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REVIEW ARTICLE

Dothistroma needle blight, weather and possible climatic triggers for the disease's recent emergenceA. J. Woods^{1,13}, J. Martín-García^{2,3}, L. Bulman⁴, M. W. Vasconcelos⁵, J. Boberg⁶, N. La Porta^{7,8}, H. Peredo⁹, G. Vergara¹⁰, R. Ahumada¹¹, A. Brown¹² and J. J. Diez^{2,3}

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Summary

Dothistroma needle blight (DNB), caused by the two fungi *Dothistroma septosporum* and *D. pini*, is a major disease of pines with a world-wide distribution. Increases in the incidence and severity of disease in areas where the disease has long been established and notable range expansions have both recently been observed. The aim of this review was to assess the relationship between DNB, weather factors and climate to better understand possible underlying causes of this recent intensification in disease. A substantial body of literature shows that the life cycles of the fungi are closely related to weather factors such as precipitation and temperature. Given the rapid response of DNB to favourable weather conditions, it seems plausible that changes in disease behaviour could be due to changes in climate. The recurrent El Niño-Southern oscillation (ENSO) phenomenon influences patterns of temperature and precipitation in many regions of the world, often resulting in warmer and wetter conditions than normal. We found that since the 1950s, four of the past five strong El Niño events appear to have coincided with reports of increased DNB activity on an intercontinental scale. The lack of long-term standardized data records limits our ability to fully interpret this relationship, but the projected future climatic conditions in the Northern Hemisphere appear to be increasingly favourable for the disease. Still, other areas of the world may become less favourable, and further research is required to be able to accurately predict DNB outbreaks and their impact on pine forests in the future.

1 Introduction

Dothistroma needle blight (DNB) caused by the fungi *Dothistroma septosporum* (Dorog.) Morelet and *D. pini* (Hulbary) (Barnes et al. 2004) has been reported from more than 63 countries, infecting over 82 different species of pine and several other non-pine species (Barnes et al. 2014). Only four decades ago forest pathologists were alarmed to find the disease in 12 countries (Parker 1972). The origin of the pathogens is not entirely clear, and hypotheses regarding any differences between the two would be speculative at best given how similar the species are and how difficult it is to tell the two apart without DNA-based identification techniques (Barnes et al. 2014). Evans (1984) suggested *Dothistroma* originated in the high elevation cloud forests of Central America though the endemic nature of the genus in native pines of north-west North America suggests it may also be indigenous to that region. Ivory (1994) proposed the remote pine forests of the Himalayas as a likely origin and more recent evidence from that region lends support to this (Barnes et al. 2008). Regardless, recent range expansions of DNB and increases in the incidence and severity of attack in areas where the genus has long been established has caught the attention of foresters and forest pathologists around the globe (Woods et al. 2005; Barnes et al. 2008; Drenkhan et al. 2014). Growing awareness of the potential threat from this genus has resulted in the creation of the International Dothistroma Alliance (IDA) in 2006 and the subsequent EU COST Action FP1102 DIAROD (Determining Invasiveness And Risk Of Dothistroma) that now includes members from 35 countries.

DNB infects needles of all ages, causing premature leaf mortality and reduced photosynthetic capacity (Bradshaw 2004). *Dothistroma* spreads primarily by means of splash-dispersed asexual conidia (Gibson et al. 1964) which may be released and germinate any time temperatures are above 5°C and moisture is available (Sinclair et al. 1987). Ascospores are thought to be more robust and capable of longer distance dispersal than conidia (Gibson 1972; Dale et al. 2011), but are only found in the Northern Hemisphere (Bradshaw 2004), are less common and are typically only released for a month (Funk and Parker 1966).

