Is an Unprecedented Dothistroma Needle Blight Epidemic Related to Climate Change?

ALEX WOODS, K. DAVID COATES, AND ANDREAS HAMANN

Dothistroma needle blight, caused by the fungus Dothistroma septosporum, *is a major pest of pine plantations in the Southern Hemisphere, where both the host and the pathogen have been introduced. In northern temperate forests where the pest and host trees are native, damage levels have historically been low; however, Dothistroma is currently causing extensive defoliation and mortality in plantations of lodgepole pine in northwestern British Columbia, Canada. The severity of the disease is such that mature lodgepole pine trees in the area are succumbing, which is an unprecedented occurrence. This raises the question of whether climate change might enable the spread of the disease by surpassing an environmental threshold that has previously restricted the pathogen's development in northern temperate regions. Establishing a causal relationship between climate change and local biological trends is usually difficult, but we found a clear mechanistic relationship between an observed climate trend and the host–pathogen interaction. A local increase in summer precipitation, not climate warming, appears to be responsible. We examine whether the recently observed climate change trend exceeds natural fluctuations in the local climate.*

Keywords: climate change, Dothistroma, environmental thresholds, forest management, species diversity

The consensus among the scientific community is that anthropogenic climate change is occurring (Oreskes 2004, Hansen et al. 2005), and that its effect on key environmental factors may have profound implications for forest dynamics (Ayres and Lombardero 2000, Aber et al. 2001, Dale et al. 2001). It is projected that continental regions and higher latitudes will warm more quickly than coastal regions and the tropics (Harvell et al. 2002).

Studies of the effects of climate change on forests have tended to focus on how the growth rates of individual tree species will be affected by changes in carbon dioxide levels, in temperature, in frost-free period, or in the length of the growing season, or by interactions among these factors (Rehfeldt et al. 1999, Shaver et al. 2000, Aber et al. 2001, Nigh et al. 2004). Others have projected the effects of climate change on the frequency or intensity of wildfires in forested landscapes (Flannigan and Van Wagner 1991, Flannigan et al. 1998, Li et al. 2000). It is important to understand how climate affects disturbances and how forests respond to them (Dale et al. 2001). Nonetheless, links between changes in climate and changes in disturbance regimes caused by pests and pathogens have seldom been directly documented (but see Brasier 1996).

The effects of climate change on the coevolved relationships between hosts and their pests may have disastrous consequences (Logan et al. 2003). The tree species at greatest risk may be those in areas where the associated pathogen has been contained at low levels because of unfavorable historic climate conditions (Coakley et al. 1999). Foliar disease fungi may be more responsive to climate change than most other forest disease organisms, as their ability to sporulate and infect is strongly tied to changes in temperature and precipitation (Peterson 1973, Gadgil 1977, Hoff 1985).

One of the most extensively studied foliar diseases is the Dothistroma needle blight of pines, caused by the fungus *Dothistroma septosporum* (Dorog.) Morelet. It is a foliar disease in temperate forests throughout the world (Harrington and Wingfield 1998, Bradshaw 2004). 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, where both the host and the pest were exotic (Gibson 1972, Zobel et al. 1978). Dothistroma needle blight is considered one of the most important diseases of pines in the world (Barnes et al. 2004).

Alex Woods (e-mail: Alex.Woods@GEMS8.gov.bc.ca) is a regional forest pathologist, and K. David Coates is a research silviculturalist, with the British Columbia Forest Service, Bag 6000, Smithers, British Columbia, V0J 2N0, Canada. Andreas Hamann was a postdoctoral researcher in the forestry department at the University of British Columbia when this article was being prepared; he is now an assistant professor at the University of Alberta, Department of Renewable Resources, Edmonton, Alberta, T6G 2H1, Canada. *© 2005 American Institute of Biological Sciences.*

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Historically, Dothistroma needle blight has had only minor impacts on native forest trees, and mortality due to any foliar disease in natural forests is rare (Harrington and Wingfield 1998). Recently, however, this has dramatically changed in the northern temperate forests of British Columbia, Canada, where Dothistroma needle blight has severely affected native lodgepole pine trees (*Pinus contorta* var. *latifolia* Dougl. ex Loud.) (Woods 2003, Bradshaw 2004). Dothistroma needle blight is now causing extensive mortality in managed plantations of lodgepole pine, and the severity of the disease is such that mature pine trees are also succumbing (Woods 2003).

