC	59.1
RWC	73.5
CRC	65.7
3. Maximum Temperature and Precipitation	
NLC	70.5
SKC	66.0
KWC	70.5
STC	69.5
RWC	75.6
CRC	63.1

Table 4.4. Correlation coefficients and p-values for current year mean seasonal precipitation and temperature variables for lodgepole pine. Spring included March, April, and May; Summer included June, July, and August; Fall included September, October, and November; Winter includes December, January, and February. *P*-values are indicated in bold.

Site	Spring precip.	Summer precip.	Fall precip.	Winter precip.	May-June precip.	May-July precip.	Winter minimum temp.	Winter mean temp.	Winter maximum temp.
KWC	0.43	0.16	0.04	0.28	0.58	0.49	0.40	0.38	0.35
p-value	**0.00**	**0.25**	**0.79**	**0.04**	**0.00**	**0.00**	**0.00**	**0.00**	**0.01**
NLC	0.35	0.22	-0.02	0.05	0.32	0.30	0.48	0.48	0.47
p-value	**0.01**	**0.12**	**0.89**	**0.64**	**0.02**	**0.03**	**0.00**	**0.00**	**0.00**
STC	0.37	0.23	-0.12	0.01	0.39	0.37	0.27	0.27	0.26
p-value	**0.02**	**0.09**	**0.45**	**0.94**	**0.00**	**0.01**	**0.02**	**0.02**	**0.03**
SKC	0.30	0.12	-0.17	0.07	0.28	0.25	0.38	0.39	0.39
p-value	**0.03**	**0.38**	**0.21**	**0.62**	**0.04**	**0.07**	**0.00**	**0.00**	**0.00**
RWC	0.33	0.13	-0.15	0.14	0.57	0.56	0.43	0.43	0.43
p-value	**0.02**	**0.36**	**0.28**	**0.32**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**
CRC	0.26	0.22	-0.08	-0.15	0.47	0.43	0.21	0.21	0.20
p-value	**0.04**	**0.12**	**0.58**	**0.28**	**0.00**	**0.00**	**0.07**	**0.07**	**0.07**

Table 4.5. Climate model statistics for the calibration period (1977-2003). Only sites with significant regression functions are listed for each climate variable. The predictor data is ring-width in the transfer function models.

Site[a]	r[b]	RSQ[c]	Equation
1. *Current year June maximum temperature*			
KWC	-0.60	0.36	$y=25.199+((-7.682)(x))$
CRC	-0.34	0.11	$y=24.713+((-3.984)(x))$
SKC	-0.35	0.12	$y=25.221+((-6.139)(x))$
STC	-0.50	0.24	$y=26.121+((-7.278)(x))$
NLC	-0.44	0.20	$y=26.864+((-8.635)(x))$
2.*Previous year August maximum temperature*			
KWC	-0.57	0.33	$y=25.876+((-7.214)(x))$
RWC	-0.43	0.19	$y=25.767+((-4.879)(x))$
SKC	-0.36	0.13	$y=26.285+((-5.638)(x))$
STC	-0.54	0.29	$y=27.287+((-7.262)(x))$
NLC	-0.28	0.08	$y=24.621+((-4.827)(x))$
3. *Total spring precipitation*			
KWC	0.54	0.29	$y=-8.984+((127.280)(x))$
RWC	0.57	0.32	$y=14.881+((166.762)(x))$
SKC	0.55	0.30	$y=-20.751+((121.952)(x))$
STC	0.60	0.36	$y=-23.230+((109.536)(x))$
4. *May-June total precipitation*			
KWC	0.62	0.38	$y=-29.459+((133.655)(x))$
CRC	0.49	0.24	$y=30.469+((79.686)(x))$
RWC	0.71	0.50	$y=-16.99+((130.004)(x))$
STC	0.56	0.31	$y=-45.585+((147.719)(x))$
SKC	0.45	0.20	$y=-22.672+((128.635)(x))$
5. May-July total precipitation			
KWC	0.51	0.26	$y=23.896+((142.629)(x))$
RWC	0.59	0.34	$y=49.503+((119.369)(x))$
CRC	0.44	0.19	$y=76.243+((96.986)(x))$
STC	0.53	0.28	$y=-12.497+((172.700)(x))$

[a] For site names see Table 1.

[b] Pearson's correlation coefficient.

[c] Squared multiple correlation.

Table 4.6. Results of the Reduction of Error (RE) and Coefficient of Efficiency (CE) statistics for the 1950-1976 verification period for each climate variable. RE and CE < 0 indicates a weak reconstruction.

Site[a]	RE	CE
1. *Current year June maximum temperature*		
KWC	0.38	0.37
CRC	0.09	0.06
SKC	0.02	0.02
STC	0.19	0.19
NLC	0.23	0.23
2.*Previous year August maximum temperature*		
KWC	0.33	0.24
RWC	0.35	0.05
SKC	0.12	0.03
STC	0.25	0.17
NLC	0.08	-0.04
3. *Total spring precipitation*		
KWC	0.09	0.02
RWC	-0.03	-0.20
SKC	-0.29	-2.83
STC	-0.38	-0.78
4. *May-June total precipitation*		
KWC	0.16	0.01
CRC	0.20	0.12
RWC	-0.16	-0.26
STC	-0.15	-1.46
SKC	-0.16	-1.92
5. *May-July total precipitation*		
KWC	0.16	0.05
RWC	0.28	0.28
CRC	0.16	-0.03
STC	-0.17	-1.13

[a] For site names see Table 1.

Table 4.7. Climate model statistics for calibration and verification periods using odd and even years. Only sites with significant regression functions are listed for each climate variable. Shaded numbers indicate sites that previously failed the verification procedure and are now positive as a result of the odd/even modeling strategy.

(A) ***Calibration (odd yrs)***			
Site	**r**	**RSQ**	**Equation**
1. *Total spring precipitation*			
RWC	0.39	0.15	$y=26.488+((162.768)(x))$
KWC	0.36	0.13	$y=21.552+((106.051)(x))$
2. *May-June total precipitation*			
KWC	0.54	0.29	$y=-2.790+(109.200)(x))$
RWC	0.39	0.15	$y=26.488+(162.768)(x))$
CRC	0.47	0.22	$y=13.984+(90.099)(x))$
3. *May-July total precipitation*			
CRC	0.54	0.30	$y=24.062+(140.528)(x))$
RWC	0.40	0.16	$y=87.628+(84.789)(x))$

(B) ***Verification (even yrs)***		
Site	**RE**	**CE**
1. *Total spring precipitation*		
RWC	-0.00	-0.09
KWC	0.27	0.27
2. *May-June total precipitation*		
KWC	0.35	0.13
RWC	0.15	0.00
CRC	0.23	0.18
3. *May-July total precipitation*		
CRC	0.02	0.01
RWC	0.40	0.37

Table 4.8a. Correlation coefficients of previous year August maximum temperature (°C) between reconstructed sites. All results are significant at the 0.05 level.

	NLC	KWC	RWC	STC	SKC
NLC	1				
KWC	0.648	1			
RWC	0.468	0.575	1		
STC	0.610	0.661	0.411	1	
SKC	0.613	0.619	0.443	0.677	1

Table 4.8b. Correlation coefficients of current year June maximum temperature (°C) between reconstructed sites. All results are significant at the 0.05 level.

	CRC	NLC	KWC	STC	SKC
CRC	1				
NLC	0.304	1			
KWC	0.373	0.642	1		
STC	0.258	0.618	0.655	1	
SKC	0.337	0.616	0.615	0.672	1

Table 4.9a. Correlation coefficients of May-June total precipitation (mm) between reconstructed sites. All results are significant at the 0.05 level.

	CRC	KWC
CRC	1	
KWC	0.373	1

Table 4.9b. Correlation coefficients of May-July total precipitation (mm) between reconstructed sites. All results are significant at the 0.05 level.

	RWC	KWC
RWC	1	
KWC	0.750	1

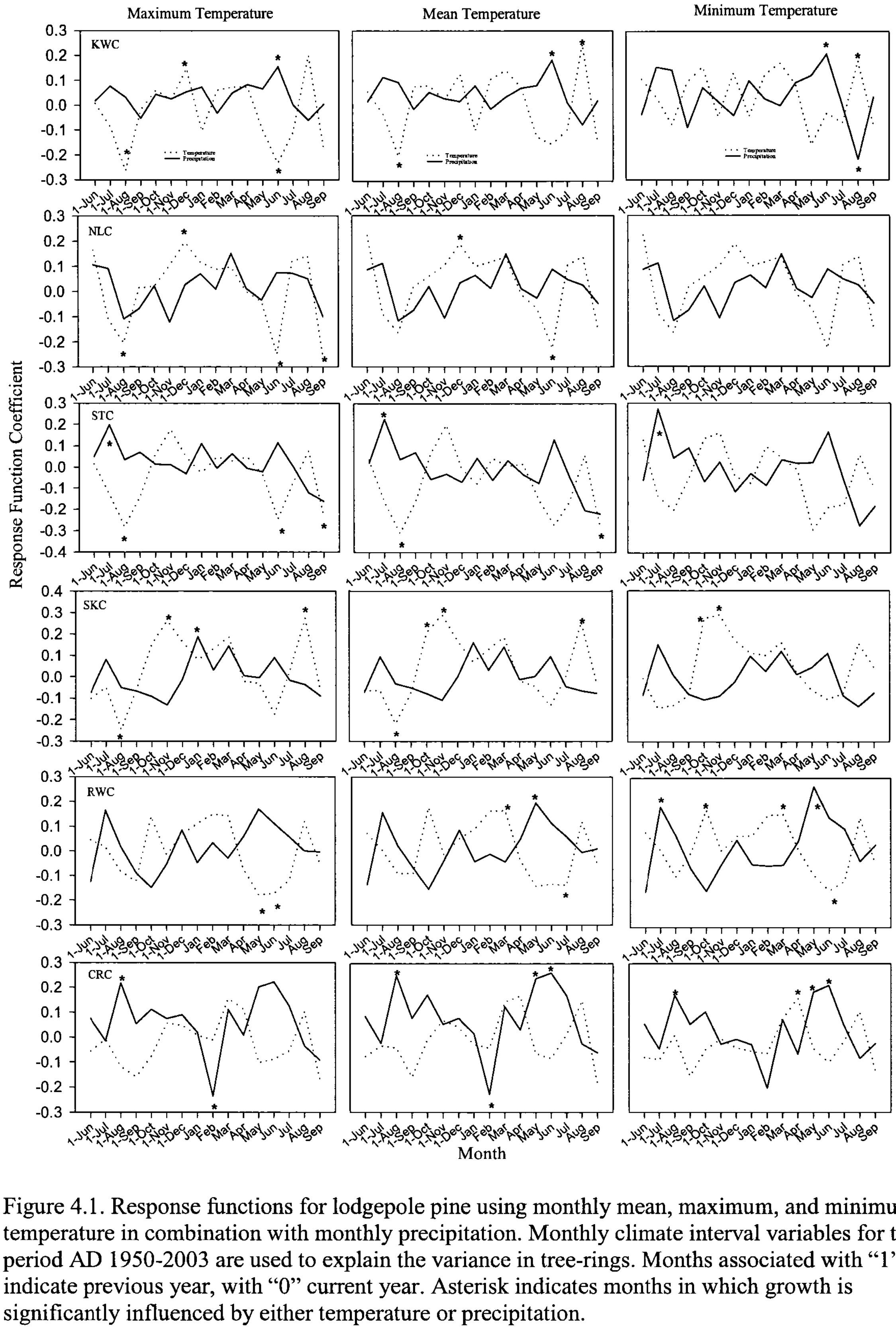


Figure 4.1. Response functions for lodgepole pine using monthly mean, maximum, and minimum temperature in combination with monthly precipitation. Monthly climate interval variables for the period AD 1950-2003 are used to explain the variance in tree-rings. Months associated with "1" indicate previous year, with "0" current year. Asterisk indicates months in which growth is significantly influenced by either temperature or precipitation.

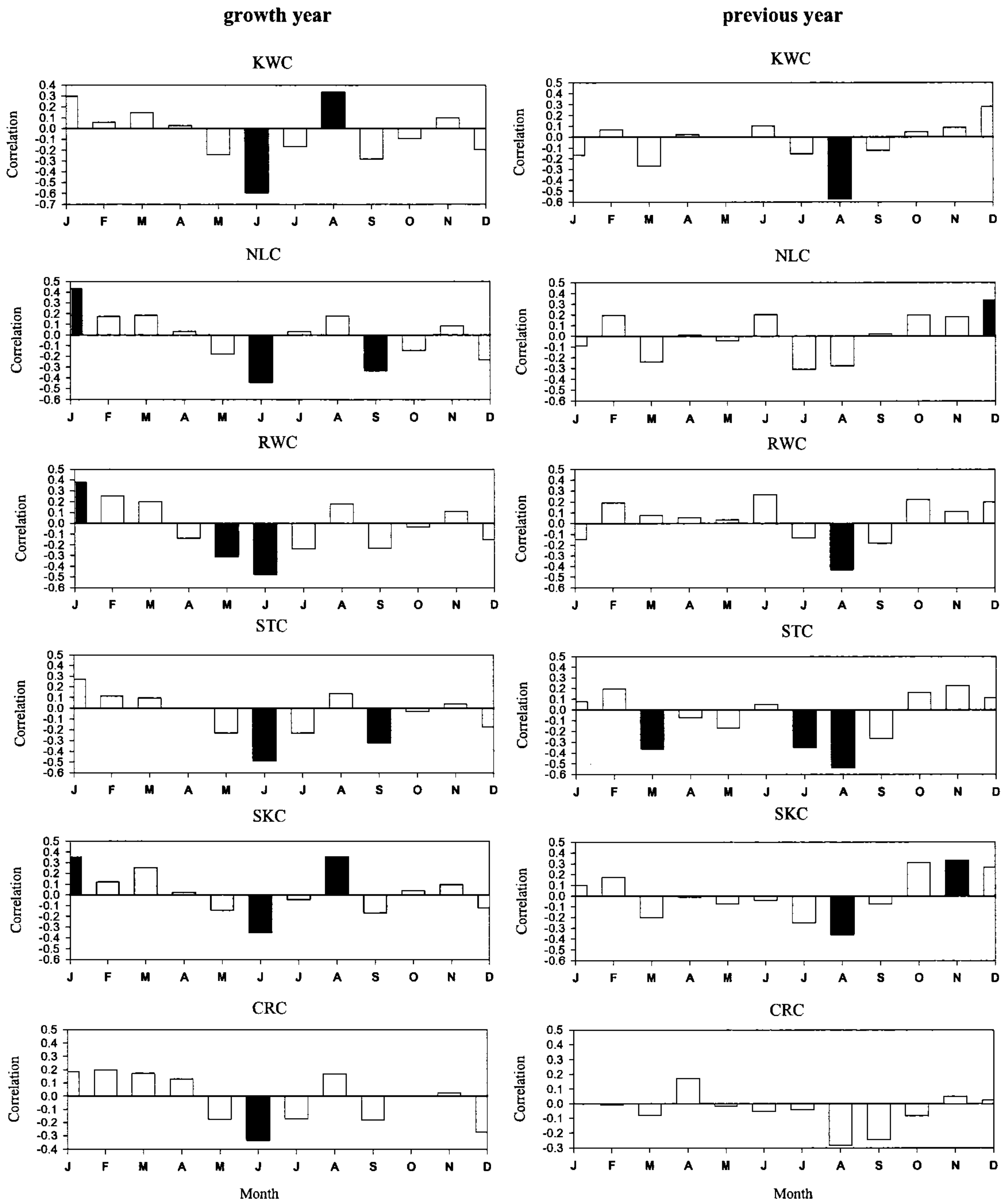


Figure 4.2. Correlation coefficients relating monthly maximum temperature to tree-rings for all climate sites. Coefficients that are significant at $p \leq 0.01$ are shaded in black. Site designations are located on the top of each graph (see Table 1 for site names).

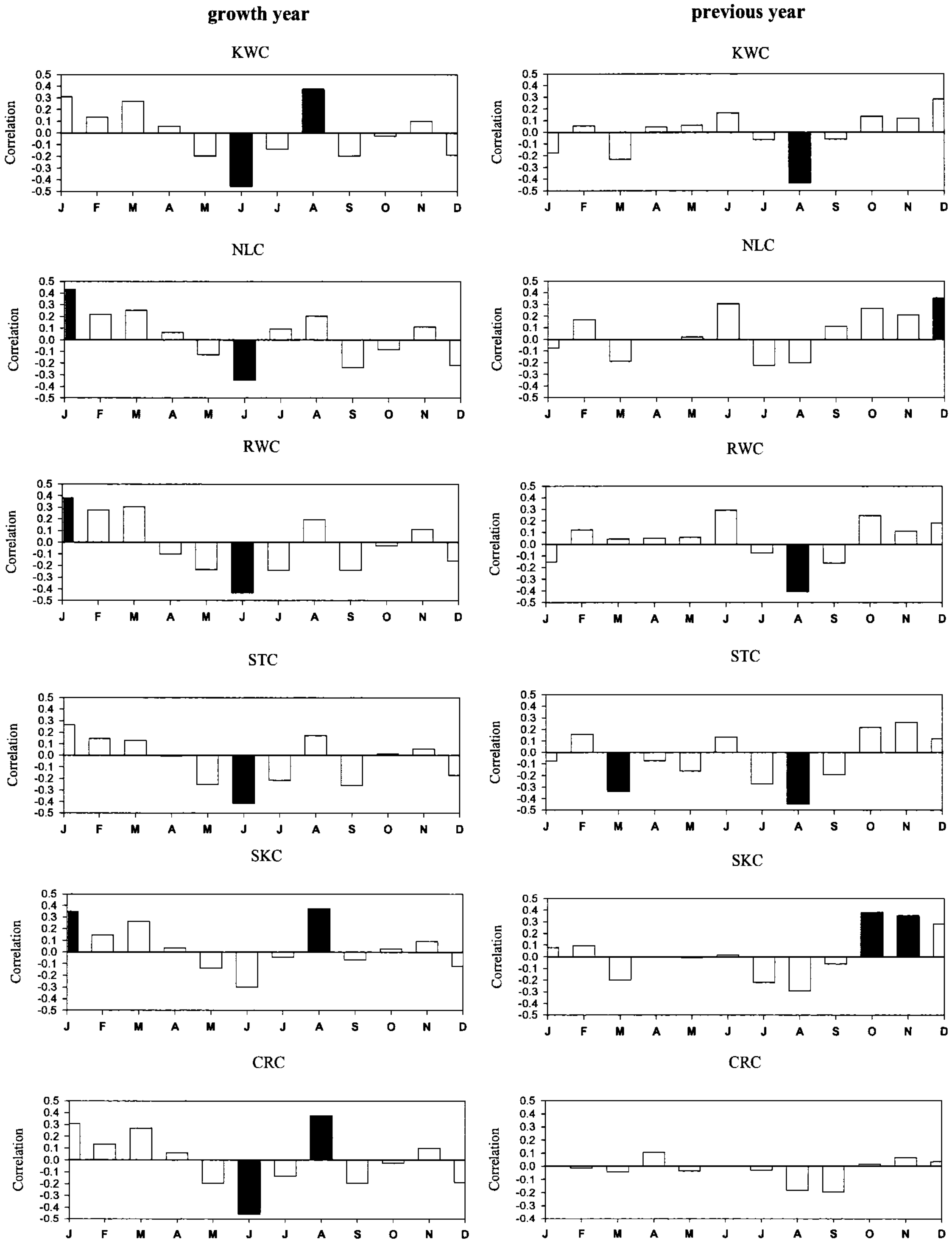


Figure 4.3. Correlation coefficients relating monthly mean temperature to tree-rings for all climate sites. Coefficients that are significant at $p \leq 0.01$ are shaded in black. Site designations are located on the top of each graph (see Table 1 for site names).