Human-mediated movement of *Dothistroma*-infected plant material is considered the primary means of spread to new host populations (Bradshaw 2004; Jankovský et al. 2004), but natural range expansions are also occurring, particularly in

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the Northern Hemisphere (Barnes et al. 2008). Recent increases in disease incidence and severity in areas with a long history of *Dothistroma* presence appear linked to environmental change (Woods et al. 2005; Fabre et al. 2012; Drenkhan et al. 2013; Welsh et al. 2014). Although relationships between the pathogen and climate factors have been modelled (e.g. Watt et al. 2009; Venette 2013), the uncertainty of model predictions and fragmented knowledge continues to limit our understanding of the epidemiology of this disease. The objective of this review is to assess and synthesize the substantial body of the literature on the relationships between DNB, weather factors and climate to better understand possible underlying causes of recent upsurges in disease incidence and impacts. Given the difficulty in identifying the species of *Dothistroma*, the two will be referred to collectively as *Dothistroma* or DNB in this review. Any differences between the two species in regard to their relationships with environmental factors represent a considerable knowledge gap.

2 The influence of weather on dothistroma needle blight

The incidence and severity of DNB infestations are strongly controlled by precipitation and temperature and are thus highly sensitive to yearly differences in weather (Peterson 1973). The life cycle of *Dothistroma* in the Northern Hemisphere generally requires 1–2 years to be completed (Peterson 1982), but the latent period between infection and subsequent sporulation is quite variable depending on temperature, rainfall, host species and provenance (Gibson 1972). The disease can develop faster under the more favourable conditions present in the Southern Hemisphere. Ivory (1972) found that symptoms of DNB on *Pinus radiata* in Kenya could appear in as little as four-and-a-half weeks following inoculation in the summer and 10 weeks in the cooler months, with a marked increase in infection when temperatures first exceeded 18°C. In New Zealand, prereproduction periods were similar, requiring as little as 5 weeks in December (summer) and up to 15–16 weeks in May to July (winter) (Gilmour 1981). Consequently, there can be considerable variability in the time lag between favourable weather conditions and subsequent disease development.

Field studies have shown that *Dothistroma* can take advantage of a wide range of environmental conditions from near optimal in New Zealand with moderate temperatures and well-distributed rainfall between 1270 and 1520 mm per annum to rainfall as low as 700 mm per annum and temperatures over 18°C in Tanzania (Gibson 1972), to the generally cooler conditions of central European, Baltic and Scandinavian countries (Drenkhan et al. 2013) and the cold and wet conditions of northern BC, Canada (McCulloch and Woods 2009). Although *Dothistroma* clearly has wide ecological amplitude, there are environmental optima for the release, spread and germination of conidia and subsequent disease development once infection has occurred. These relationships have been well studied and are described below. Both precipitation and temperature have a great influence on the biological processes of the pathogen, and a combination of both factors is a key to disease development. As with many pathosystems, studies that consider individual climatic factors separately could be misleading (Thompson et al. 2014).

2.1 Precipitation

In the Northern Hemisphere, the amount of rainfall during June to September is thought to be a good indicator of disease severity based on evidence from the US mid-west (Peterson 1973), though Karadzić (1989) also considered wet periods in May as a critical period for infection in Central Europe and the Western Baltic region. Likewise, in the Southern Hemisphere, Ades et al. (1992) reported the importance of summer precipitation noting severe outbreaks of *Dothistroma* in Australia on *Pinus muricata* following unusually wet summers. In New Zealand, Gilmour (1981) found that major infections took place from November to February, with a second less aggressive infestation period from March to April, both related to high precipitation periods (Gilmour 1981). Rainfall in late spring was considered the best predictor of disease severity in New Zealand (Watt et al. 2011b). In Chile, Pérez (1973) related severe defoliation from DNB to heavy summer rains and Henriquez (1998) found that precipitation from December to February was strongly associated with the percentage of defoliation in the current year, with subsequent effects on diameter growth becoming evident 2 years later. In other work by Rack (1986), conidia were found throughout the year in Chile, but mainly during the last week of January and the first week of February (Chilean summer), and the higher the summer precipitation, the higher the conidia concentration. In contrast, Ahumada and Bulman (unpubl. data) found that disease levels in Chile generally started increasing in late winter and peaked in late spring/early summer and then decreased over late summer and autumn. In the three consecutive years of their study, winter rainfall was more than double that measured in summer. It was concluded that winter rainfall influenced disease more than summer rainfall because of the greater frequency and quantity of rainfall over winter. Throughout much of the literature, spring and summer rainfall and in particular peaks in spring and summer rainfall above long-term normals are associated with reports of DNB (Gibson 1972; Peterson 1973; Villebonne and Maugard 1999; Brown et al. 2003; Woods et al. 2005; Bulman et al. 2013). The observations from Chile, where temperatures are suitable for the life cycle of *Dothistroma* throughout much of the year, show how important rainfall is for the pathogen regardless of the season.