All diseases are a result of the relationships among host availability, environmental factors, and the pathogen's ecological requirements, which make up the so-called disease triangle (Gäumann 1950). The unprecedented severity of Dothistroma needle blight observed in northern British Columbia must also be a function of the interplay among these three factors. Establishing a causal relationship between climate change and local biological trends is difficult, and short-term, single-species studies of limited geographical scale may not be useful (Harvell et al. 2002, Parmesan and Yohe 2003). If such a causal relationship is to be established, long-term disease records are required, and they are rare. In northern British Columbia, the incidence of Dothistroma needle blight has been documented from 1963, when the disease was first identified (Parker and Collis 1966), to the present (Woods 2003). The Canadian Forest Service's annual Forest Insect and Disease Survey (FIDS) monitored disease incidence for the period 1949–1995 (e.g., Molnar 1963). Crucial information is available on all three parts of the disease triangle that have contributed to this disease history: (1) host availability, from inventory data of the British Columbia Ministry of Forests (Woods 2003); (2) environment, consisting of daily and harmonized monthly weather station records used to evaluate regional and local climate change trends over the past five decades (Mekis and Hogg 1999, Vincent et al. 2002, Environment Canada 2005a); and (3) extensive research on the influence of environmental parameters on the behavior of the pathogen (Peterson 1967, 1973, Gadgil 1974, 1977). Two principal factors appear to have played a role in the development of the Dothistroma needle blight epidemic now occurring in northwestern British Columbia. First, extensive plantations of lodgepole pine have greatly increased host abundance in the area, starting in the early 1980s (Woods 2003). Second, there has been a marked increase in the frequency of weather events favorable to the disease. We hypothesize that this second factor is due to directional climate change, and this proposed relationship is the focus of our study.

The Dothistroma needle blight epidemic study area

The most severe Dothistroma needle blight infestation in northern British Columbia is located in the Kispiox Forest District (figure 1). Low-elevation northern temperate forests in this area are transitional between the coastal rainforests to the west and the more continental sub-boreal forests to the east.



Figure 1. Map of British Columbia, Canada, showing the location of the Kispiox District study area, the range of* Pinus contorta *(shaded gray), and the location of selected weather stations with long-term records.

Within the biogeoclimatic classification system for British Columbia, these mixed forests are part of the Interior Cedar–Hemlock (ICH) zone. (See Pojar and colleagues [1987] or Meidinger and Pojar [1991] for a description of this system of vegetation classification, and Banner and colleagues [1993] for a detailed description of the ICH zone in northwestern British Columbia.)

Industrial forest management in northwestern British Columbia began approximately 30 to 40 years ago, with clearcutting being the dominant management practice. Approximately 11% of the forested land base has been logged. Unmanaged stands, generally of wildfire origin, are stratified mixtures of coniferous and deciduous tree species, usually dominated by western hemlock (*Tsuga heterophylla* [Raf.] Sarg.). Lodgepole pine is typically a seral component of these forests, mixed with 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.); subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.); amabilis fir (*Abies amabilis* Dougl. ex Forbes); paper birch (*Betula papyrifera* Marsh.); trembling aspen (*Populus tremuloides* Michx.); and black cottonwood (*Populus balsamifera* ssp. *trichocarpa* Torr. & Gray). Pollen samples identified in lake sediment cores indicate that lodgepole pine has been a substantial component of these forests for the past 9000 years (Gottesfeld et al. 1991).

Dothistroma needle blight in northwestern British Columbia

The first recorded incidence of Dothistroma needle blight in northwestern British Columbia's Kispiox Forest occurred in the early 1960s (Parker and Collis 1966). The next reference to the disease in the study area occurred in the FIDS

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annual reports for the years 1984–1986. These reports followed the development and decline of a small (10-hectare [ha]) but intense Dothistroma needle blight infestation in a young lodgepole pine stand in the ICH zone of the study area (Unger and Humphreys 1984). The 1984 annual FIDS report noted that "occasional tree mortality had occurred" in 8-meter-tall trees, suggesting the disease was present for a number of years before that observation. The 1986 FIDS report stated that the disease infestation was reduced to trace levels in the same 10-ha pine stand. There were no further reports of Dothistroma needle blight in the FIDS surveys up to 1995, when the survey program was discontinued.

We have been monitoring the development of the current Dothistroma needle blight epidemic since 1997, when the first instance of a lodgepole pine plantation failing because of the disease was identified. The magnitude of the epidemic was not fully appreciated until 2002, when a low-level aerial survey was conducted over more than 21,000 ha of lodgepole pine plantations (Woods 2003). Since then, low-level flights over neighboring jurisdictions have extended the survey to more than 40,000 ha of pine plantations, 92% of which show some signs of Dothistroma needle blight infection (table 1). Nine percent of the plantations surveyed are so severely defoliated that recovery seems unlikely (figure 2a, 2b). Since intensive monitoring of the epidemic began, we have observed very few instances of trees recovering after infection. Up to this point, the damage caused by the epidemic has predominantly been varying levels of defoliation; however, mortality of individual trees has occurred in nearly 7% of the monitored stands. These severely affected stands are widely distributed. Given the ubiquitous nature of the disease in the study area, we anticipate continued mortality and plantation failures. The wide-scale damage to plantations, some as old as 25 years, is requiring managers to replant using a variety of nonhost species. We expect the need for this reforestation program to continue.