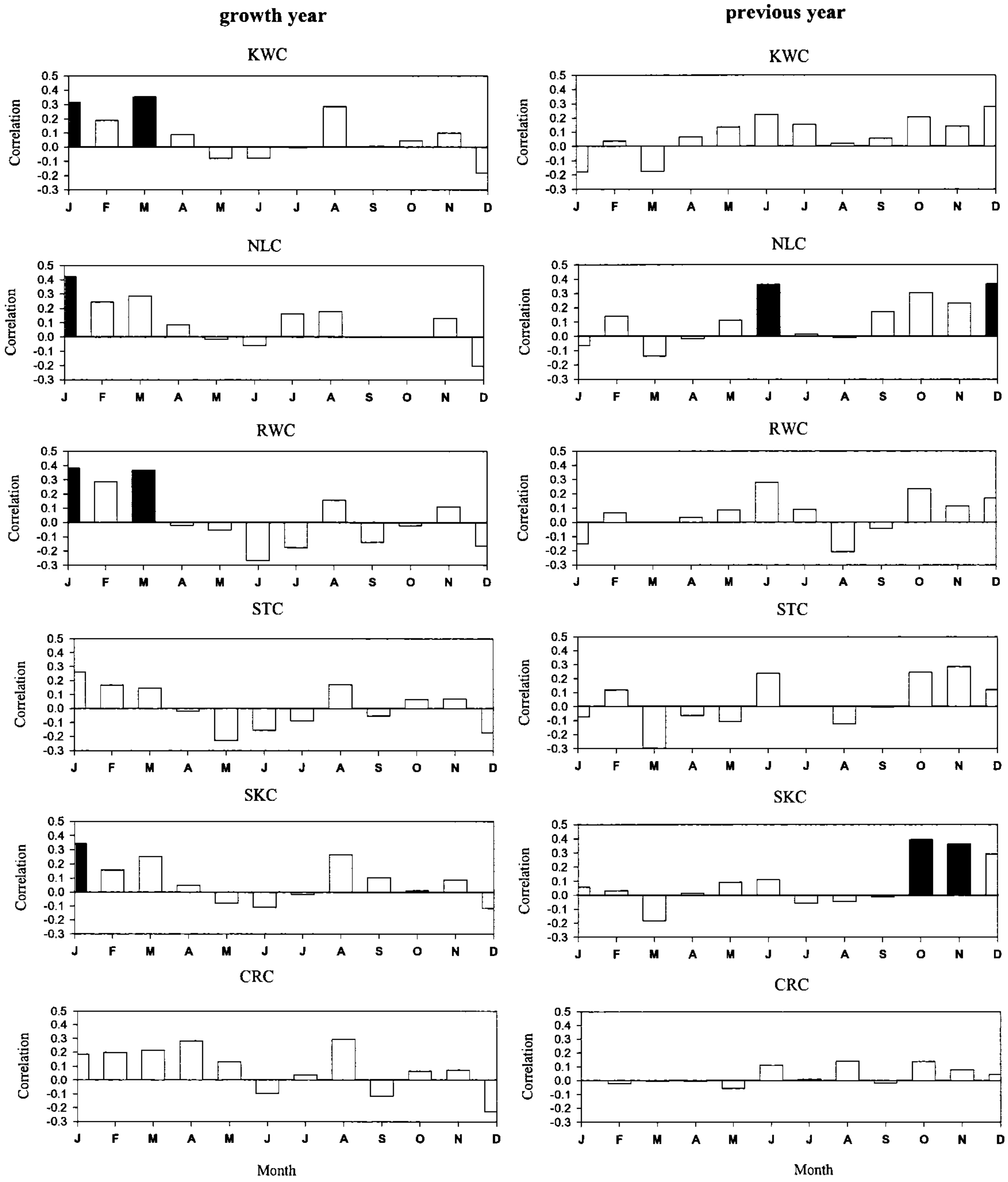


Figure 4.4. Correlation coefficients relating monthly minimum temperature to tree-rings for all climate sites. Coefficients that are significant at $p \leq 0.01$ are shaded in black. Site designations are located on the top of each graph (see Table 1 for site names).

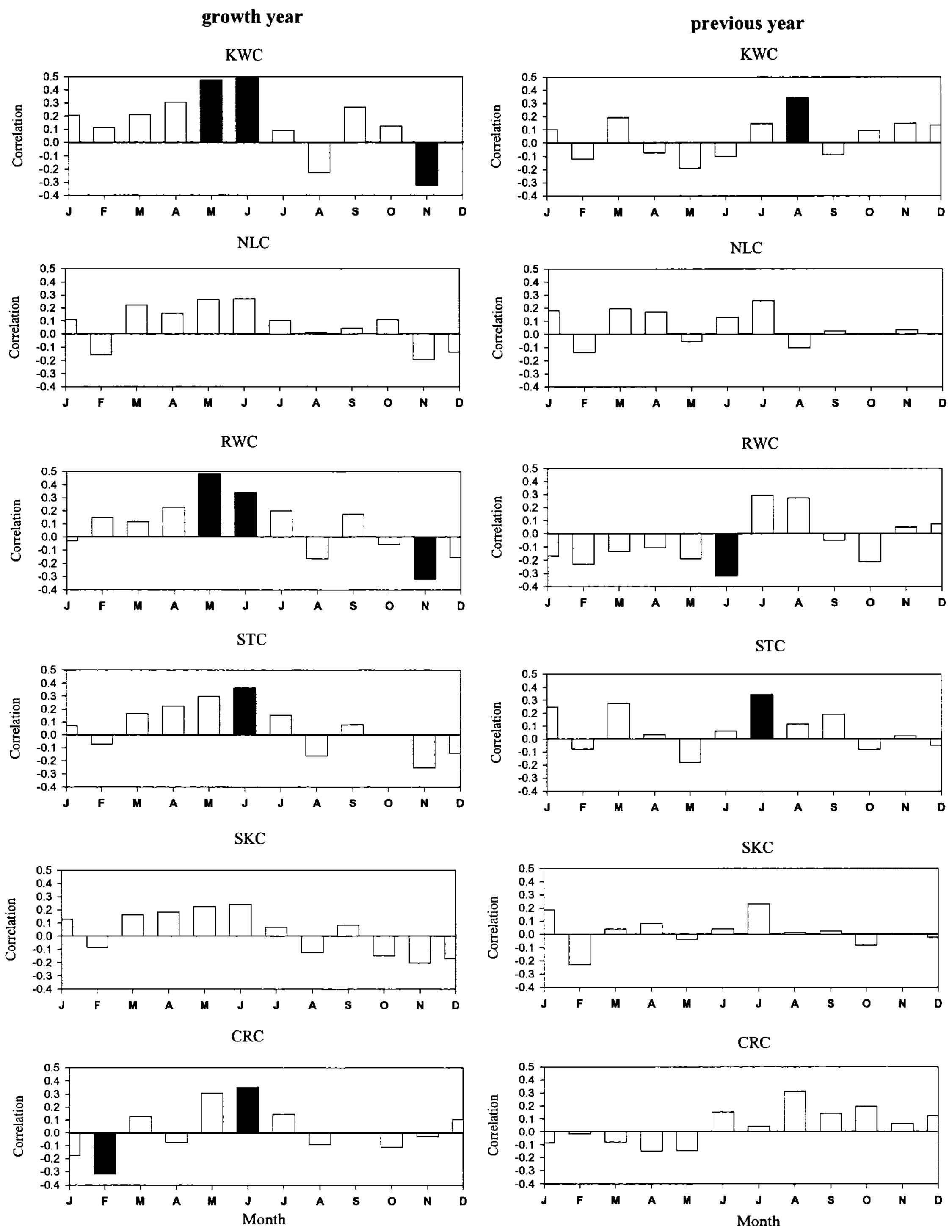


Figure 4.5. Correlation coefficients relating monthly total precipitation to tree-rings for all climate sites. Coefficients that are significant at $p \leq 0.01$ are shaded in black. Site designations are located on the top of each graph (see Table 1 for site names).

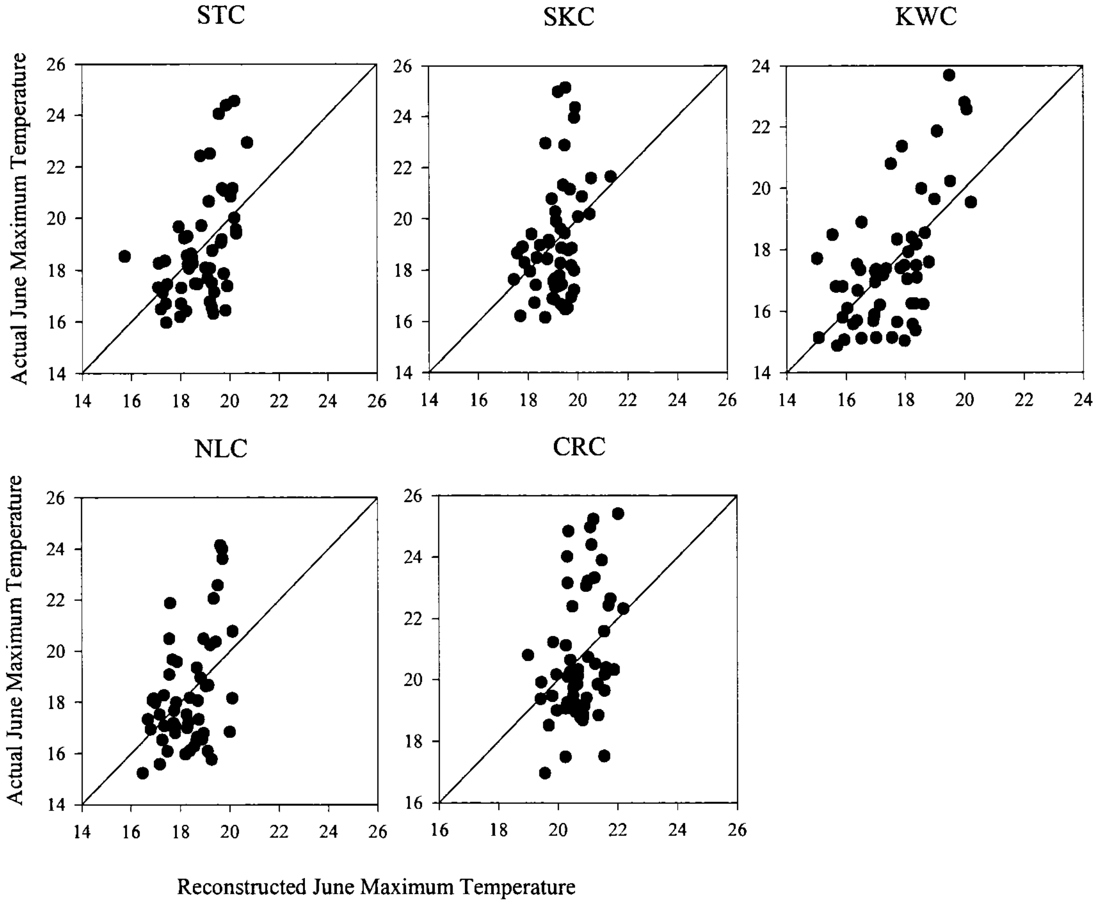


Figure 4.6a. Scatter plot of the estimated values compared to actual data to determine if a linear relationship exists between the two series. The data represents actual and reconstructed mean June maximum temperature for climate sites. Site designations are located on the top of each scatter graph (see Table 1 for site names).

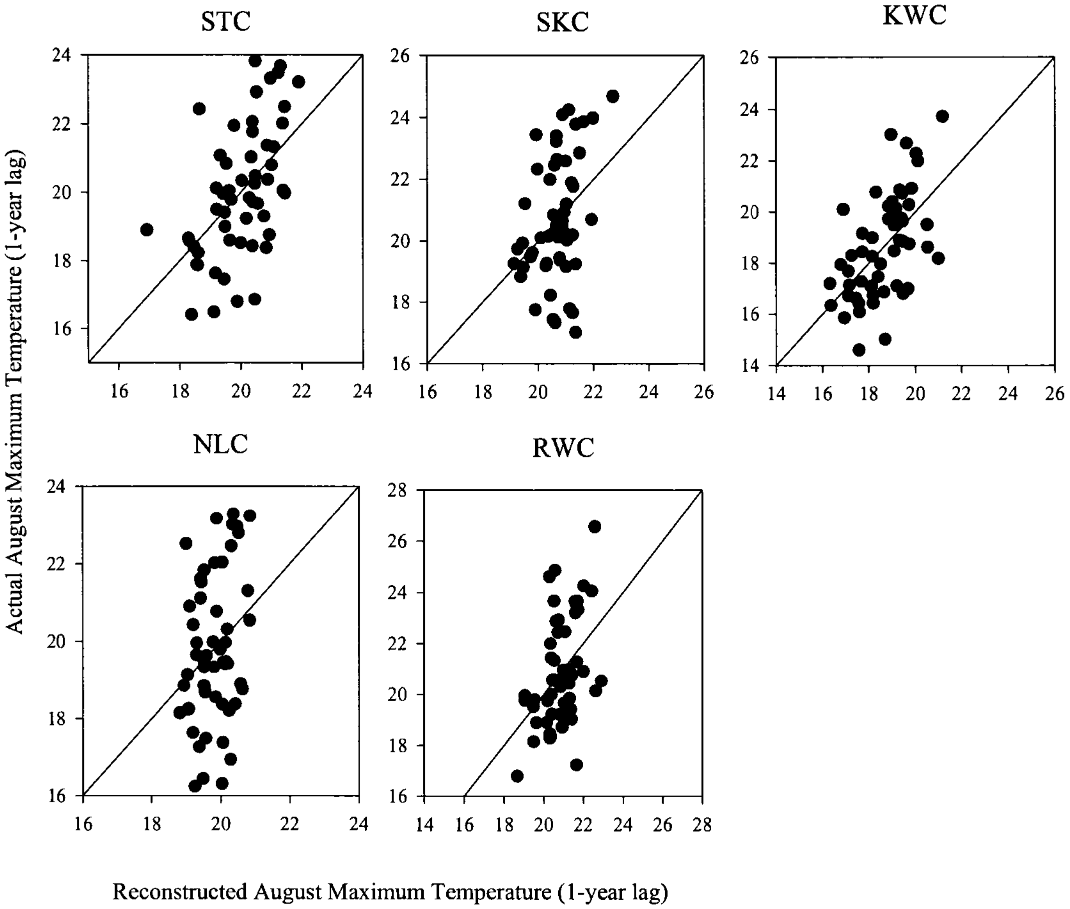


Figure 4.6b. Scatter plot of the estimated values compared to actual data to determine if a linear relationship exists between the two series. The data represents actual and reconstructed previous year mean August maximum temperature for climate sites. Site designations are located on the top of each scatter graph (see Table 1 for site names).

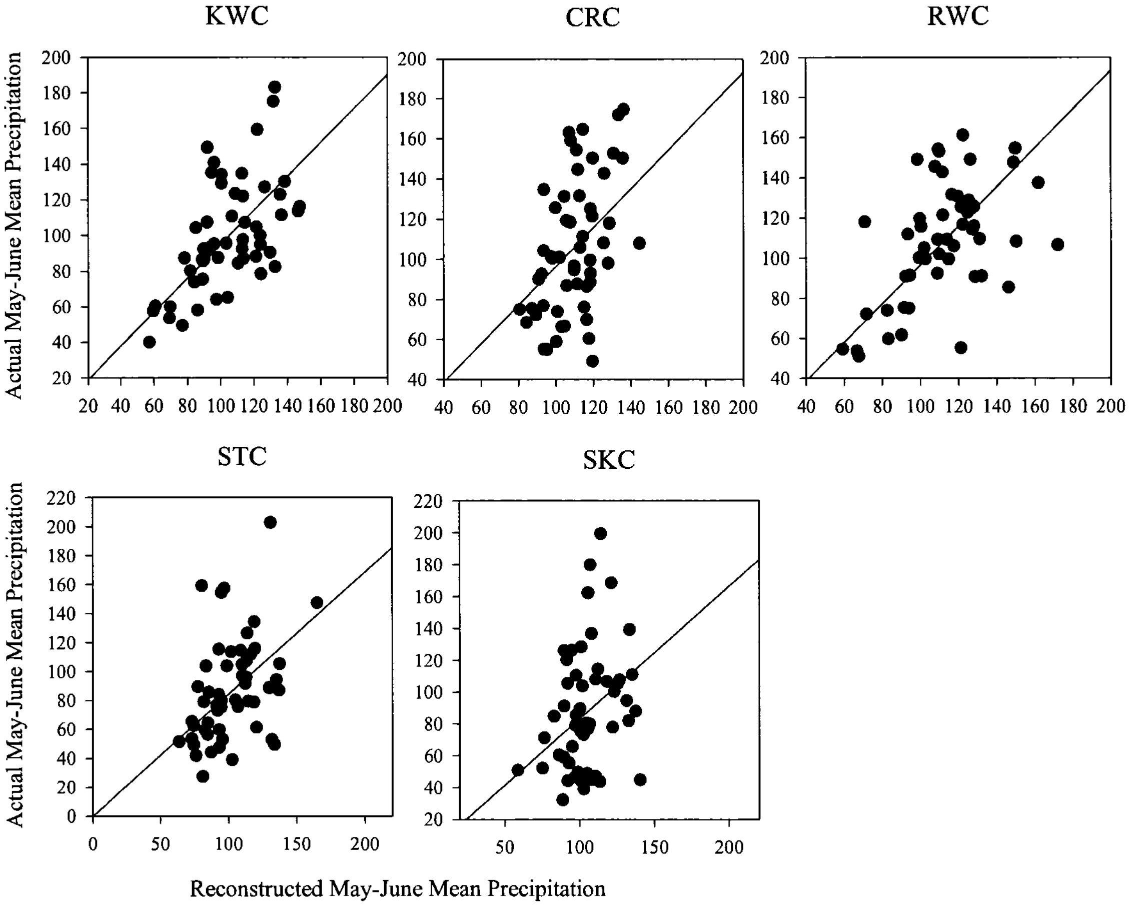


Figure 4.6c. Scatter plot of the estimated values compared to actual data to determine if a linear relationship exists between the two series. The data represents actual and reconstructed May-June total precipitation for climate sites. Site designations are located on the top of each scatter graph (see Table 1 for site names).