Severe DNB in pine nurseries in the United Kingdom was recorded in years where rainfall from June to September ranged from 315 to 450 mm, while no infection was seen when rainfall ranged from 160 to 175 mm (Murray and Batko 1962). A DNB outbreak in Chile during the summer of 1964/1965 was attributed to rainfall accumulations from December 1964 to February 1965 of 368 mm, significantly higher than the mean of 157 mm for this period (Dubin 1967). In the US mid-west, Peterson (1973) found low infection levels when rainfall accumulations over the period of June–September were 280 mm, while heavy infection was observed when rainfall ranged from 380 to 580 mm. Marks and Hepworth (1986) reported outbreaks of DNB in *P. radiata* plantations in Australia soon after rainfall accumulations of over 100 mm were

recorded in 9 months out of ten from March 1983 to January 1984. Similarly, in New Zealand, Bulman et al. (2013) found that disease outbreaks occurred after rainfall exceeded 120 mm per month from November to February and disease was suppressed after periods when rainfall was less than 70 mm per month. The literature consistently shows that disease outbreaks occur where rainfall in warmer periods averages 100 mm per month or more, while DNB is far less likely to reach damaging levels if rainfall is less than 50 mm per month.

The magnitude of differences in rainfall accumulations associated with *Dothistroma* epidemiological field studies suggests that the total amount of rainfall may be a misleading predictor of disease development. For instance, 4 days of heavy rainfall (i.e., over 50 mm/day) followed by 1 month of dry weather will result in less disease than 15 days of over 0.1 mm rain or high relative humidity. The combination of total rainfall and number of rain-days significantly improved disease prediction models over those that used total rainfall alone (L.S. Bulman, unpubl. data). Pine plantations infected with DNB are treated with applications of copper fungicide in New Zealand when average disease levels exceed 20%. The percentage of susceptible plantation area sprayed every year is, therefore, a good indicator of annual disease variation (Bulman et al. 2004). The relationship between November to February rainfall and area sprayed the following spring was satisfactory ($R^2 = 0.50$), but was improved to $R^2 = 0.70$ when the number of rain-days over 0.1 mm were included in the model (L.S. Bulman, unpubl. data). In north-west BC, Canada, no conidia were observed on rainless days and rainfall frequency was found to be a more important driver of conidia numbers than rainfall amount (Boateng and Lewis 2015). Gadgil (1977) found a close to exponential increase in the severity of *Dothistroma* infections with decreasing number of dry days under optimal temperatures. Woods et al. (2005) found that the development of a DNB epidemic in north-west BC coincided with an increase in the frequency of weather events consisting of three or more consecutive days of warm rain, when at least a trace of precipitation fell and temperatures reached 18–20°C. A similar relationship between consecutive days of warm rain and DNB expression was found in the United Kingdom by Archibald and Brown (2007). In a DNB epidemiology study, the success of inoculations of *P. radiata* and *P. muricata* seedlings was found to be significantly greater under a variable fluctuating moisture and temperature regime than in a constant one (Muir and Cobb 2005). Relationships between consecutive daily weather events which combine both precipitation and temperature in relation to disease expression are less frequently reported in the literature. Such analyses are perhaps more complicated and data acquisition itself is more laborious than monthly and seasonal weather correlations, but given our understanding of DNB, they are worth further investigation.