Table 1. Extent, in hectares, of Dothistroma needle blight (DNB) damage in lodgepole pine plantations in the Kispiox District and neighboring jurisdictions in northwestern British Columbia, Canada, based on low-level aerial surveys conducted in the years 2002–2004.

District	Area surveyed	Area infected by DNB	Area with trees killed by DNB	Area currently requiring replanting
Kispiox	21,888	19,706	1350	1670
Bulkley	3866	3748	60	345
Nass/Kalum	15,144	14,210	1331	1666
Total	40,898	37,664	2741	3681

Note: The Bulkley District lies immediately to the east of the Kispiox; the Nass/Kalum lies to the west. Natural regeneration of other conifer species may reduce the area that requires replanting.

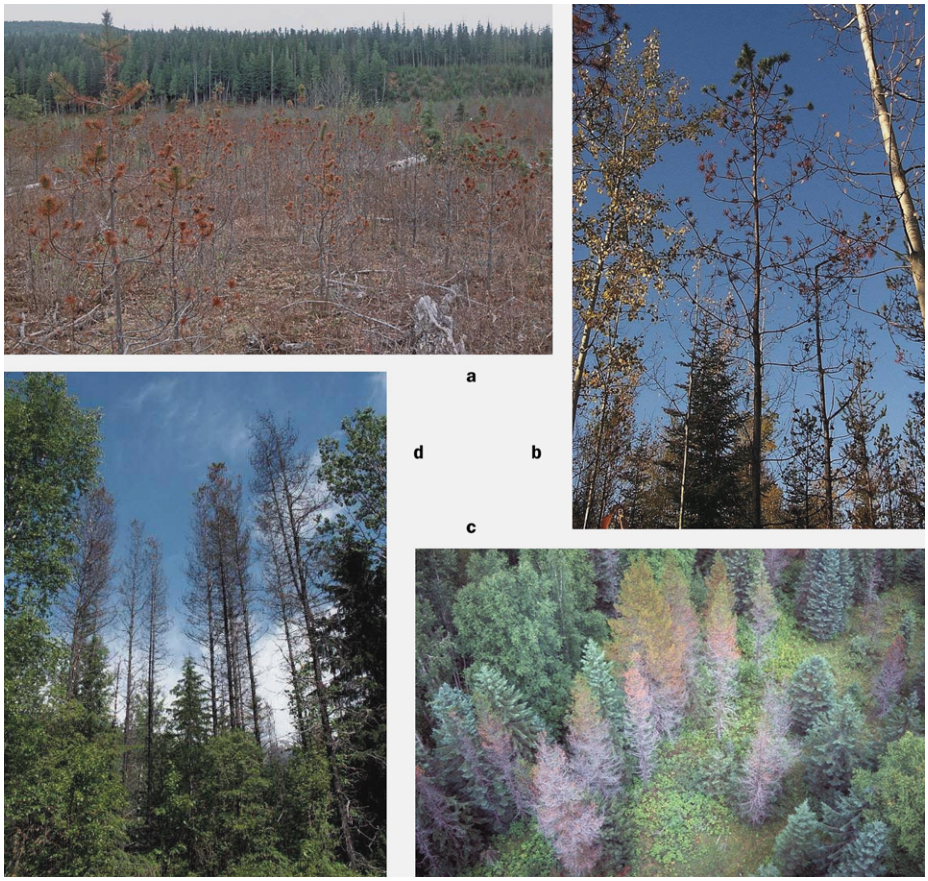


Figure 2. Scenes from the current Dothistroma needle blight epidemic in northwestern British Columbia, Canada, including severely damaged lodgepole pine plantations (a, b) and a mature (60-year-old) mixed-species stand containing lodgepole pine trees dying from the foliar disease (c, d). The plantation depicted in (a) is one of the most severely damaged stands. The extent of defoliation visible in (b) is found in 15% of the lodgepole pine plantations in the study area. Isolated pockets of severe defoliation and mortality in mature stands such as those depicted in (c) and (d) are distributed throughout the study area but are not common. Photographs: Alex Woods (a, c, and d); Paul Hanna, Silverwood Consulting (b).

In addition to plantations, we have monitored the extent of defoliation and mortality in isolated stands of mature lodgepole pine throughout the study area. The landscape-level incidence of disease symptoms in mature stands is not as uni-

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versal as that in plantations, but where disease expression is severe, it is altering the species composition of the mature stands (figure 2c, 2d). Some of the most severely damaged mature stands are located in the transition zone between the ICH and SBS (sub-boreal spruce) biogeoclimatic zones (Pojar et al. 1987), where lodgepole pine is a more abundant species because of the area's wildfire history.