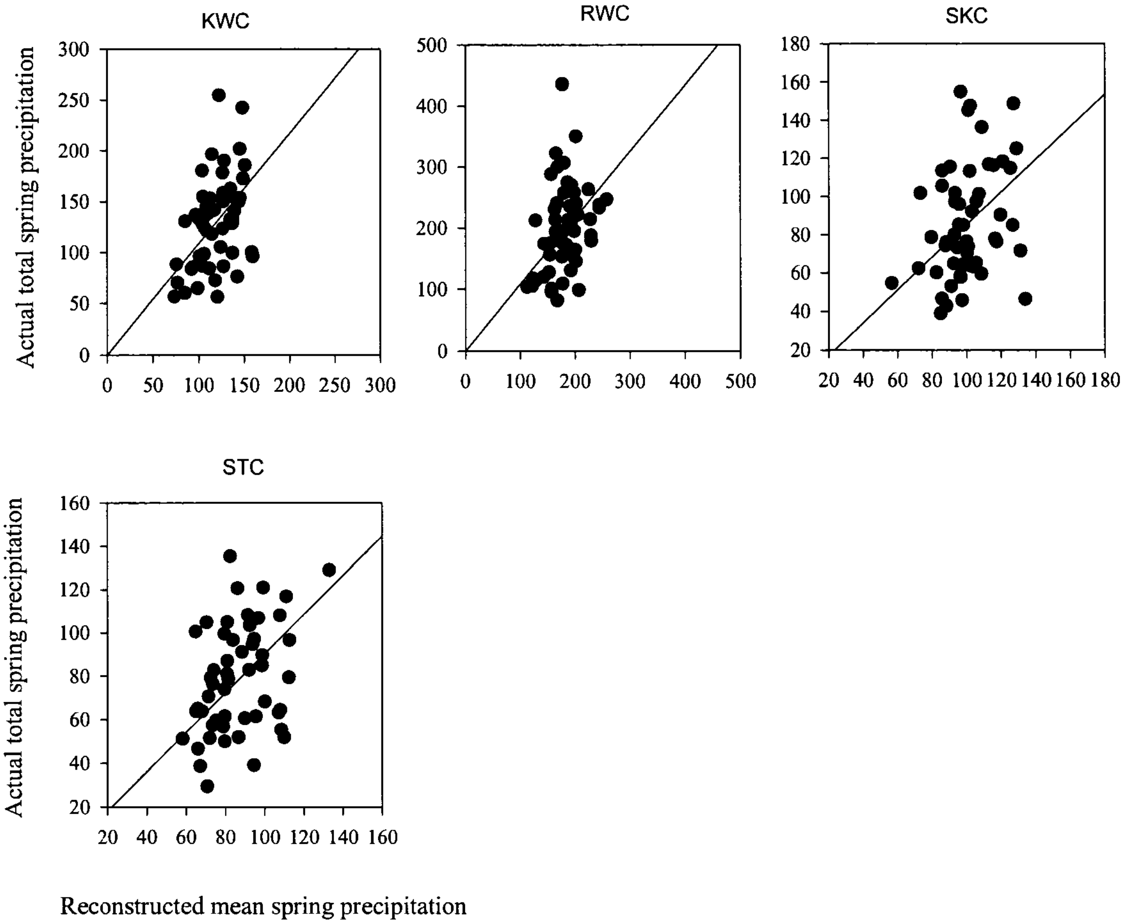


Figure 4.6d. Scatter plot of the estimated values compared to actual data to determine if a linear relationship exists between the two series. The data represents actual and reconstructed total spring precipitation for climate sites. Site designations are located on the top of each scatter graph (see Table 1 for site names).

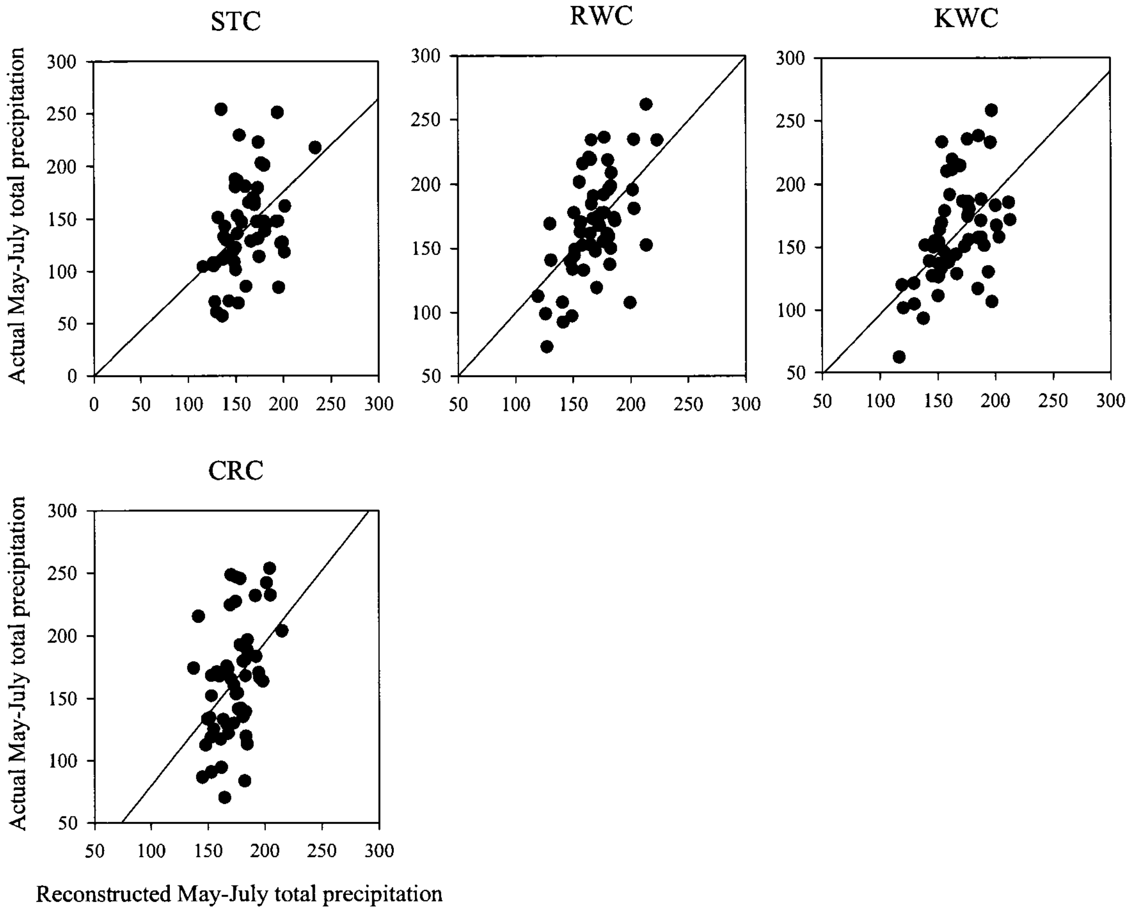


Figure 4.6e. Scatter plot of the estimated values compared to actual data to determine if a linear relationship exists between the two series. The data represents actual and reconstructed total May-July precipitation for climate sites. Site designations are located on the top of each scatter graph (see Table 1 for site names).

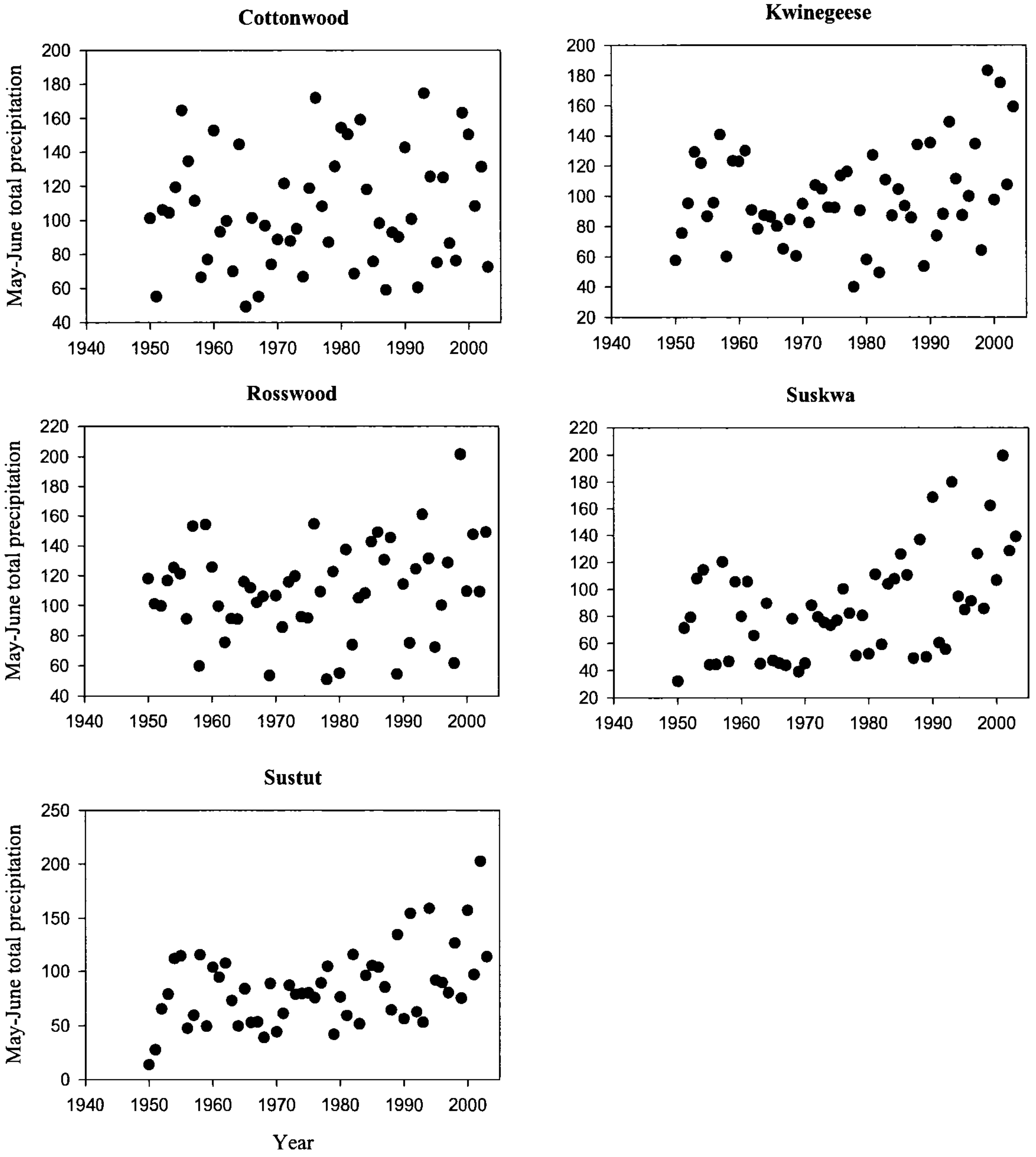


Figure 4.7a. Scatter plots of May-June total precipitation for the entire instrumental period. Note the shift towards an increase in precipitation during the mid-to-late 1970s.

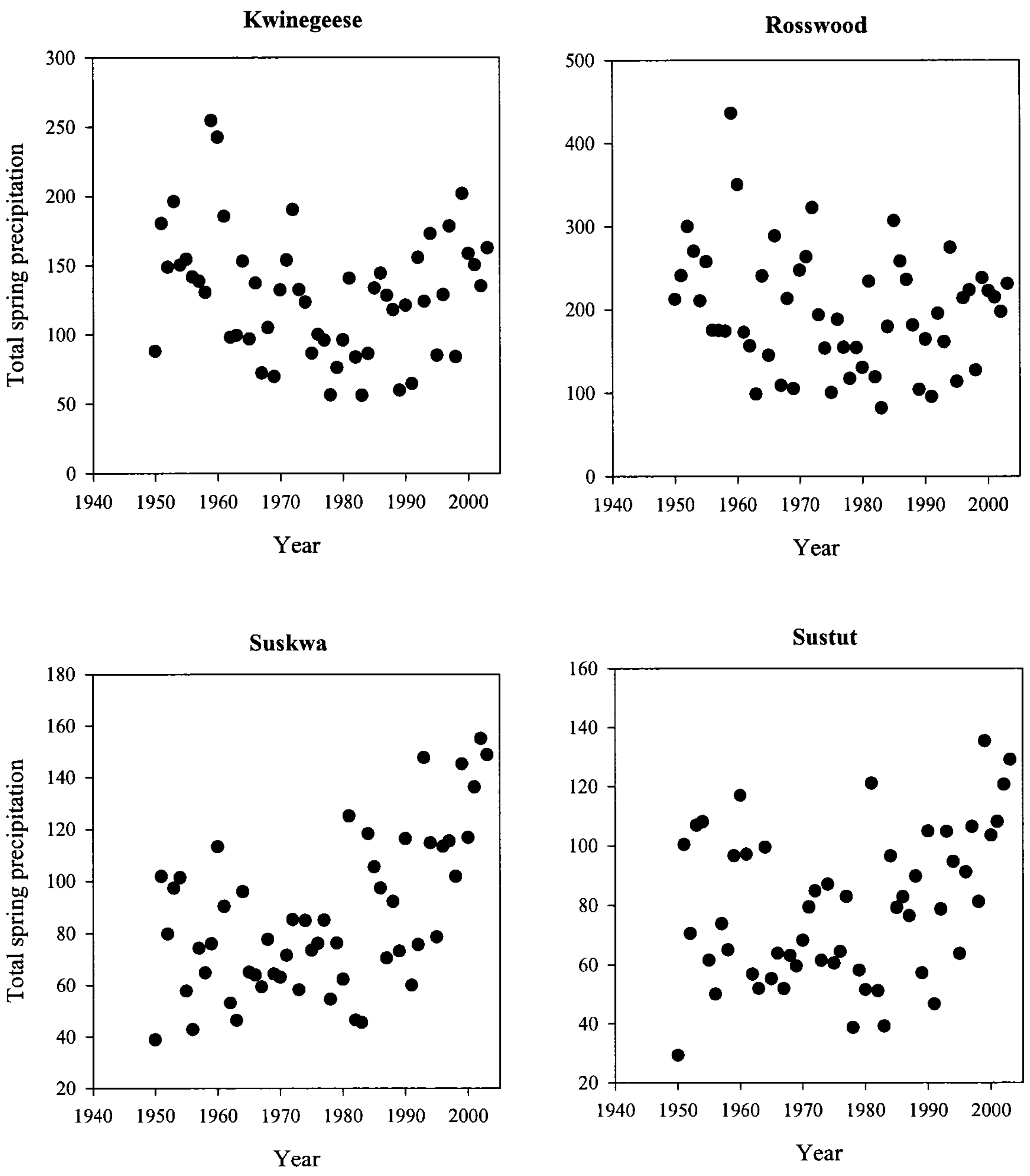
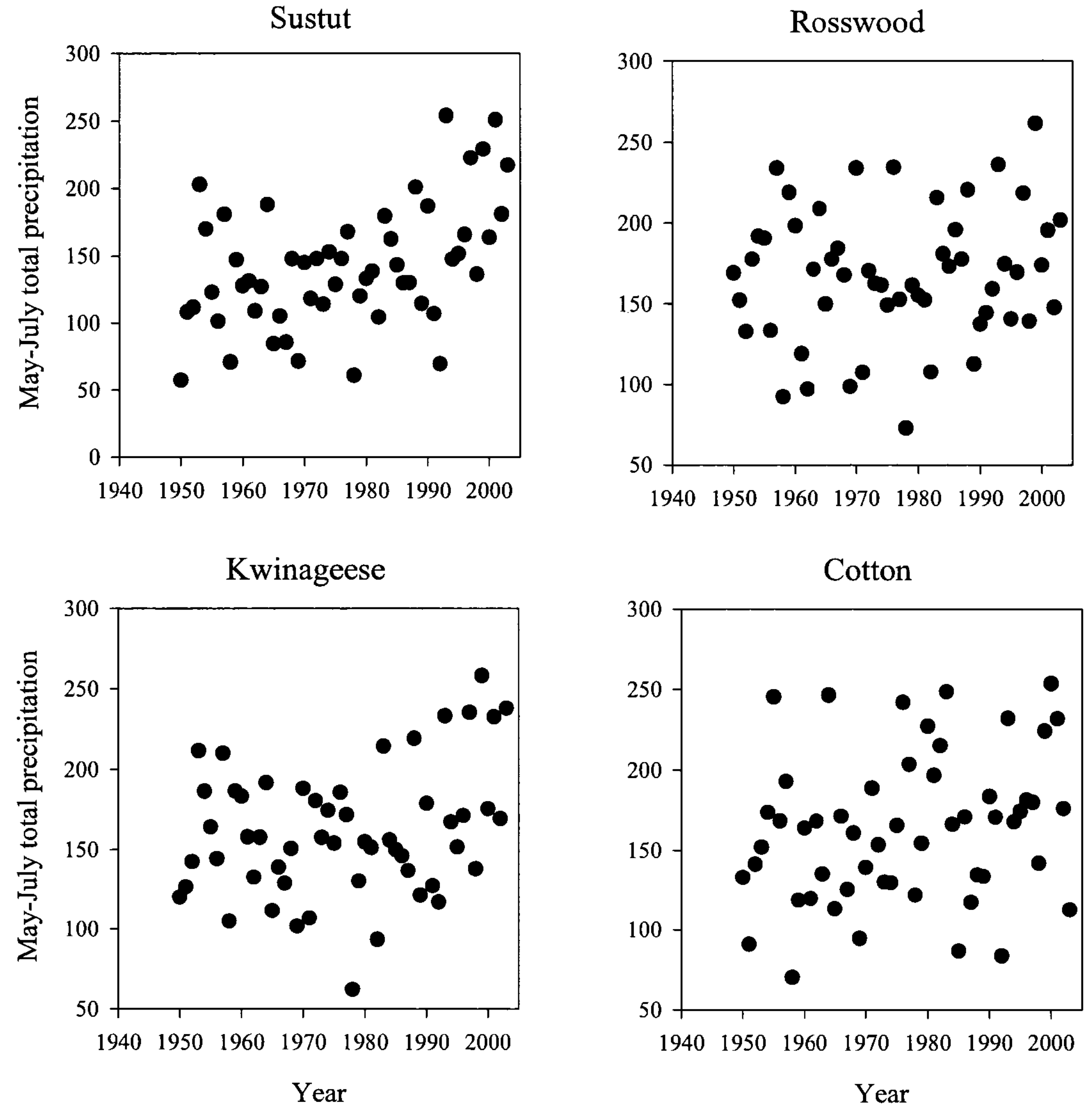


Figure 4.7b. Scatter plots of total spring precipitation for the entire instrumental period. Note the shift towards an increase in precipitation during the mid-to-late 1970s.