An increase in summer precipitation over the period of 1998–2002 of up to 30% above the 1961–1990 normal was implicated in the initiation of a DNB epidemic on *Pinus contorta* subsp. *latifolia* Engelm. ex S. Watson in north-west BC (Woods et al. 2005). Summer rain accumulations (June–September) of more than 300 mm occurred only four times in the 14-year record prior to 1997 when that epidemic was first noticed, and eight times in the same length of time following 1997, the greatest occurring in 2007 with 375 mm (A. Woods unpubl. data). An increase in precipitation since 1997 has also been implicated in the mounting impacts of DNB in the United Kingdom (Archibald and Brown 2007). Wet springs (March–May) during the period of 1999–2002, when average precipitation amounts were more than 100 mm above the long-term normal of 167 mm, could partly explain this increase in disease severity (Brown et al. 2003). More recently, increased summer precipitation has also been connected to the development of DNB in a new host species, *Abies concolor*, in Estonia (Drenkhan et al. 2014). Generally, increases in summer rainfall have been associated with defoliation due to foliar pathogens resulting in more transparent tree crowns (Sanz-Ros et al. 2008) and in a growing number of areas of temperate pine plantations and forests, DNB is the agent responsible.

2.2 Temperature

The growth of cosmopolitan, adaptable fungal pathogens like *Dothistroma*, is often limited by the specific environmental characteristics of the affected area. In areas with a warm Mediterranean climate, the limiting factor is typically precipitation (Desprez-Loustau et al. 2007). In cooler areas such as central Europe, Karadzić (1989) suggested the amount of rainfall was of less importance than temperature and that rainfall was not strongly correlated with the amount of infection. Higher mean winter temperatures have been associated with increased DNB on *Pinus nigra* in France (Landmann 2000). Dvorak et al. (2012) found that *Dothistroma* spore production only took place on days with an average temperature above 10°C and minimum temperatures above freezing. In a study using dendrochronology to relate past suspected DNB outbreaks to weather, Welsh et al. (2014) found that August minimum temperature was the most influential climate variable out of a wide range of monthly and seasonally averaged temperature and precipitation variables. Fabre et al. (2012) found that mean temperature over the months of June–August was more closely related to the presence of *D. pini* than the amount of total rainfall over the same period but did not specify the same relationship for *D. septosporum*. The Fabre et al. (2012) study represents the only documented attempt to determine whether the two *Dothistroma* species have different environmental requirements. Their work suggests a tendency for *D. septosporum* to favour cooler conditions than *D. pini*, but DNB severity, regardless of species, was more closely related to the amount of rain in the period June to August. In agreement with earlier work of Desprez-Loustau et al. (2007), Fabre et al. (2012) concluded that temperature influenced pathogen presence, while rainfall better explained disease severity.

Cold stress in conjunction with low humidity has been considered as a possible limiting factor for the ability of DNB to reach epidemic levels in American, European and Asian countries (Evans 1984; Venette 2013). Using a threshold of –30°C, Watt et al. (2009) suggested that cold temperatures limited the extent of the pathogen in Canada. Nonetheless, the existence of *Dothistroma* in locations of the boreal white and black spruce biogeoclimatic zone (Pojar et al. 1987) of north-west BC (McCulloch and Woods 2009) where temperatures often reach –40°C suggests that cold stress is not a strongly limiting factor. The recent discovery of *Dothistroma* and DNB in native stands of *Pinus sylvestris* in northern Scandinavia provides

further evidence of the pathogens' cold tolerance (Solheim and Vuorinen 2011). The climate of that region has not been considered as particularly suitable for the disease (Watt et al. 2009), and *P. sylvestris* has been considered as one of the more resistant pine species to DNB (Peterson 1982; Karadzić 1989; Watt et al. 2009), although considerable intraspecific variation in DNB susceptibility within Scots pine provenances has recently been found (Fraser et al. 2014). Recent findings of high genetic diversity in *Dothistroma septosporum* populations in Estonia and Finland imply that the pathogen may have been present in this region for a long time (Drenkhan et al. 2013) again suggesting cold temperatures are not limiting for *Dothistroma*.