Biology of Dothistroma needle blight

Dothistroma septosporum (Dorog.) Morelet belongs to a group of fungi that cause needle blights. Dothistroma infects pine needles of all ages, causing premature leaf mortality and reducing photosynthetic capacity. The fungus produces both sexual spores (ascospores) and asexual spores (conidiospores), the conidial stage being the most common (Gibson 1972), although both spore forms are found in British Columbia (Funk and Parker 1966). The first splash-dispersed conidiospores of the fungus are released in the spring from dead needles infected the previous year (Bradshaw 2004). Conidiospores continue to be released and new infections initiated throughout the year, provided temperatures are above 5 degrees Celsius (°C) and moisture is present (Sinclair et al. 1987). The incidence of Dothistroma needle blight infection is thus highly sensitive to yearly differences in weather (Peterson 1973). Rapid development of disease epidemics can occur during prolonged wet periods in the growing season (Harrington and Wingfield 1998).

The life cycle of Dothistroma needle blight generally requires one to two years to complete (Peterson 1982). Consequently, there is often a delay between a season of favorable weather conditions and subsequent disease development. Although the fungus can sporulate and germinate over a wide range of conditions, temperatures between 15°C and 20°C, combined with extended periods of moisture, are optimal for infection (Peterson 1967, Gadgil 1974, Harrington and Wingfield 1998). Peterson (1967) found that even small amounts of rain were sufficient for spore dispersal. Gadgil (1974) observed that a combination of 20°C days and 12°C nights, under continuous moisture, produced significantly more Dothistroma needle blight infection than other tested temperature regimes.

Regional climate change trends

To evaluate recent changes compared with baseline climate, we used harmonized monthly long-term records for temperature (Vincent et al. 2002) and precipitation (Mekis and Hogg 1999) from 76 weather stations in western Canada, available from Environment Canada (2005a). For these stations, 1961–1990 normals, defined as climate-variable averages over a 30-year period (WMO 1989), and 1998–2002 averages were calculated. We expressed the difference between the two as a percentage for monthly precipitation and as a measurement in °C for monthly temperature. We interpolated weather station data using ANUSPLIN software (Hutchinson 2005) to generate spatial coverages at 1° resolution for observed climate changes (figure 3).

We did not find a warming trend for the study area that was capable of explaining the current disease outbreak. Most of the already observed increase in mean annual temperature (figure 3a) occurred during the winter months (figure 3c) and should therefore have had no impact on the level of *Dothistroma* infections. The observed increase in temperature during the coldest months is in accordance with predictions from climate change models (e.g., Flato et al. 2000, Johns et al. 2003). The increased winter temperatures have been identified as a major contributing cause of the massive mountain pine beetle (*Dendroctonus ponderosae* Hopkins.) epidemic that is devastating lodgepole pine in the interior of British Columbia (Carroll et al. 2004). We found a pronounced increase in mean summer precipitation (MSP) for the study area (figure 3e). The spatial correlation between the area subjected to increased MSP and the area affected by the current *Dothistroma* epidemic is striking. In the sections that follow, we investigate in more detail the relevance of an increase in MSP for Dothistroma needle blight.

Long-term records of climate and infection thresholds

On the basis of the known environmental relationship between temperature, precipitation, and Dothistroma needle blight, we investigated the frequency of climatic events that would favor infection, namely consecutive days of rain (at least three days) with mean daily temperature above a certain threshold (16°C, 18°C, or 20°C). These events were extracted from a database of daily climate records for individual weather stations (Environment Canada 2005b). We used data from three weather stations surrounding the study area: Smithers, Terrace, and Fort St. James (figure 1). The station at the center of the study area, Hazelton, unfortunately closed in 1976. Smithers was found to be a very close match to Hazelton, using a multivariate distance measure describing similarity based on multiple climate variables (Mahalanobis distance). However, the record at Smithers dates back only to 1950. To evaluate climate variability over longer periods of time, we added Fort St. James and Terrace to the analysis (Fort St. James, with records since 1895, is climatically fairly similar to the study site but geographically distant; Terrace, with records since 1914, has a more maritime climate but is geographically close).

All three weather stations recorded an increase in three-day rain events above temperature thresholds of 16°C, 18°C, and 20°C since the 1970s (figure 4a, 4b, 4c). The trend is most pronounced at Smithers (figure 4a). In addition, peaks of MSP at Smithers (figure 4d) mirrored the historical records of Dothistroma needle blight. Spikes in precipitation that occurred in the early 1960s and 1980s correspond to the timing of the first published record of Dothistroma needle blight in British Columbia and the 1984–1986 outbreak observed by the FIDS surveyors. The trend toward increased frequency of warm rain in the mid-to-late 1990s has coincided with a sharp increase in the extent and severity of the current epidemic.