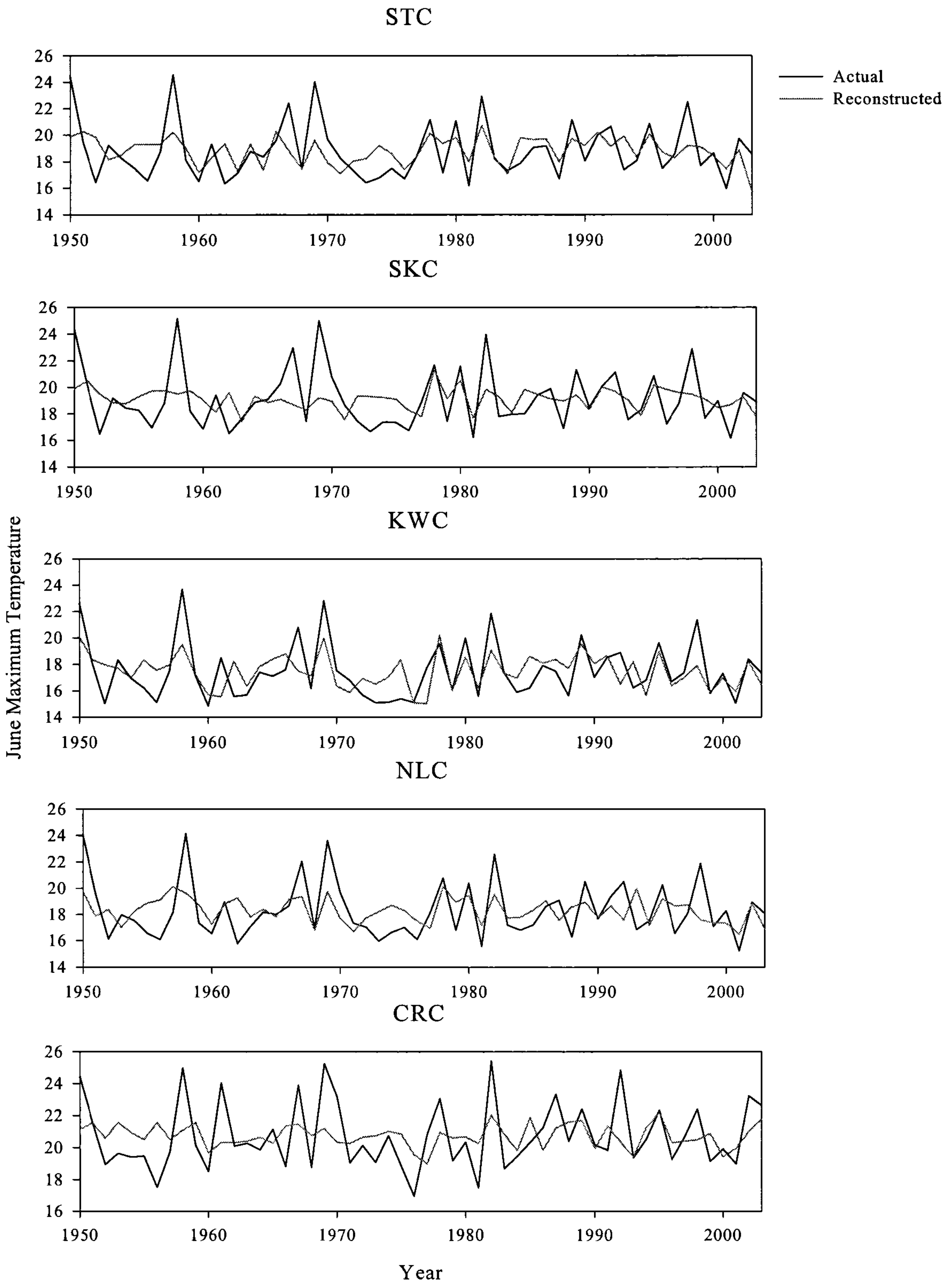

Sustut

Rosswood

Kwinageese

Cotton

Figure 4.7c. Scatter plots of May-July precipitation for the entire instrumental period. Note the shift towards an increase in precipitation during the mid-to-late 1970s.


STC

SKC

KWC

NLC

CRC

Figure 4.8a. Actual instrumental data of average June maximum temperature compared to the estimate values (or reconstructed values) as a function of time. Site designations are located on the top of each graph (see Table 1 for site names).

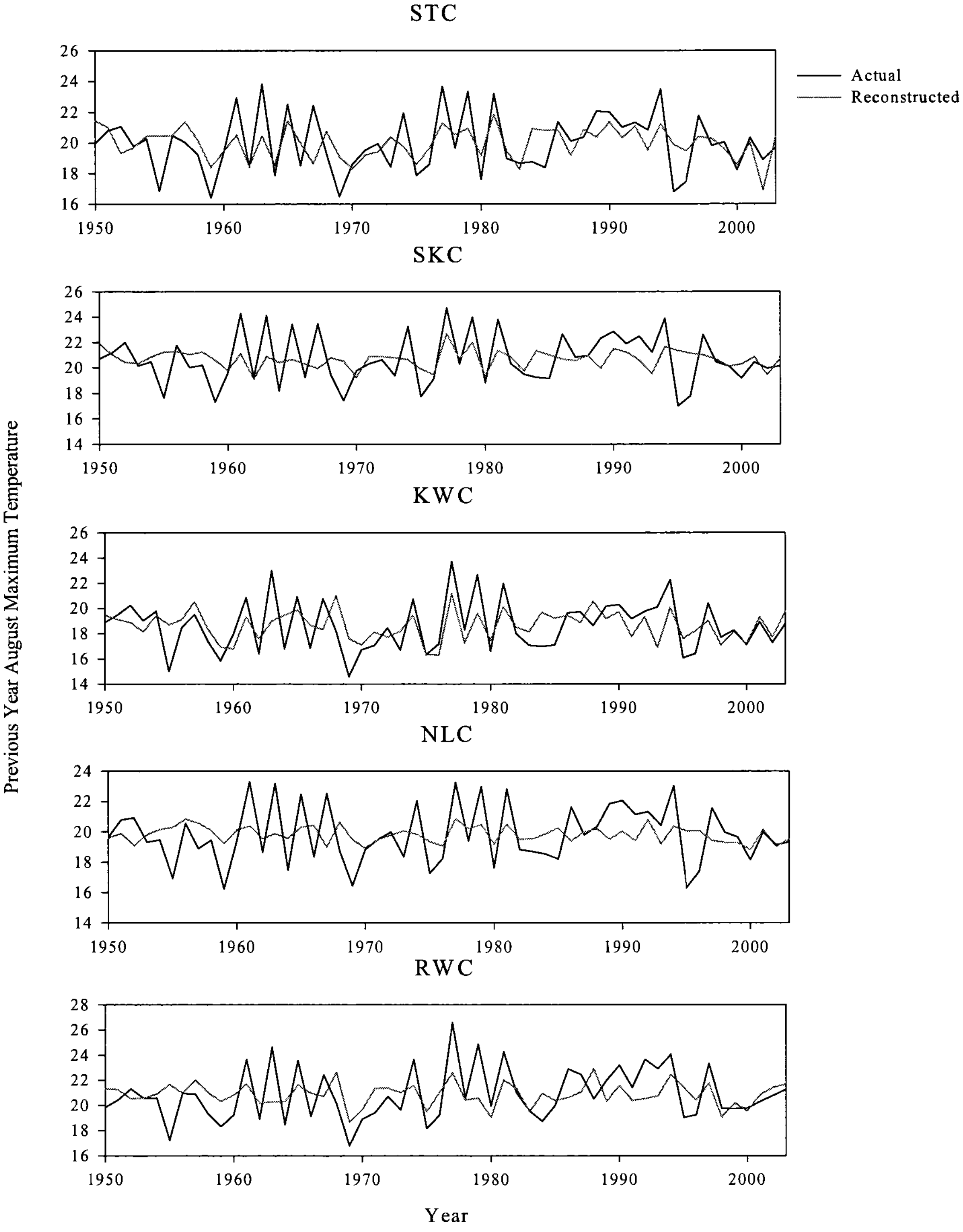


Figure 4.8b. Actual instrumental data of previous year average August maximum temperature compared to the estimate values (or reconstructed values) as a function of time. Site designations are located on the top of each graph (see Table 1 for site names).

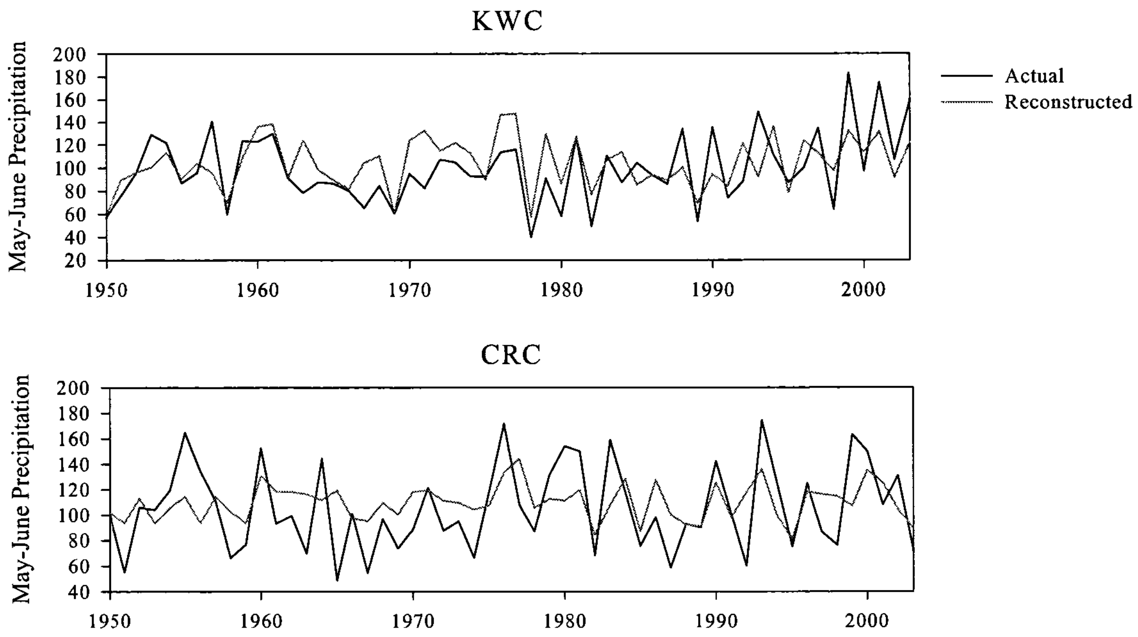


Figure 4.8c. Actual instrumental data of May-June total precipitation compared to the estimate values (or reconstructed values) as a function of time. Site designations are located on the top of each graph (see Table 1 for site names).

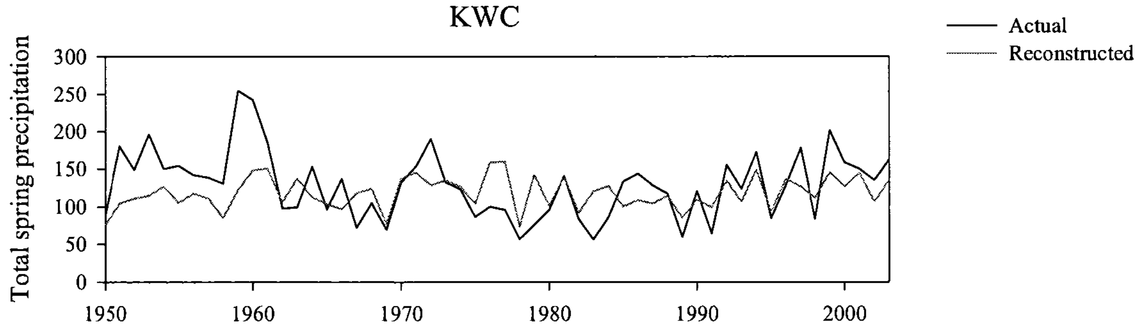


Figure 4.8d. Actual instrumental data of total spring precipitation compared to the estimate values (or reconstructed values) as a function of time. Site designations are located on the top of each graph (see Table 1 for site names).

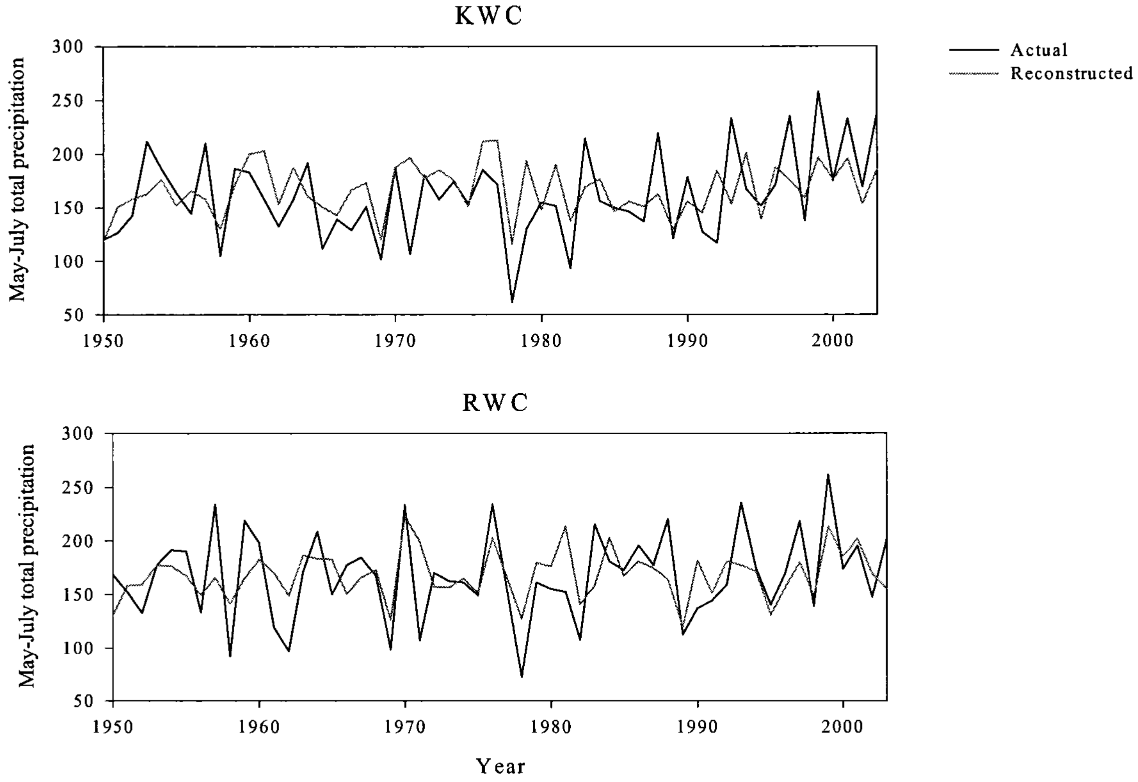


Figure 4.8e. Actual instrumental data of May-July total precipitation compared to the estimate values (or reconstructed values) as a function of time. Site designations are located on the top of each graph (see Table 1 for site names).

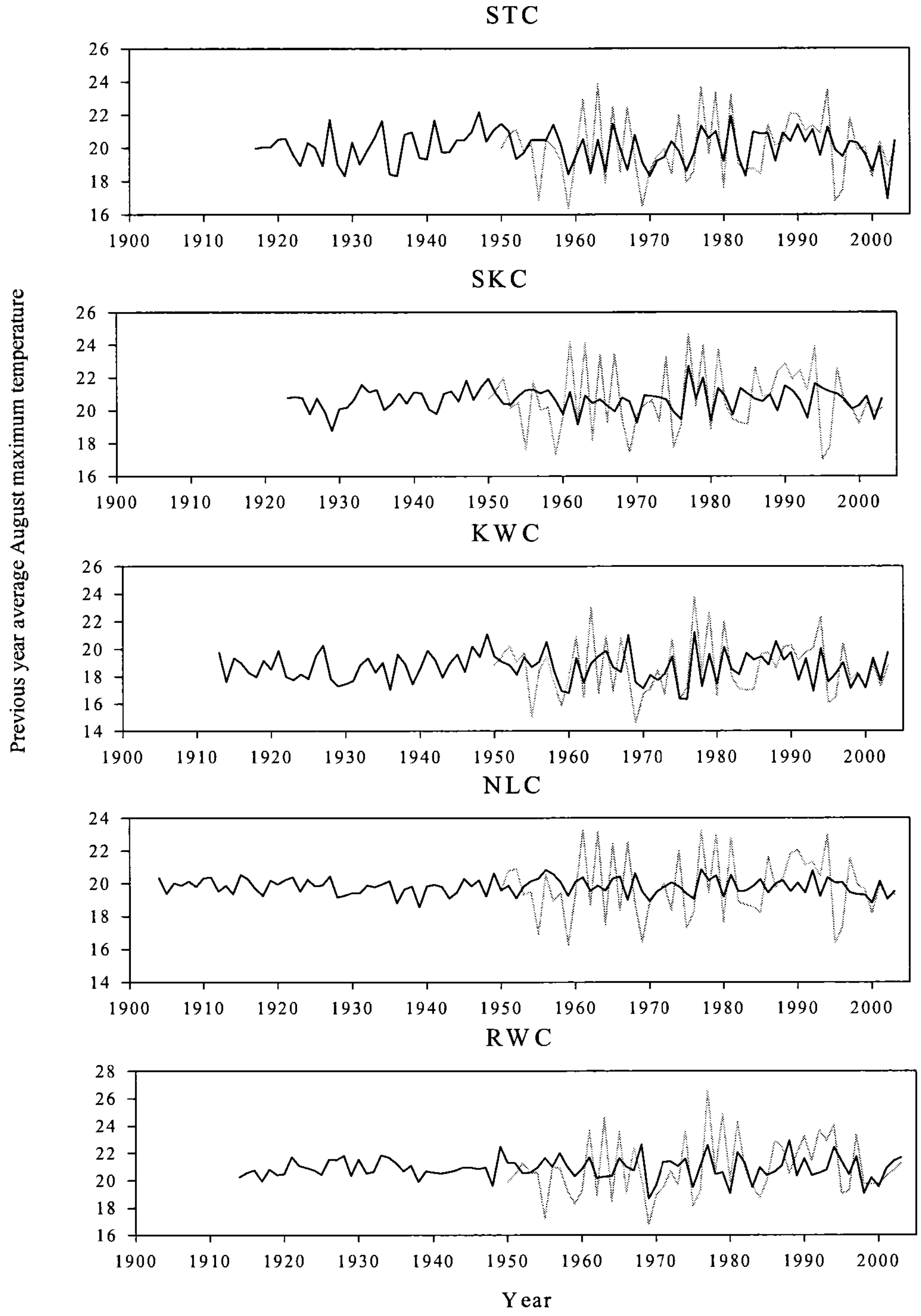


Figure 4.9a. The observed (grey) and reconstructed (black) average previous year August maximum temperature for northwest British Columbia.

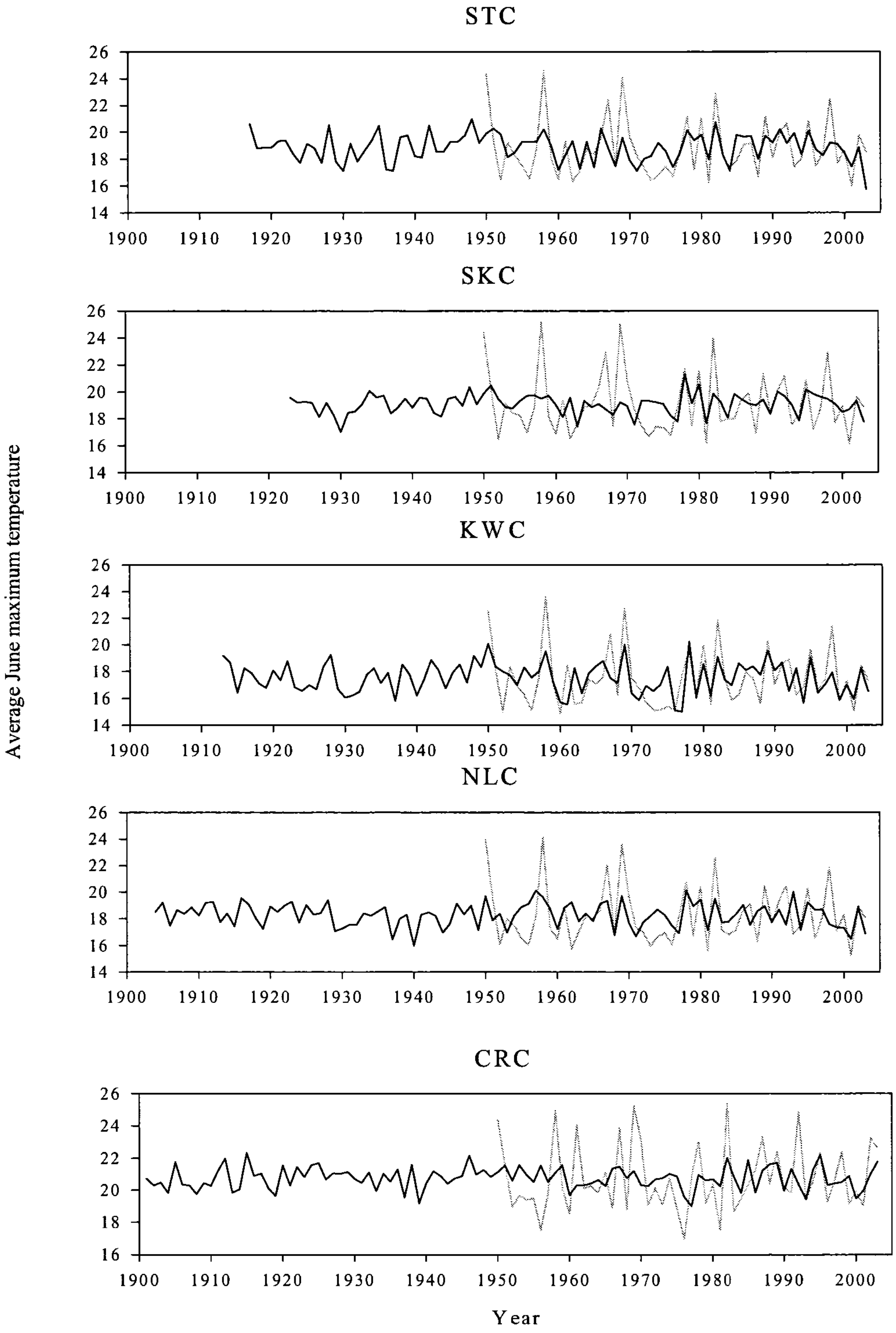


Figure 4.9b. The observed (grey) and reconstructed (black) average June maximum temperature for the northwest and central interior of British Columbia.

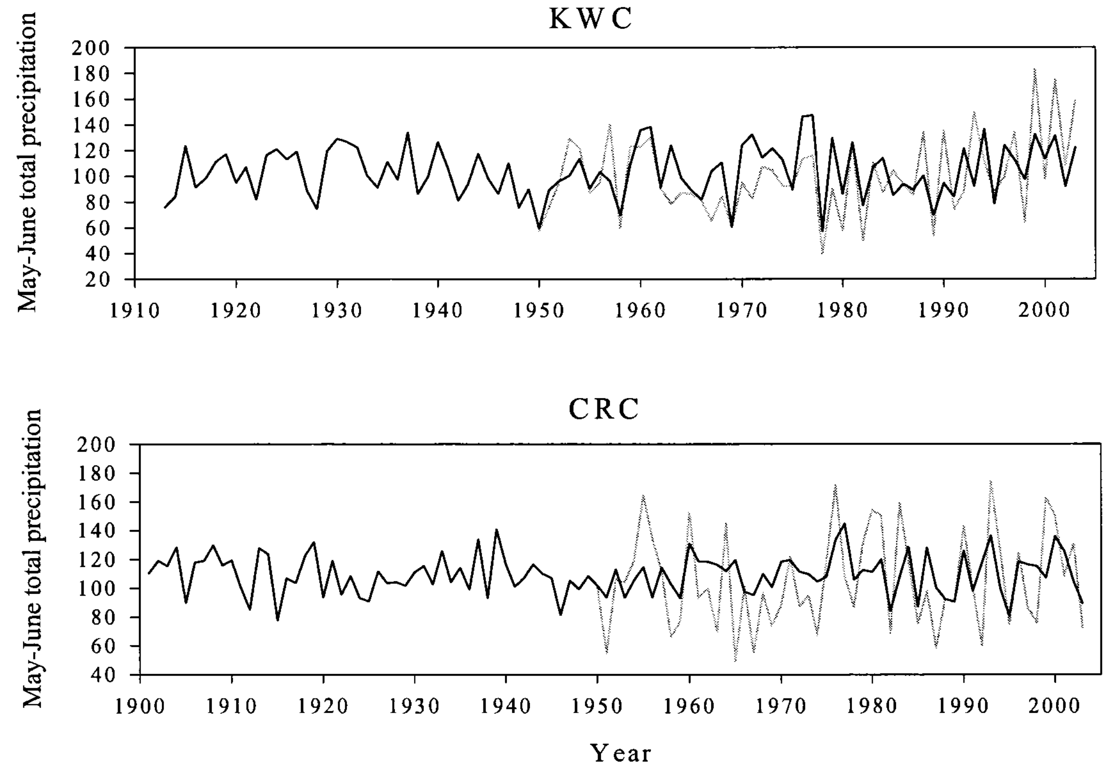


Figure 4.9c. The observed (grey) and reconstructed (black) May-June total precipitation for the northwest and central interior of British Columbia.

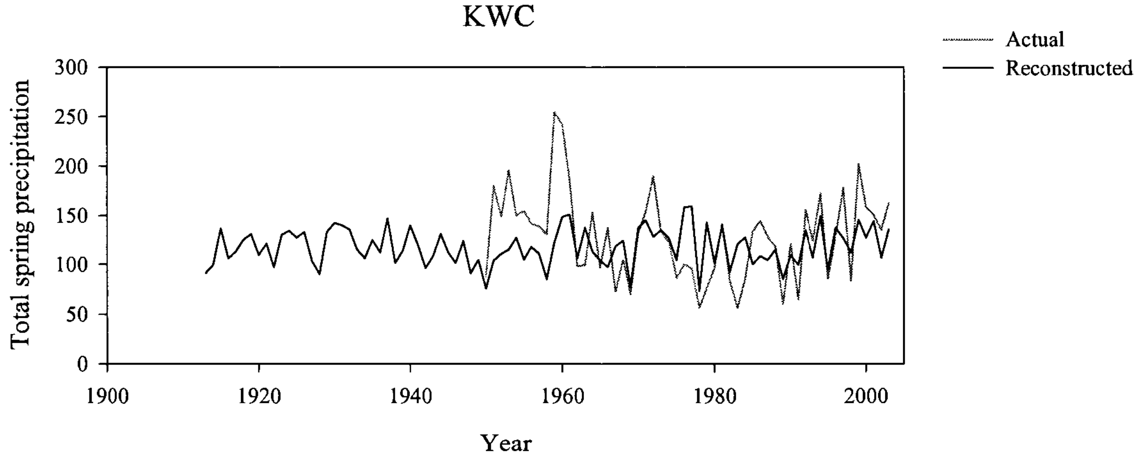


Figure 4.9d. The observed (grey) and reconstructed (black) total spring precipitation for the northwest and central interior of British Columbia.

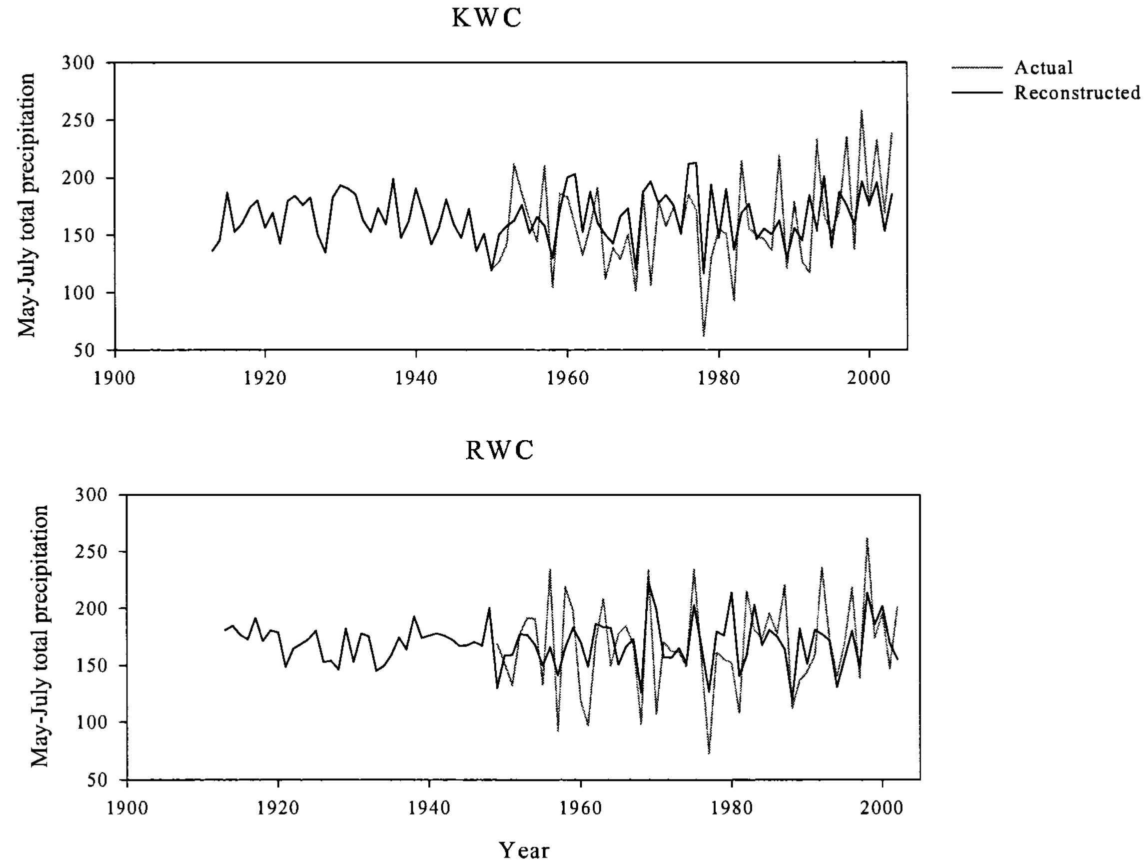


Figure 4.9e. The observed (grey) and reconstructed (black) May-July total precipitation for the northwest and central interior of British Columbia.

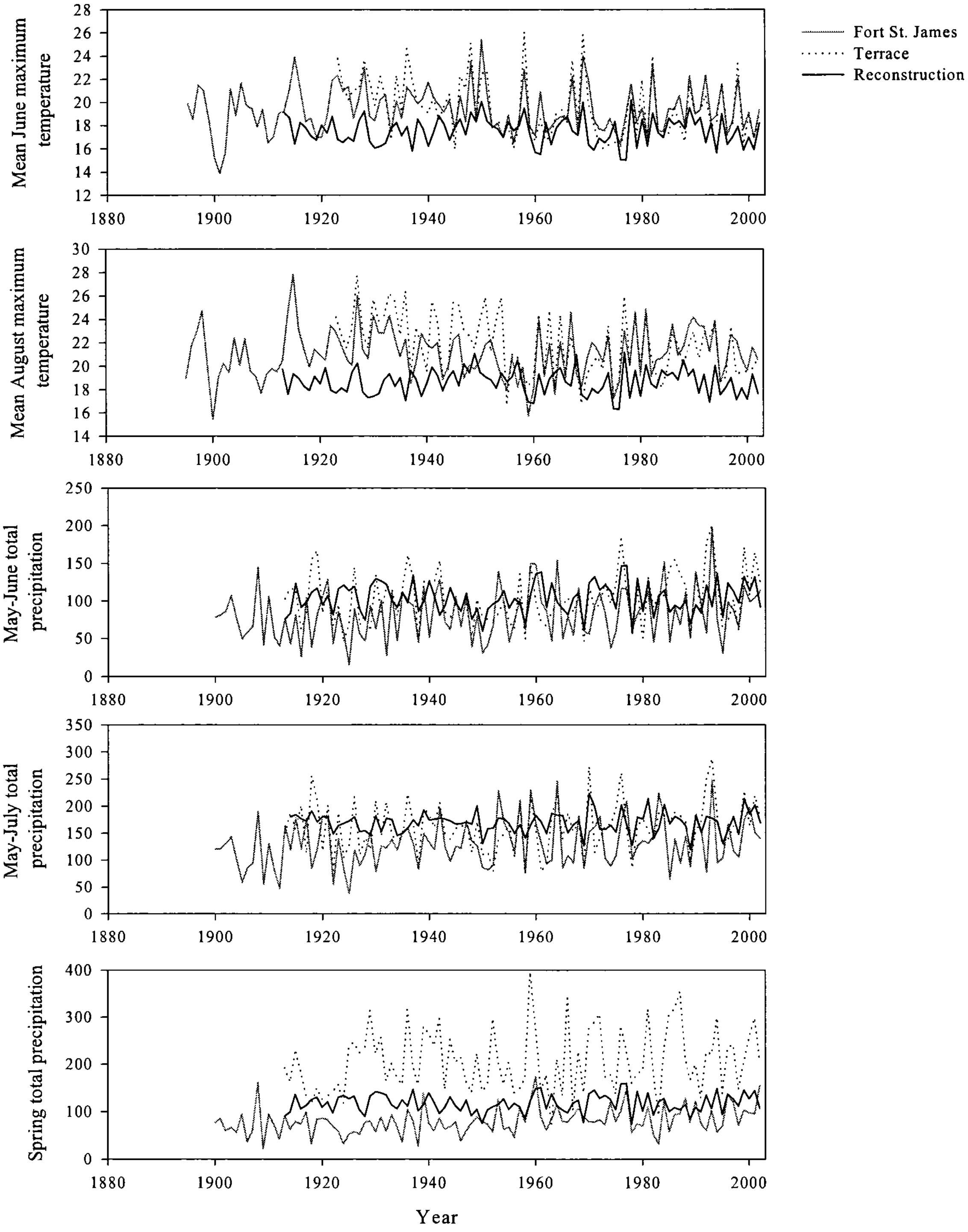


Figure 4.10. A comparison of the temperature and precipitation reconstructions with weather records from Fort St. James and Terrace stations over the entire time span of each. The May-July total precipitation reconstruction was provided by Rosswood (RWC), the rest from the Kwinageese (KWC) site.