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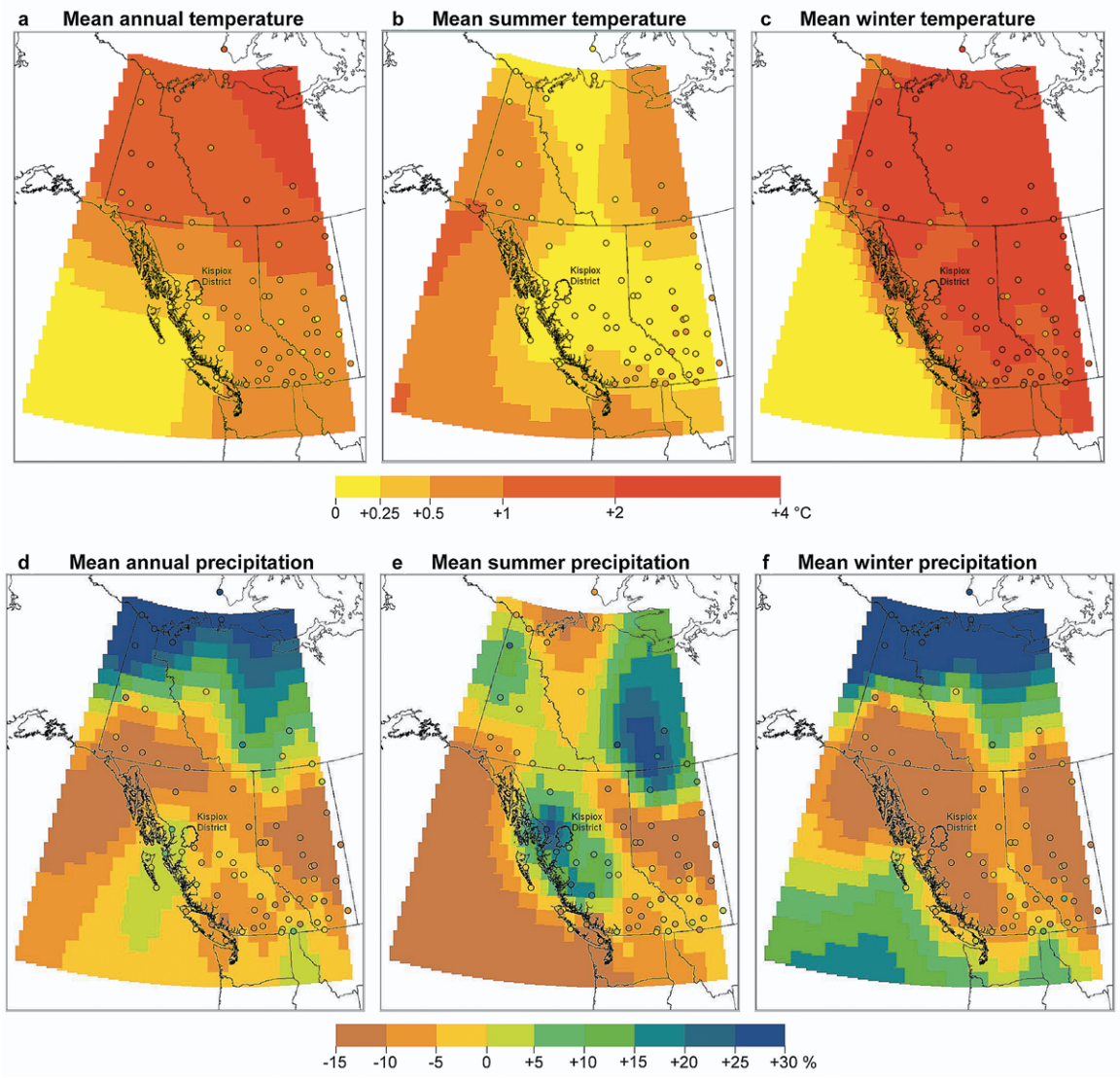


Figure 3. Changes in temperature and precipitation from the 1960–1991 normal period to the 1998–2002 average, observed by weather stations (circles) and interpolated using thin plate spline techniques (colored areas). Areas beyond weather station coverage (northeast, south, and ocean) are not valid as interpolations.

In their current state, global circulation models are unreliable in predicting future trends in precipitation (Barron 1995). Furthermore, the low spatial resolution of these models does not allow the identification of localized trends like those observed in this study. This leaves open the question of whether the observed local increase in precipitation is part of directional global climate change (with an expectation of continued increase) or whether it is attributable to recurring long-term fluctuations (with an expectation of subsequent decrease).

A known mechanism causing long-term fluctuations in climate patterns in western North America is the Pacific Decadal Oscillation (PDO), which represents the Northern Pacific ocean surface temperature (Mantua 2001). It is comparable to the El Niño–Southern Oscillation (ENSO), but persists for decades (20 to 30 years) instead of months. The climatic fingerprint of the PDO is observed primarily in North America and has only a marginal impact in the tropics, while the opposite applies for ENSO. Warm phases of the PDO (positive PDO index values; figure 5) are correlated with El Niño–like North American temperature and precipitation anomalies, while cool phases of PDO (negative index values; figure 5) are correlated with La Niña–like climate patterns (Mantua 2001).

We found no relationship between the PDO index (figure 5) and our directional increase in precipitation and warmer temperatures since the mid-1990s. The correlation coefficients for the investigated variables had low correlation coefficients ranging from –0.02 to +0.36, which were not significant after the adjustment for multiple inference (Rice 1989). The major increase in precipitation around 2000 that has contributed to the current epidemic appears to be entirely

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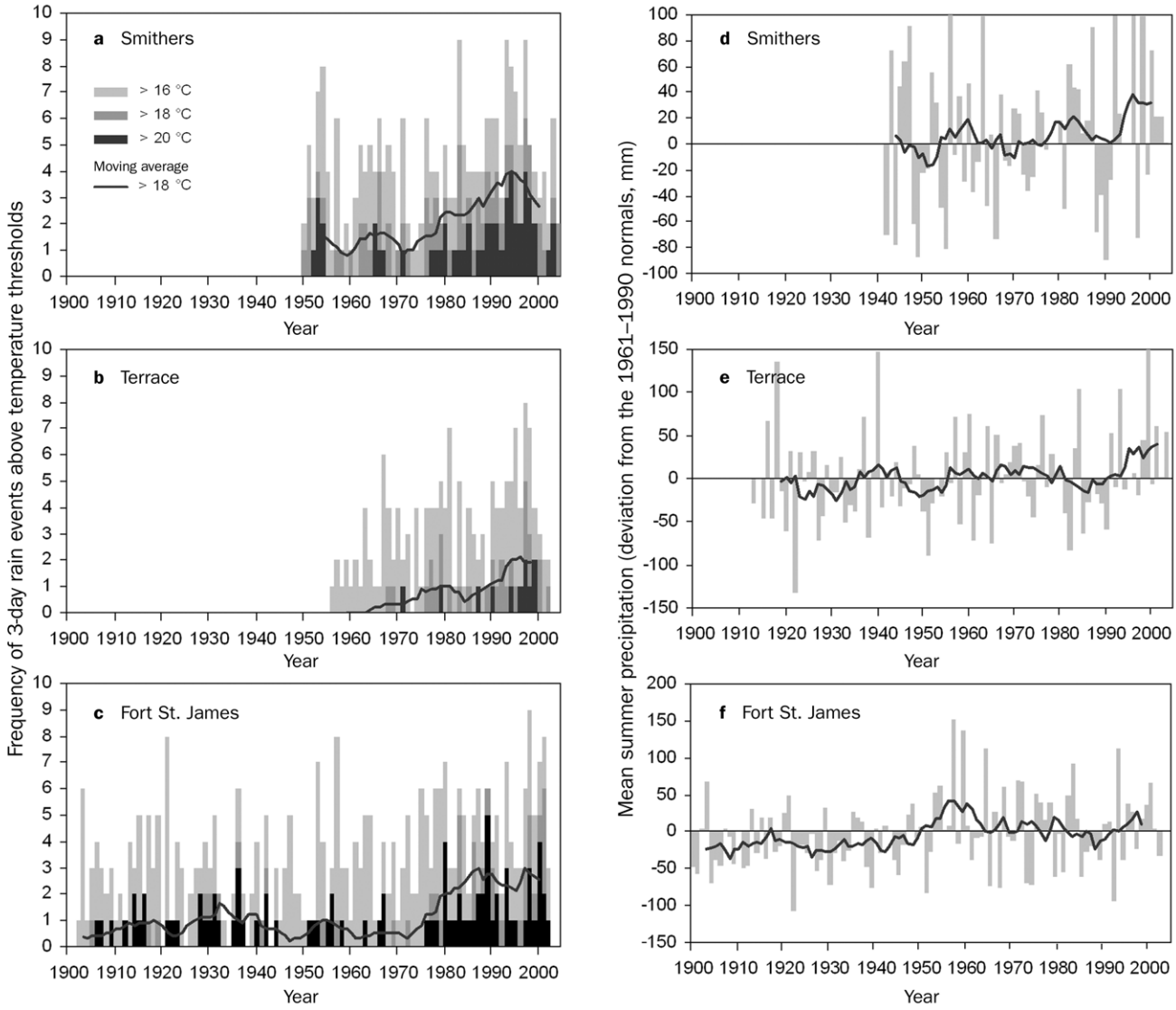


Figure 4. Long-term climate trends observed at the Smithers, Terrace, and Fort St. James weather stations. A 10-year moving average is added to help visualize trends in noisy data ("noise" refers to random error due to the method of data collection, missing data, etc.). Temperature thresholds of 16 degrees Celsius (°C), 18°C, and 20°C (a, b, c) correspond with the known biology of Dothistroma needle blight.

independent of the trend in the PDO index (figure 5). We conclude that it is more likely that the current trend is part of a directional global change pattern.