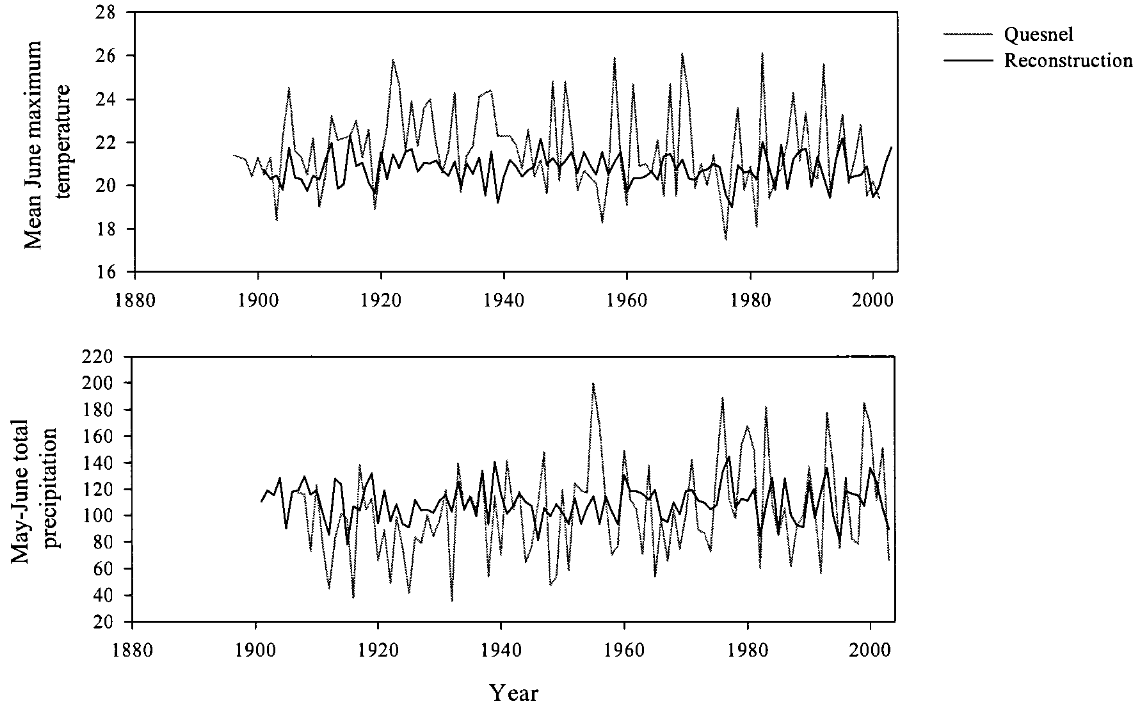


Figure 4.11. A comparison of the temperature and precipitation reconstructions for the central interior site with weather records from Quesnel weather station over the entire time span of each.

CHAPTER 5

RELATIONSHIP BETWEEN CLIMATE AND OUTBREAKS: A PERSPECTIVE ON THE REGIONAL OUTBREAK PATTERNS OF DOTHISTROMA NEEDLE BLIGHT IN NORTHWEST BRITISH COLUMBIA, CANADA

5.1 Abstract

Multicentury tree-ring reconstructions of Dothistroma needle blight (*Dothistroma septosporum* (Dorog.) Morlet) outbreaks were compared with the longest available climate record to examine the relationship between climate and regional outbreak patterns. Precipitation and temperature records from the weather station at Fort St. James, British Columbia were used to represent regional climate conditions in our study area. We compared outbreak reconstructions with mean monthly temperature and total precipitation during the individual spring (March, April, May) and summer (June, July, August) months. The cumulative effects of both total spring and summer precipitation were also examined. Few statistically significant relationships were found between the selected temperature and precipitation variables and the regional outbreak chronology. However, a trend towards increased August minimum temperatures appears to be the most important climate factor contributing to the spread of the disease. Graphical comparisons of total spring precipitation reveal that periods of above average precipitation coincided with periods of outbreak increase during the mid-1960s, late 1970s, and the late 1980s. Decreases in both precipitation and August minimum temperature also correspond to decreases in outbreak extent. It is also apparent that consecutive years of high spring and summer precipitation during the early-1950s and 1960s could have caused the sudden increase in outbreak extent and severity observed

during the 1960s. Even more pronounced was the recent increase 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 Dothistroma needle blight behavior. The extent and severity of the current disease epidemic raises the possibility that the key factors which have driven outbreaks in the past have changed. If this is due to climate change, as has been suggested, then there are serious implications for the future extent of Dothistroma needle blight and the health of lodgepole pine in British Columbia.

5.2 Introduction[1]

Outbreaks of Dothistroma needle blight (*Dothistroma septosporum* (Dorog.) Morelet) in northwest British Columbia have been detected as early as 1831 (Chapter 3). Historically, Dothistroma needle blight has had only minor impacts in native forest trees in western North America (Harrington and Wingfield 1998). During the past decade, however, prevalence of the disease has increased in the northwestern forests of British Columbia (Bradshaw 2004, Woods *et al.* 2005). Since the mid-1990s, a trend towards increased summer precipitation and more specifically, warm rain events has been recorded in the area (Woods *et al.* 2005). This trend towards increased summer precipitation has been suggested to be a part of a directional global change, and it has undoubtedly played a role in the extent and severity of the current disease epidemic in northwest British Columbia (Woods *et al.* 2005).

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[1] A version of this document will be submitted for publication under multiple authors. All data used in this study were collected by C. Welsh and a number of field and lab assistants. In this thesis I use 'we' and 'our' to reflect the involvement of others in various aspects of this work.

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). Climate change has the potential to modify host physiology and resistance and to alter stages and rates of development of the pathogen. Tree species most vulnerable to damage may be those where the associated pathogens are at low disease levels because of unfavourable climate conditions (Coakley *et al.* 1999, Woods *et al.* 2005). Very few studies have quantified the potential impact of climate change on forest pathogens and the diseases they cause. This is despite the fact that forest diseases are heavily dependent on prevailing weather events and no disease can develop in the absence of conducive weather conditions (Chakraborty *et al.* 1998). Foliar disease fungi may be some of the most responsive pathogens to climate change (Woods *et al.* 2005). Therefore, it is imperative that we quantify the effects of climate variability on the occurrence of Dothistroma needle blight to allow better predictions of future impacts of climate change on forest health.

Dothistroma needle blight is an economically important forest disease worldwide (Gibson 1972, Bradshaw *et al.* 2004). The disease first gained prominence as a pest of *Pinus radiata* in the Southern Hemisphere, devastating extensive plantations in Brazil, Kenya, Zimbabwe, New Zealand, and South Africa (Gibson 1972, Bradshaw *et al.* 1997). Currently, the disease has been reported to affect over 60 *Pinus* species in 45 countries (Ivory 1994). The magnitude of the disease outbreaks stimulated research aimed at understanding its biology and impact (Gibson 1972, Gadgil 1977, Gilmour 1981, Bradshaw 2004, Woods *et al.* 2005). In northwest British Columbia, damage is recorded as most severe in the Interior Cedar-Hemlock (ICH) zone (Woods 2003), an area transitional between the coastal rainforests to the west and the more continental sub-boreal forests to the east (Banner *et al.* 1993). Recent low-level aerial surveys conducted over 40,000 ha of lodgepole pine-dominated managed stands showed 92% to be suffering varying degrees of damage (Woods 2003). Scattered mortality attributable to the foliar pathogen has also been recorded among isolated mature pine trees in mixed-species stands in the area (Woods *et al.* 2005). The foliar disease is now so prevalent and chronic that entire plantations are failing, and the severity of the disease is such that mature pine trees are also succumbing (Woods 2003, Woods *et. al.* 2005).

The effect of defoliation on growth is strongly influenced by the species, resistance, and the physiological condition of the tree (Ivory and Paterson 1969, Gibson 1972). The most immediate impact of defoliation by Dothistroma needle blight is the reduction in growth (Ades *et al.* 1992). Wood yield loss is approximately proportional to disease severity (defoliation level), particularly when young photosynthetically active needle are affected (Gibson 1972). Tree-ring studies of live trees in northwest British Columbia indicate reductions in early and late wood production in the past, suggesting that these trees were capable of surviving multiple outbreaks (Chapter 3). This no longer seems to be the case as high levels of mortality are now occurring. The mortality found in mature lodgepole pine stands is globally unprecedented and illustrates the unpredictable nature of a changing climate on forest diseases (Woods *et al.* 2005).

The causal agent of Dothistroma needle blight belongs to a group of fungi that cause needle blights. The fungus produces both sexual spores (ascospores) and asexual spores (conidiospores), the conidial stage being more common (Gibson 1972). Both spore forms are found in British Columbia, which has lead to speculation of its indigenous origins in the area (Funk and Parker 1966). The first splash-dispersed conidiospores are released in the spring (Peterson 1973), and under conditions of prolonged leaf wetness and temperatures above 5 °C can release spores for up to seven months (Karadzic 1989). 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). The incidence of Dothistroma needle blight infection 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).

Although only limited research has been undertaken to examine the effects of climate on Dothistroma needle blight outbreaks in northwest British Columbia, Woods *et al.* (2005) have emphasized the importance of climate change in the form of increased summer precipitation on the current epidemic. The purpose of this research was to document the relationship between historical Dothistroma needle blight 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 Dothistroma needle blight outbreaks were compared with the longest available climate record to examine the relationship between climate and the onset of the outbreaks. It was anticipated that these findings would provide an opportunity to better understand the likely responses of Dothistroma needle blight to climate change in northwest British Columbia.

5.3 Methods

5.3.1 Historical reconstructions of Dothistroma needle blight outbreaks

In this study, a regional outbreak chronology of historical Dothistroma needle blight outbreaks developed for northwest British Columbia from host lodgepole pine trees (Chapter 3) was compared to local climate records. The regional time series of outbreaks was based on criteria in which greater than 40% of host trees in each site had to show a specific reduction pattern identified by the program OUTBREAK (Holmes and Swetnam 1996) to be included as an outbreak in a given year. The regional outbreak chronology indicates reoccurring outbreak events since 1831. Outbreak chronologies developed for sites outside the northwest study area were also used in the analysis: one in the central interior near Cinema, British Columbia, and one southwest of the general study area, around Rosswood near Terrace, British Columbia (Chapter 3). The Cinema outbreak chronology was computed from the combined outbreak history of two stands where an outbreak had been previously identified in FIDS records. The Rosswood outbreak chronology represents the outbreak history of one site. These distant outbreak reconstructions were used to determine whether the same climate variables were related to outbreaks across different areas.

5.3.2 Climate records

Weather records for northwest British Columbia area were limited. Although a number of weather stations were established in the area, few records extended the necessary length for any meaningful analysis. In Chapter 4, it was determined that the climate data from the Fort St. James weather station were representative of regional climate variability in the study area. Woods *et al.* (2005) also found the Fort St. James weather records climatically similar to areas near Smithers, which represent the more easterly portions of our study area. Temperature records at the Fort St. James weather station extend from 1895 to 2003 but because of missing data, precipitation records were shorter, extending from 1900-2003.

The closest weather stations with records extending the length of the outbreak reconstructions were chosen for comparisons at Cinema and Rosswood (i.e., Quesnel and Terrace weather stations, respectively). Missing temperature and precipitation data for the Terrace weather station were estimated by regression from the neighbouring Prince Rupert climate records. The mean monthly temperature record for Terrace extended from 1914-2003, and total precipitation between 1913-2003.

5.3.3 Analysis of climate and outbreak history

Woods *et al.* (2005) found a strong spatial correlation between increased mean summer precipitation and the area affected by the current epidemic in northwest British Columbia. Spikes in precipitation levels were also shown to correspond to the 1960s and 1980s documented outbreaks in the area. Other studies have indicated the importance of moisture and warm temperatures in disease development (Peterson 1967, Gibson 1972, Parker 1972, Gadgil 1977, Bradshaw 2004). Gadgil (1974) showed that the highest infection percentages were recorded on needles during continuous high humidity and warm temperature regimes (i.e., 20/12°C). Thus, rainfall, humidity, and temperature are the most important climatic factors in relation to disease occurrence. Since relative humidity data were not readily available for our study area, we compared the outbreak reconstructions with mean monthly temperature and total precipitation during the individual spring (March, April, May) and summer (June, July, August) months. The cumulative effects of both total spring and summer precipitation were also examined.

The coincidence of Dothistroma needle blight outbreaks and favourable climatic events was examined using a stepwise regression analysis with backwards elimination. The regional time series of disease outbreaks were compared with the temperature and precipitation variables to determine whether temporal changes in the outbreak patterns were related to favourable climate variations. Any significant relationships were then used to identify climate variables that would correlate with the Cinema and Terrace reconstructions. A correlation analysis was used to further identify other possible climate variables that may be related to the occurrence of the disease in these areas.

5.4 Results

Few relationships were found between the selected temperature and precipitation variables and the regional outbreak chronology. Only March and cumulative spring precipitation contributed significantly to the prediction of the outbreaks among all the precipitation variables tested. However, the relationships were weak ($r^2 = 0.04$ and 0.05, respectively). Mean August temperatures also contributed significantly to the prediction of the regional outbreaks, but the relationship was weak ($r^2 = 0.09$). We further explored the temperature relationship with August minimum and maximum temperature values using a linear regression and identified a positive relationship between minimum August temperatures and outbreak occurrence ($r^2 = 0.17$).

Graphical comparisons of total spring precipitation reveal that periods of above average precipitation coincided with periods of disease increase during the mid-1960s, late 1970s, and the late 1980s (Fig. 5.1). In addition, yearly spikes in spring precipitation levels during 1908, 1939, 1953, 1960, 1977, and 1988 are either followed by the appearance of an outbreak or a peak in outbreak levels. The trend towards increased spring precipitation during the mid-1990s directly corresponds to the timing of the current epidemic. Although not as pronounced, summer precipitation showed the same increasing trend associated with the current outbreak (Fig. 5.2). Prior to the late-1950s, both spring and summer precipitation levels typically remained below the long-term average. However, a period of increase in summer precipitation levels in the late-1950s, followed by a spike in spring precipitation in the early-1960s coincided with a sudden increase in outbreak extent in the 1960s. A period of precipitation increase during the 1950s was also apparent in comparison with total March precipitation and the outbreak chronology (Fig. 5.3).

Since the 1960s, there was an obvious increasing trend in August minimum temperature levels in our graphical comparisons (Fig. 5.4). It is apparent that the regional outbreak chronology was in phase with August minimum temperature cycles. More specifically, spikes in August minimum temperature in 1965, 1977, and 1990 corresponded exactly to each peak in outbreak levels in the regional chronology. In addition, prior to the 1960s, outbreak peaks were also associated with increases in August minimum temperature in the mid-1910, 1930s, and early-1940s. Similar to comparisons with spring precipitation, decreases in minimum temperature values were also accompanied by decreases in outbreak levels. It is also important to note that since the 1960s, increases in August minimum temperature coincided with increases in spring precipitation levels.

Graphical comparisons of total spring precipitation with the Cinema and Rosswood outbreak chronologies indicate that relationships were similar to comparisons of the regional outbreak chronology (Fig. 5.5 and 5.6). For instance, all outbreaks from both sites were accompanied by some increase in spring precipitation. In the Terrace records, spikes in spring precipitation observed since the 1960s were similar to those observed in the Fort St. James precipitation records. However, these same peaks in spring precipitation occurred without the presence of an outbreak. This was also observed in the Cinema comparisons where no outbreaks were present during an increase in precipitation in the late-1970s, which was not the case a decade earlier. The increasing trend in August minimum temperature was largely absent in both Cinema and Terrace weather records and the peaks did not coincide with any outbreak at these sites (Fig. 5.7 and 5.8). In addition, peaks in August minimum temperature in the Terrace weather record during the mid-1960s, late 1970s, and 1990s coincided with decreases in spring precipitation levels.

Correlation analyses indicated that outbreaks at the Cinema site were positively correlated with total April and July precipitation (Table 5.1). Graphical comparisons indicate that the 1950s, 1960s, and 1990s outbreaks coincided with increases in April precipitation and July precipitation (Fig. 5.9 and 5.10). The 1960s and 1990s outbreaks were the two largest outbreaks in the chronology and occurred during major periods of precipitation increase. No significant correlations were found between climate and the outbreak chronology at Terrace (Table 5.2).

5.5 Discussion

Comparisons of climate and the regional outbreak chronology show that strong, but temporally variable, Dothistroma needle blight events in northwest British Columbia were in phase with August minimum temperature cycles. We found that although outbreak events were not related in a statistically significant manner to increases in precipitation levels, outbreak events occurred during periods of increased spring precipitation. Decreases in spring precipitation and August minimum temperature levels were also accompanied by decreases in the individual outbreak periods. In contrast, peaks in spring precipitation at the Rosswood site corresponded to low August minimum temperature, which may explain the absence of outbreaks during most periods of precipitation increase (i.e., 1960s, 1970s, late-1980s) at that site. These results suggest that Dothistroma needle blight is limited by weak spring precipitation and low summer minimum temperature cycles.

Yearly differences in weather are known to result in considerable yearly variations in the amount of infection by Dothistroma needle blight (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 temperatures are above 5°C and moisture is present (Karadzic 1989). In eastern Nebraska, conidia of Dothistroma needle blight have been found on stromata (fruiting bodies) on needles of Austrian (*Pinus nigra* Arnold) and ponderosa pine (*P. 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 amount of defoliation increased to 75% of the tree's foliage in several plantations after 10 months of very wet weather. In northwest British Columbia, periods of increased spring precipitation (as early as March) were accompanied by increases in the extent and severity of outbreaks of Dothistroma needle blight in the regional chronology. Since precipitation has an important influence on the amount of disease, it seems likely that increases in spring rainfall could have played a role in the observed increases in the historical outbreaks. This relationship has been exemplified over the last ~40 years, where the frequency of outbreaks and peaks in spring precipitation have increased. Even more pronounced was the recent increase in spring precipitation associated with the current epidemic (Fig. 5.1).

Periods in which spring rainfall is sufficient to disseminate large numbers of conidiospores may not be accompanied by conditions that result in infection. Peterson (1973) found that dry weather during the summer months caused no infection even though high numbers of conidia were found on needle surfaces. In another study, only 4 hours of desiccation (24°C and 30% relative humidity) was sufficient to stop further germ tube development of germinated conidia (Peterson and Walla 1978). This suggests that a brief drying period, occurring after the dispersal of the conidiospores and after germination has commenced, could result in little or no infection. It is apparent, therefore, that factors other than spring precipitation also determine whether an outbreak can occur. Precipitation during the summer is often a good indicator of the amount of infection to be expected (Peterson 1973). Woods *et al.* (2005) found peaks in mean summer precipitation that occurred in the early 1960s and 1980s corresponded to the timing of the first published record of Dothistroma needle blight in British Columbia in 1963 and the 1984-1986 outbreak observed by the FIDS surveyors. Comparisons of summer precipitation with the regional outbreak chronology support these findings. During the late 1950s summer precipitation reached record highs. A large spike in spring precipitation followed this increase in summer precipitation, which was subsequently accompanied by an increase in Dothistroma needle blight activity. One can expect that this spike in summer precipitation may have resulted in conditions favourable for large amounts of infection (Peterson 1973, Marks *et al.* 1989). Years of wet spring weather following this increase may have provided conditions favourable for substantial increases in disease incidence (i.e., early spore release and the production of high inoculum loads). We suggest that these successive years of increased precipitation is the principle cause of the initial increase in the severity of Dothistroma needle blight in the study area.