The Dothistroma epidemic: A function of host abundance and climate change

It is reasonable to expect the impacts of climate change to materialize first in forests at higher latitudes, such as those investigated in our study (Hansen et al. 1998, Harvell et al. 2002). The climatic data analysis we have presented supports this claim. Clearly, summer precipitation and, more specifically, warm rain events from the mid-1990s to the present have increased markedly from earlier decades. The trend appears to be part of a directional global change, rather than a decadal oscillation.

Dothistroma needle blight is considered native in the Northern Hemisphere (Harrington and Wingfield 1998). Lodgepole pine has been a component of the northern temperate forests of the study area for millennia (Gottesfeld et al. 1991). Since the late 1990s, Dothistroma needle blight has caused extensive defoliation in young lodgepole pine plantations (up to 25 years old). Now tree mortality is occurring in the pine plantations that were affected earliest, and we have observed scattered mortality among mature pine canopy trees in mixed-species stands, where pine represents only a small proportion of stand composition. This mortality of mature lodgepole pine caused by the Dothistroma needle blight is a globally unprecedented occurrence that has not been previously documented in the scientific literature. To date, this disease has caused most damage in exotic plantations in the

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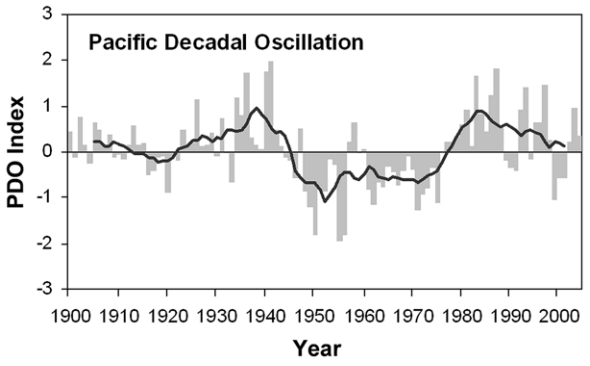


Figure 5. The magnitude of the Pacific Decadal Oscillation (PDO). A 10-year moving average is added to help visualize trends in noisy data. The PDO index corresponds to changes in the northern Pacific Ocean surface temperature. The PDO index has been in a declining trend since the early 1980s. This is not consistent with the increased summer precipitation trends shown in figure 4. Data are from Zhang and colleagues (1997), available from the Joint Institute for the Study of the Atmosphere and Ocean Climate Data Archive (JISAO 2005).

Southern Hemisphere, where both the host and the pathogen have been introduced (Gibson 1972, Bradshaw 2004). However, even in these exotic plantations, the most serious impacts of the disease have been reduced growth rates rather than mortality, which is rare (Bradshaw 2004).

We believe the current Dothistroma needle blight epidemic represents the interplay between host abundance and short-term directional climate change. Forest management practices of the past 30 years have demonstrably increased host abundance; more than 40,000 ha of young lodgepole pine plantations now exist in the study area. These lodgepole pine–dominated stands represent approximately 40% of the managed stands in the study area, compared with a historical level of 10% before active forest management began (Woods 2003).

While it is difficult to assess how forest management and increased host availability have affected the risk of Dothistroma needle blight, it is evident that the disease has been present for a long time and has previously infected pine trees, but has not reached epidemic levels because of unfavorable climatic conditions for the pathogen. The previously documented Dothistroma needle blight outbreak in the study area from 1984 to 1986 occurred before the creation of many of the current managed lodgepole pine plantations. The affected trees recovered after the 1984–1986 outbreak. That apparent recovery coincided with a reduction in the frequency of warm rain events in the remainder of that decade. The current, much more severe Dothistroma epidemic coincides with a prolonged period of increased frequency of warm rain events throughout the mid-to-late 1990s. Despite the influence of forest management, it is unlikely that the current disease epidemic could have developed without a change in climate that favored Dothistroma needle blight.

The limited literature on the impacts of climate change regarding fungal pathogens has focused primarily on predicted rather than realized impacts, and mostly in agricultural settings (Coakley et al. 1999). Climate change studies that have considered pathogens have tended to look at how the impacts of drought and associated stress on host organisms (plants) have affected fungal pathogens (Brasier 1996, Lonsdale and Gibbs 1996). Drought stress was not a factor in our study area. If anything, temperature and moisture conditions for lodgepole pine populations should have improved during the 1990s, resulting in possibly improved growth performance (Rehfeldt et al. 1999, Nigh et al. 2004). Instead, these environmental conditions have favored the development of a foliar pathogen that has far outweighed any benefits the improved environmental conditions may have had on tree growth.

The current Dothistroma needle blight epidemic in northwestern British Columbia illustrates the unpredictable nature of the influence of climate change on forest ecosystems. Brasier and Scott (1994) warned that attempts to forecast an interaction of climate change with ecologically complex processes such as host–pathogen relationships must be treated with circumspection. We agree, and have documented an example of such an interaction, one that would have been very difficult to forecast given previous experience with Dothistroma needle blight. Our study shows how a relatively small change in climate can have serious implications for a tree species, particularly if that change surpasses an environmental threshold that has hitherto restricted the development of a pathogen.