Temperature is an important factor influencing the occurrence and development of disease. Favourable temperatures may shorten the period between infection and the production of new spores, and so influence the number of spore generations occurring during a season (Colhoun 1973). This effect on the supply of inoculum during the season may determine whether or not an epidemic can develop. In this study, the trend towards increased summer minimum temperatures appears to be the most important climate factor contributing to outbreak of the disease. Since the 1960s, the frequency of peaks in August minimum temperatures has increased (Fig. 5.3). In addition, peaks in August minimum temperature have increased ~ 2°C since that time. 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. Woods (*pers comm.*) has also found a strong positive correlation between defoliation severity due to Dothistroma needle blight and changes in August minimum temperature between the 1920s and the 1990s at 25 lodgepole pine provenance test sites across central British Columbia. He speculates 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. 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, infection could spread to adjacent areas. Temperature increases were not observed in the climate records at Terrace and Quesnel, and neither were increases in disease severity. However, the 1960s outbreak identified at Cinema did correspond to a slight increase in August minimum temperatures, a relationship that was absent during the most recent outbreak recorded at the site. It is possible that increased August minimum temperature, by influencing nighttime humidity levels, could have contributed to the development of the disease epidemic in the northwest.

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 August minimum temperatures were accompanied by increases in outbreak levels. 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 suggests that climate might be influencing synchronicity of Dothistroma needle blight. However, because even the smallest amount of rain is sufficient for spore dispersal (Peterson 1966) synchrony of a disease event must be more a factor of conditions conducive for successful infection. Therefore, we suggest that for Dothistroma needle blight outbreaks to be synchronized among the sampled sites, specific regionally stochastic weather events must be present during specific stages of disease development. It is possible that wet summers in which minimum temperatures extend the length of the infection period could represent a common trigger for outbreak events.

Clearly, precipitation levels from the mid-1990s to the present have increased markedly from earlier decades (Woods *et al.* 2005, see Fig. 5.1 and 5.2). In this study, an increase in disease severity and spread was most notable during the current outbreak when spring precipitation increased to previously unrecorded levels over the last ~100 years. Because moisture is important in disease development, the mid-1990s increase in precipitation is likely responsible for the current and unprecedented levels of the disease (Woods *et al.* 2005). In the same study, Woods *et al.* (2005) found that a sharp increase in summer precipitation in northwest British Columbia appears entirely independent of decadal oscillations (i.e., the Pacific Decadal Oscillation), suggesting that the current trend is a part of a directional global change.

Global circulation models suggest that increases in temperature are likely to be similar for daily maximum and minimum temperature, except where there are changes in rainfall and cloudiness (Chakraborty *et al.* 1998). Wetter, cloudier conditions will lead to a greater increase in minimum temperature, whereas drier, clearer conditions will produce a greater increase in maximum temperature (Chakraborty *et al.* 1998). This may explain why warmer minimum temperatures accompanied increases in precipitation in the northwest. Because the possible mechanisms of temperature and moisture control over Dothistroma needle blight have been identified, this current climate change may have more serious implications for the future extent of the current outbreak in northwest British Columbia. For instance, Hamann and Wang (2006) predict that the northern portion of the current Sub-boreal Spruce (SBS) zone in central British Columbia will experience a shift in climatic conditions to more closely resemble the Interior Cedar Hemlock (ICH) zone by 2025. Because the current epidemic is largely concentrated in the ICH, this is a concern for the SBS zone where pine is a dominant species. If this change in climate and the associated foliar disease spread further east to the SBS zone, lodgepole pine forests could be severely impacted (A. Woods *pers comm.*).

Dothistroma needle blight has a long history of coexistence with lodgepole pine in northwest British Columbia (Funk and Parker 1966, Woods *et al.* 2005). Regular outbreaks have recurred in the forests for at least the past 174 years (Chapter 3). Relationships between climate and reconstructed Dothistroma needle blight outbreaks over the past ~100 years indicate that outbreaks prior to the 1960s were restricted by periods of unfavourable climate conditions (i.e., decreases in precipitation levels). These findings support survey records suggesting that, until recently, outbreaks of Dothistroma needle blight have been uncommon and of little concern in these forests (Woods *et al.* 2005). Since the 1960s, spring and summer precipitation levels have increased to previously unrecorded levels along with increases in August minimum temperatures. It appears obvious that this climate change has created conditions favourable for Dothistroma needle blight to reach epidemic levels.

5.6 Literature cited

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Table 5.1. Correlation coefficients between the outbreak chronology from Cinema and the temperature and precipitation records from the Quesnel weather station.

	Temperature						Precipitation					
	Mar	Apr	May	Jun	Jul	Aug	Mar	Apr	May	Jun	Jul	Aug
Outbreak	-0.132	-0.148	-0.134	-0.109	0.032	0.006	0.048	0.302	0.041	0.036	0.284	-0.024
P-value	**0.255**	**0.203**	**0.248**	**0.351**	**0.786**	**0.956**	**0.677**	**0.008**	**0.722**	**0.753**	**0.012**	**0.836**

Table 5.2. Correlation coefficients between the outbreak chronology from Rosswood and the temperature and precipitation records from the Terrace weather station.

	Temperature						Precipitation					
	Mar	Apr	May	Jun	Jul	Aug	Mar	Apr	May	Jun	Jul	Aug
Outbreak	-0.081	0.062	0.006	-0.017	-0.084	0.033	0.200	0.015	0.001	0.097	0.034	0.016
P-value	**0.496**	**0.605**	**0.961**	**0.885**	**0.484**	**0.783**	**0.094**	**0.903**	**0.993**	**0.421**	**0.779**	**0.898**

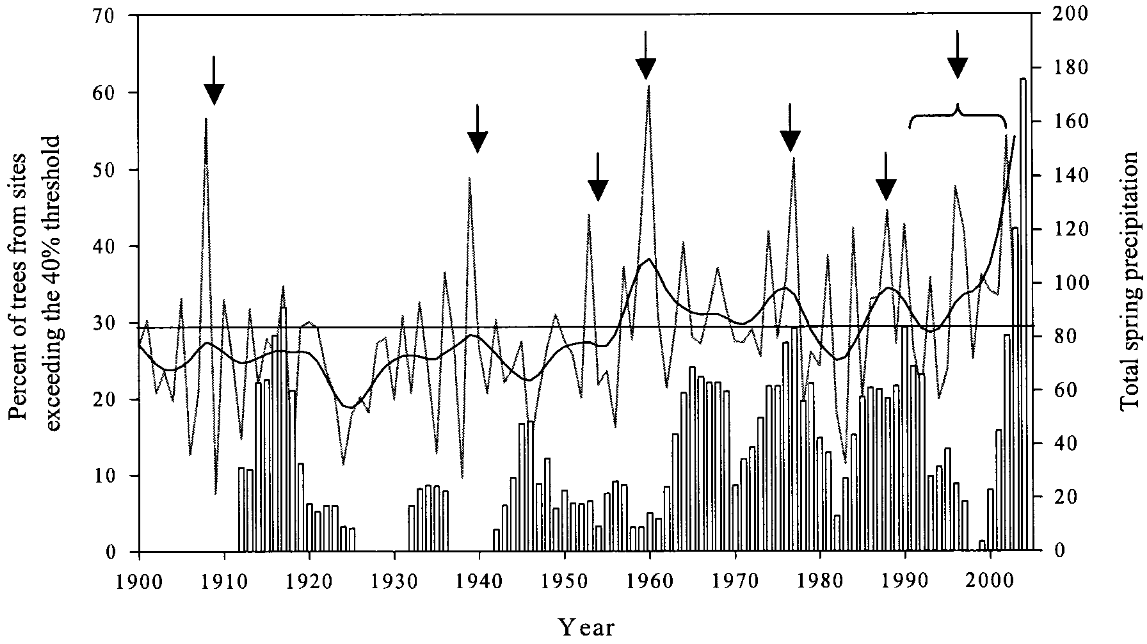

Figure 5.1. Comparison of spring (June-August) precipitation (AD 1900-2003) with Dothistroma needle blight outbreak periods (vertical bars). Arrows indicate spikes in precipitation that correspond to increases outbreak levels. Straight line indicates the mean of the climate variable. Gray line represents yearly weather record. A 10-year spline was added to help visualize trends (black line).

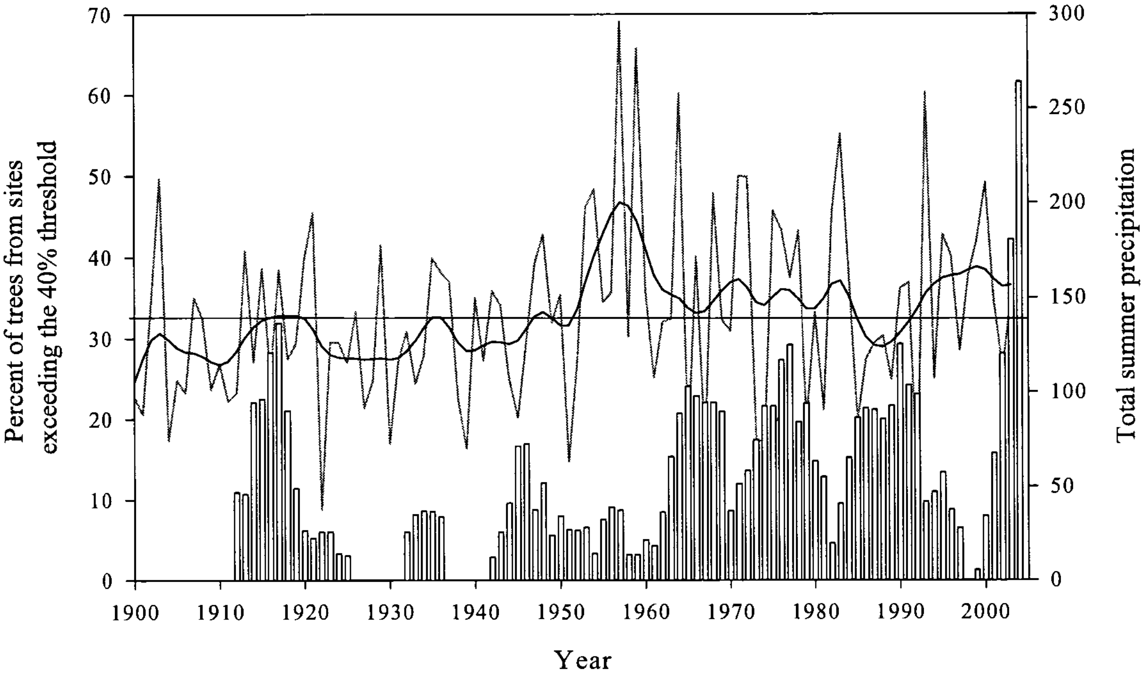

Figure 5.2. Comparison of summer (March-May) precipitation (AD 1900-2003) with Dothistroma needle blight outbreak periods (vertical bars). Straight line indicates the mean of the climate variable. Gray line represents yearly weather record. A 10-year spline was added to help visualize trends (black line).

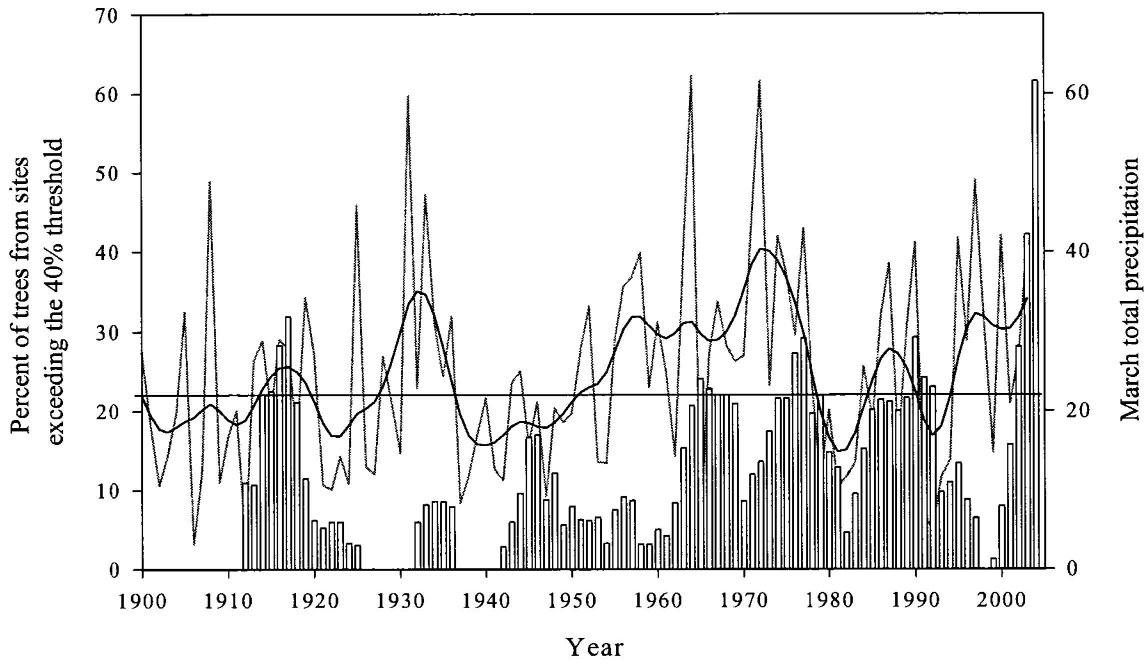

Figure 5.3. Comparison of March precipitation (AD 1900-2003) with Dothistroma needle blight outbreak periods (vertical bars). Straight line indicates the mean of the climate variable. Gray line represents yearly weather record. A 10-year spline was added to help visualize trends (black line).

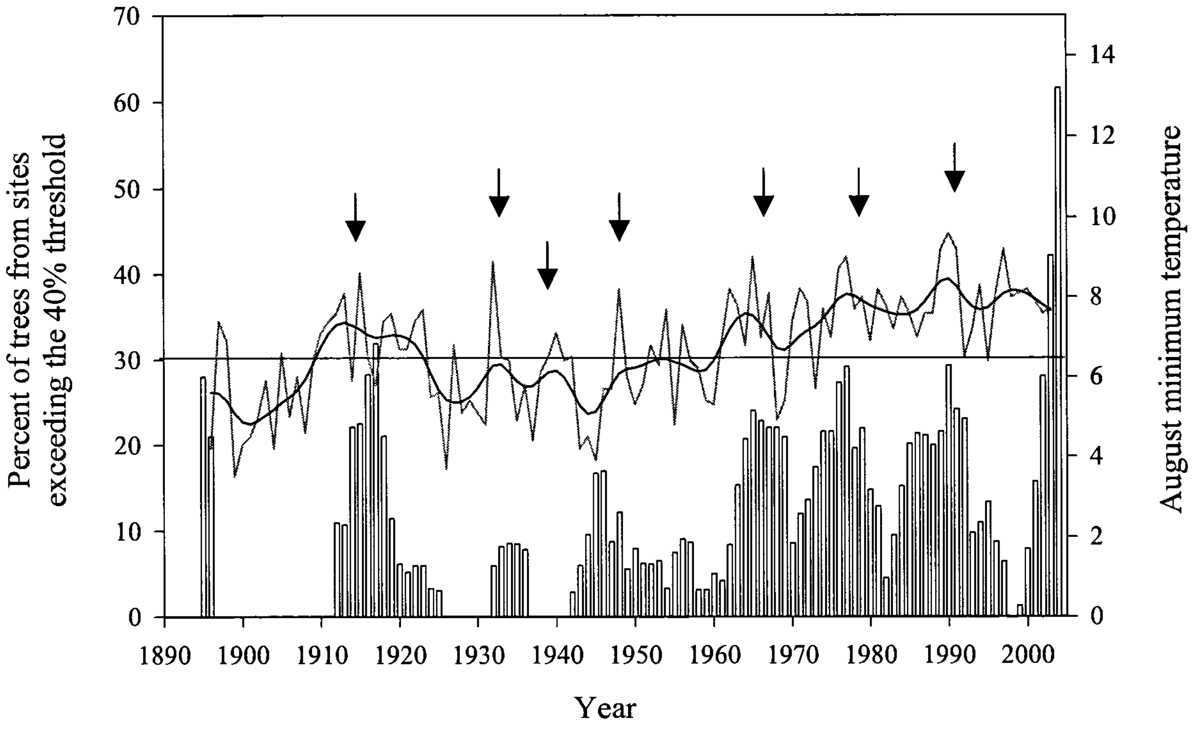

Figure 5.4. Comparison of August minimum temperature (AD 1895-2003) with Dothistroma needle blight outbreak periods (vertical bars). Arrows indicate spikes in minimum temperature that correspond to increases outbreak levels. Straight line indicates the mean of the climate variable. Gray line represents yearly weather record. A 10-year spline was added to help visualize trends (black line).

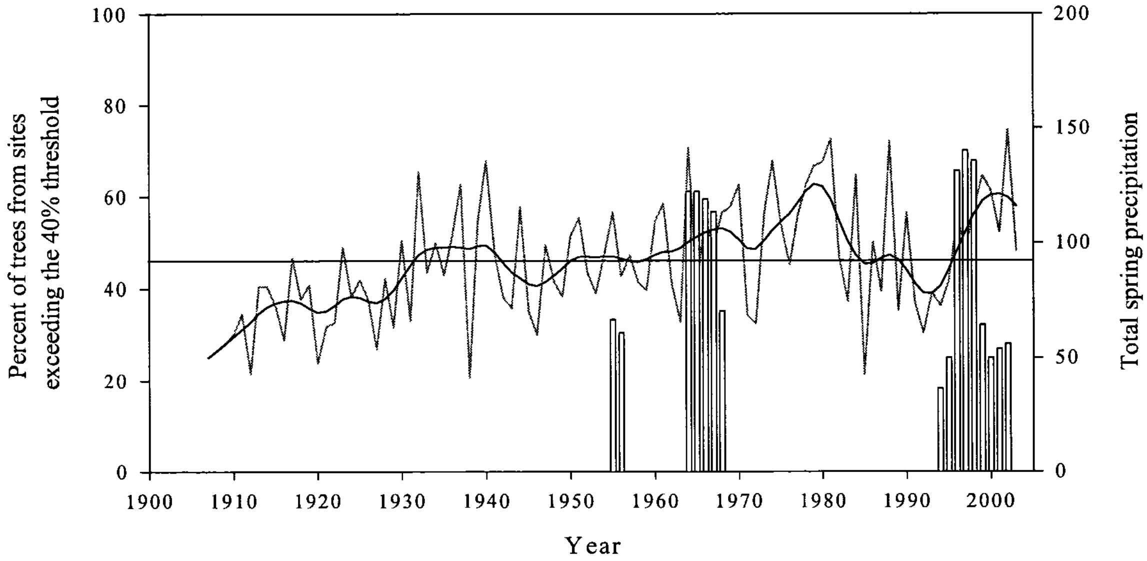

Figure 5.5. Comparison of spring (March-May) precipitation (AD 1907-2003) with Dothistroma needle blight outbreak periods (vertical bars) from Cinema. Straight line indicates the mean of the climate variable. Gray line represents yearly weather record. A 10-year spline was added to help visualize trends (black line).

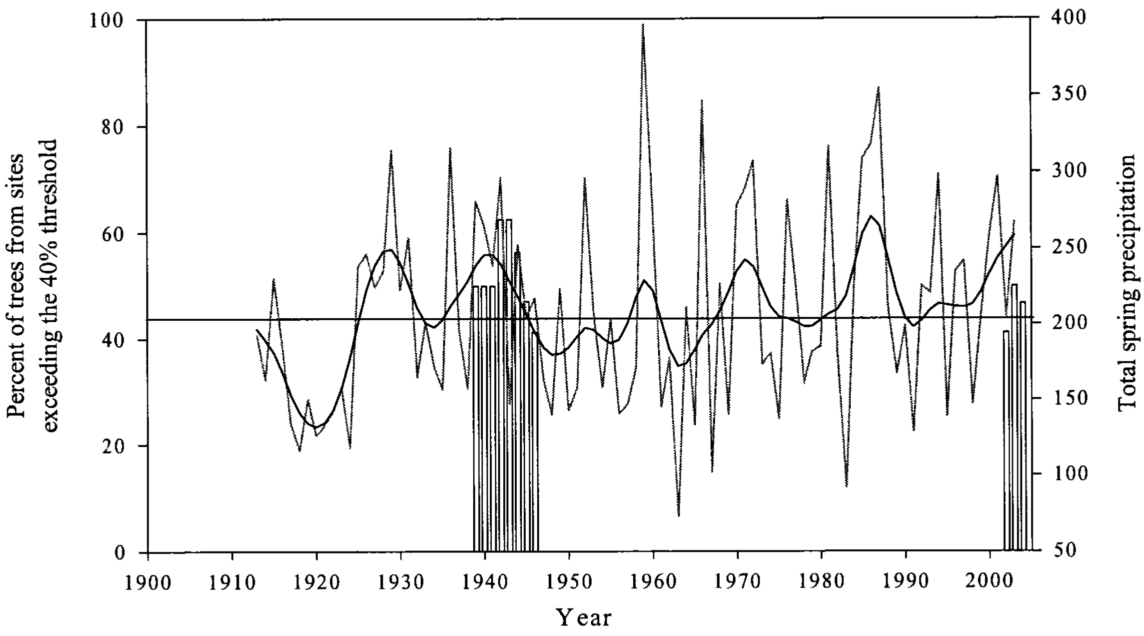

Figure 5.6. Comparison of spring (March-May) precipitation (AD 1913-2003) with Dothistroma needle blight outbreak periods (vertical bars) from Rosswood. Straight line indicates the mean of the climate variable. Gray line represents yearly weather record. A 10-year spline was added to help visualize trends (black line).

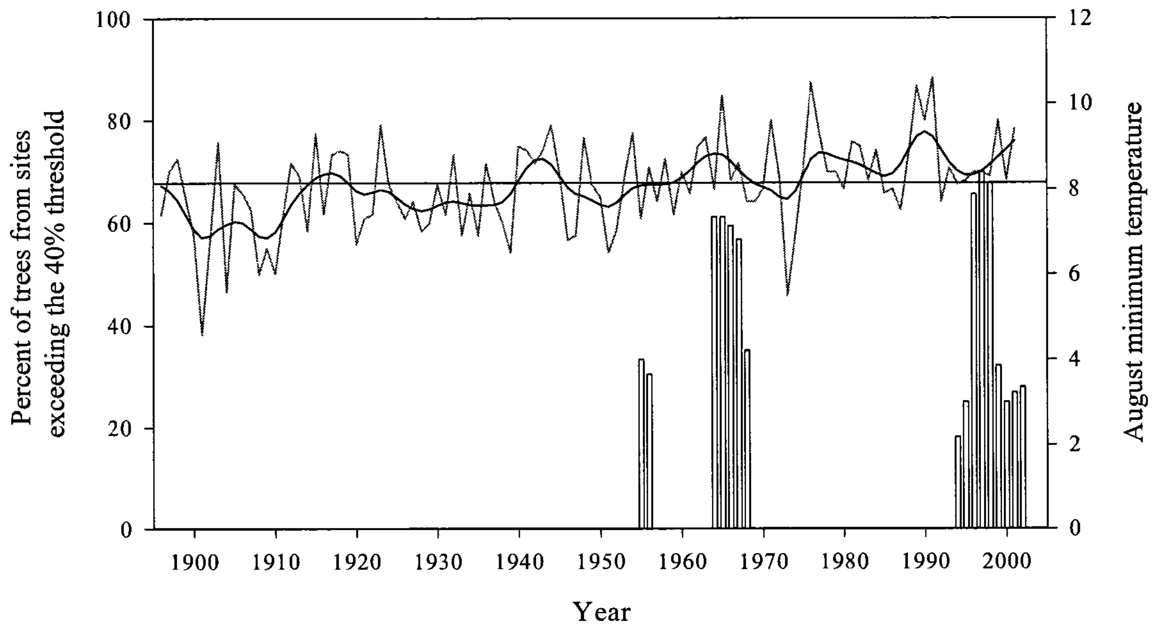

Figure 5.7. Comparison of August minimum temperature (AD 1896-2003) with Dothistroma needle blight outbreak periods (vertical bars) from Cinema. Straight line indicates the mean of the climate variable. Gray line represents yearly weather record. A 10-year spline was added to help visualize trends (black line).

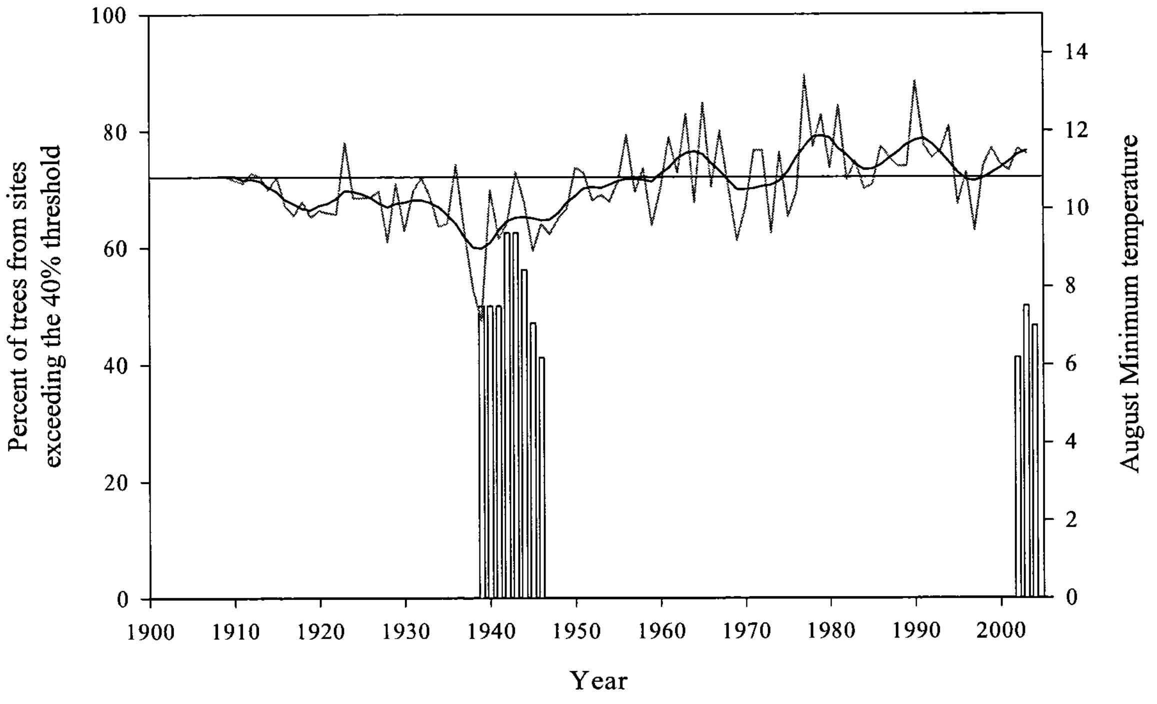

Figure 5.8. Comparison of August minimum temperature (AD 1914-2003) with Dothistroma needle blight outbreak periods (vertical bars) from Rosswood. Straight line indicates the mean of the climate variable. Gray line represents yearly weather record. A 10-year spline was added to help visualize trends (black line).

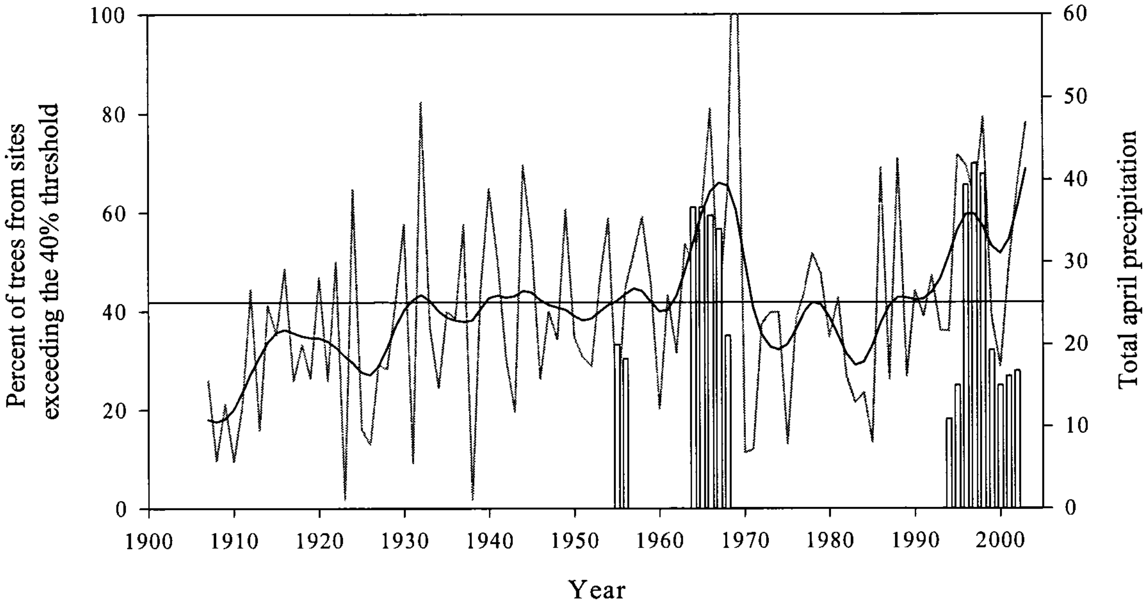

Figure 5.9. Comparison of April precipitation (AD 1907-2003) with Dothistroma needle blight outbreak periods (vertical bars) from Cinema. Straight line indicates the mean of the climate variable. Gray line represents yearly weather record. A 10-year spline was added to help visualize trends (black line).

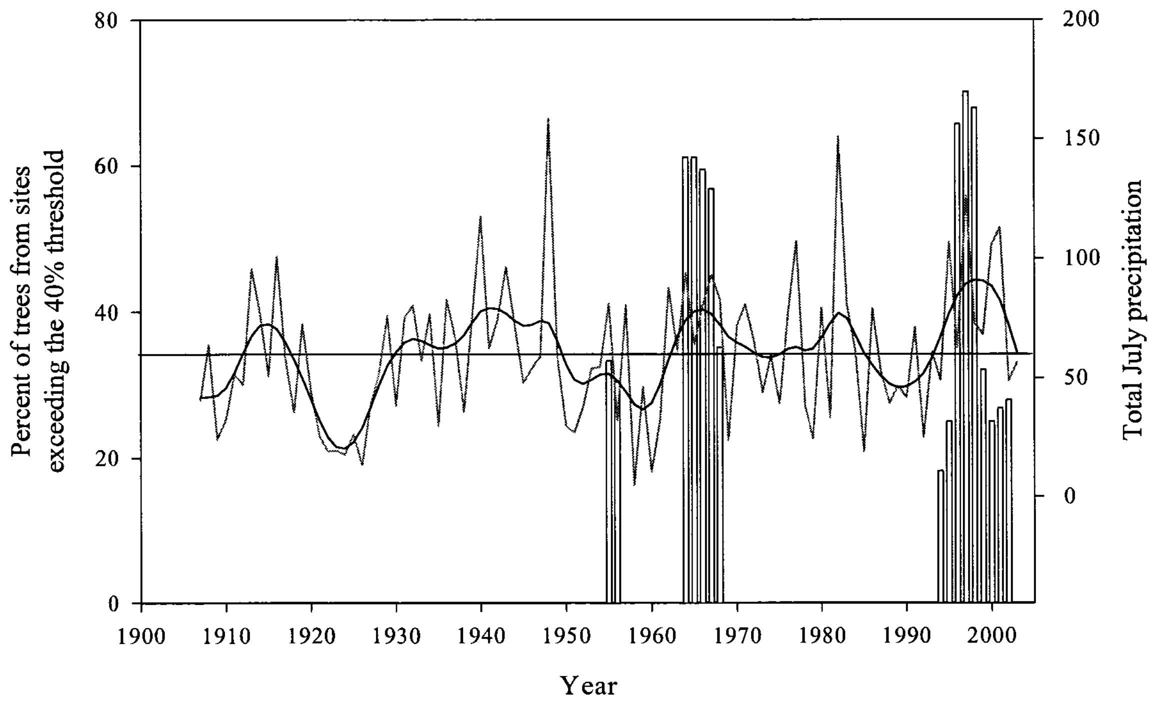

Figure 5.10. Comparison of July precipitation (AD 1907-2003) with Dothistroma needle blight outbreak periods (vertical bars) from Cinema. Straight line indicates the mean of the climate variable. Gray line represents yearly weather record. A 10-year spline was added to help visualize trends (black line).

CHAPTER 6

CONCLUSION

Dothistroma needle blight leaves a distinctive signature in the ring-width series of severely defoliated lodgepole pine trees. The consistent recurrence of the signature in association with historically documented outbreaks enabled us to identify 10 regional Dothistroma needle blight outbreak periods in northwest British Columbia, extending back to A.D. 1831. We used conservative criteria and eliminated other disturbance agents (i.e., insect defoliators and weaker foliar pathogens) and climate as possible causes of the ring-width pattern, therefore we are confident that the identified outbreaks were Dothistroma needle blight.

One of the most important uses of multicentury outbreak reconstructions is to evaluate the hypothesis that outbreaks have become more frequent, widespread, or severe (Speer *et al.* 2001). Our reconstructions demonstrate that Dothistroma needle blight 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 was the greater severity and synchronicity among the sites during the current outbreak. These findings support recent survey reports of an increase in disease spread and severity in the area since the mid-1990s (Woods *et al.* 2005). Differences in outbreak patterns were also observed between the ecological variants (ICHmc1, ICHmc2, SBSmc2), which may be a factor of varying climate and land-use histories.

To determine the relationship between climate and outbreak history of Dothistroma needle blight in northwest British Columbia it was important to use the longest and most spatially representative climate information available. Because the climate sensitivity of long-lived tree species offered an opportunity to develop histories of past climate, we examined the use of dendrochronology to reconstruct local climate unique to the study area. However, it was apparent that our climate reconstructions did not represent local climate variability, but rather a reconstruction of larger regional climatic processes. We found that climate data from long-term weather stations though geographically distant, were equally representative of climate variability in the study area, and we used this data to evaluate relationships between climate and Dothistroma needle blight outbreaks.

Our climate and outbreak comparisons indicated that increases in spring precipitation coincided with increases in the extent and severity of outbreaks. Since 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. It is obvious from our comparisons that an increase in disease severity and spread during the current outbreak coincided with recorded precipitation levels.

The trend towards increased minimum temperatures appears to be the most important climate factor contributing to outbreaks of the disease; peaks in the outbreaks directly coincide with peaks in August minimum temperature. It also appears that peaks in these warm periods correspond to increases in spring precipitation levels, and both show an increasing trend over the last ~40 years. This suggests that climate in northwest British Columbia 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 Dothistroma needle blight 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 Dothistroma needle blight over the last ~100 years in northwest British Columbia are in phase with spring precipitation and minimum temperature cycles. It is also evident that other climate factors, such as summer precipitation, are important in the development of disease. Woods *et al.* (2005) suggests that past outbreaks of Dothistroma needle blight 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. Currently, however, precipitation levels have increased to 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.

Although difficult to assess the impacts on disease development, industrial forest management over the past 30 years has increased host abundance in the study area (Woods *et al.* 2005). Management policies have resulted in the conversion of a landscape comprised primarily of western hemlock and true firs to one dominated by interior spruce and lodgepole pine (Woods 2003). This is most evident in the Interior Cedar-Hemlock (ICH) zone of northwest British Columbia, where the current epidemic is most severe. This increase in host abundance has undoubtedly played a role in the increase in the extent and severity of the disease. However, it is unlikely that the outbreaks of

Dothistroma needle blight could have developed without favourable climate conditions. We suggest that forest managers should diversify managed stands to mitigate further risk of disease outbreaks. In addition, planting of pine in areas of high disease incidence and areas known to receive weather conditions conducive to disease spread should be avoided.

We have also demonstrated that dendrochronological reconstructions of outbreaks of foliar fungi provide a rich opportunity for research. Long-term reconstructions provide an opportunity to present a perspective in the likely responses of pathogens to impending climate changes. Because of the unpredictable nature of climate change on forest ecosystems, it is imperative we quantify the effects of climate variability on disease occurrence to allow for better predictions of future impacts of climate change on forest health.

6.1 Literature cited

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