Implications for forest management

Historically, forest research has focused on tree-related issues such as reproduction methods, provenance testing, genetics, growth and yield prediction, and development of planting, tending, and harvesting techniques. Management practices (e.g., competition control, short rotations, use of genetically improved seed in single-species plantations) have tended toward simplification, with the implicit assumption that this will lead to increased yields compared with those of unmanaged stands. Such management practices may have contributed to the current Dothistroma needle blight epidemic in northwestern British Columbia by increasing and concentrating host abundance.

We have demonstrated that climate changes can make trees more vulnerable to damage from pathogens, specifically pathogens that have not been important because of unfavorable climate. Such interactions between climate and tree health, which are difficult to predict, may place managed plantations at high risk. Lodgepole pine in our study area, once considered a favored species and planted extensively, is now a major restoration liability. We believe forest managers should diversify managed stands to mitigate unexpected negative effects of climate change on forest productivity.

We have also demonstrated how the interplay between management practices and short-term climate change

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during the past decade probably resulted in a major increase in Dothistroma needle blight, which has devastated native pine in northwestern British Columbia. Our study illustrates the unpredictable nature of the influence of climate change on forest ecosystems. Loehle (1996) suggested that there has been a systematic bias toward alarmist predictions in projections of tree health response to climate change. Our study supports the claim of Harvell and colleagues (2002) that links between climate change and disease are likely to increase the severity of threats associated with climate warming.

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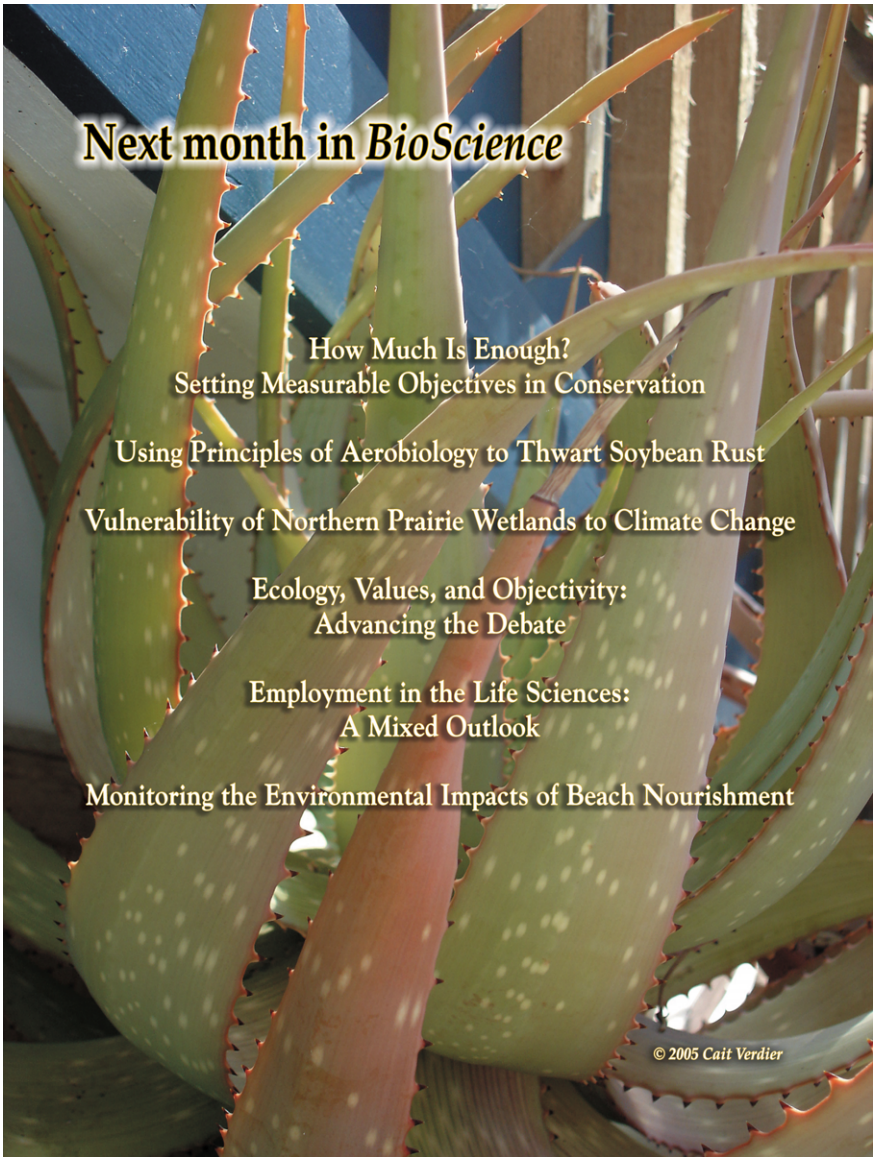
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