Under controlled conditions, Gadgil (1974) observed that a combination of 20/12°C (days/nights) with continuous moisture produced significantly more DNB infection than other tested temperature regimes. The more frequently these optimal environmental conditions were reached in field conditions, the greater the risk for losses due to this pathogen. The close to exponential increase in disease severity that Gadgil (1977) observed when the number of dry days between those optimal 20/12°C (days/nights) was 7 days or less illustrates how quickly *Dothistroma* can take advantage of favourable environmental conditions. When these findings are coupled with the knowledge that the period over which conidia are produced did not depend on season and that conidia survival did not depend on climate (Gadgil 1970), then a story emerges. DNB can remain latent until environmental conditions favour its development and then quickly erupt during optimal weather events. Field-based evidence of the rapid expansion that DNB is capable of under such optimal conditions has recently been observed in Colombia (Rodas et al. 2016).

Given our understanding of the close relationships between DNB and weather, it seems plausible that changes in disease behaviour could be due to changes in climate.

3 The influence of climate on forest diseases

The relationship between forest pathogens and climate and the potential for changes in climate to have serious implications on pathogen impacts has been considered for decades (Hepting 1963). A change in climate can lead to both the emergence of pre-existing pathogens as major disease agents and the provision of novel climatic conditions enabling introduced pathogens to establish (Anderson et al. 2004; Desprez-Loustau et al. 2007; La Porta et al. 2008; Sturrock et al. 2011; Pautasso et al. 2012).

Over a hundred studies have linked forest declines to drought and heat stress (Allen et al. 2010; Jactel et al. 2012), revealing emerging climate change risks. Relatively little attention has been paid to climate change acting as a predisposing factor for disease outbreaks through the creation of more favourable conditions for pathogens. Foliar fungi are particularly responsive to temperature and water availability for both infection and sporulation (Harvell et al. 2002), and the environmental conditions that typically favour foliar pathogens are often seen as favourable to the host in the absence of the pathogen (Wang et al. 2006; Woods 2011). In this sense, foliar diseases provide a clearer picture of the direct influence of climate change on pathogens than disease relationships where host stresses such as drought are involved. Foliar diseases are probably some of the most effective early warning indicators of environmental change (Harvell et al. 2002; Garrett et al. 2009), and DNB is the best understood foliar disease of temperate forests (Bradshaw 2004). The pathogen is an ideal model organism to study as it is established both in the Northern and Southern Hemisphere, where it can be viewed alternatively as a native or an alien invasive pathogen, influenced by planting practices, other human activities and for the purposes of this review, environmental change (Barnes et al. 2014).

4 Possible climatic triggers for the recent emergence of *Dothistroma* needle blight

4.1 ENSO (El Niño-Southern Oscillation)

The dominant mode of interannual variability in global and hemispheric land precipitation is the El Niño-Southern Oscillation (ENSO) (New et al. 2001). ENSO is considered second only to the seasonal cycle in its impact on climate variability (Nicholls 1993). ENSO influences patterns of temperature and precipitation including extreme events such as droughts, floods and tropical cyclones in many regions of the world (Zebiak et al. 2014). The 5th report of the IPCC (Stocker et al. 2013) states that there is high confidence that ENSO will remain the dominant mode of interannual variability in the tropical Pacific with global effects in the 21st century and due to the increase in moisture availability associated with greater rates of evaporation, ENSO-related precipitation variability on regional scales will likely intensify.

The onset of an El Niño event is often phase-locked to the seasonal cycle, with the peak of an El Niño episode occurring around late December (Van Oldenborgh 2000). The entire period influenced by El Niño, however, has been defined as covering a span of 24 months starting in July of the year before the episode and running to June the following year (Ropelewski and Halpert 1987). The same authors found an ENSO-related precipitation pattern in many areas of the globe with greatly enhanced precipitation in the Northern Hemisphere summer and fall, specifically southern Europe in April through November, greater than normal precipitation in East Africa in October to April, and in southern South America in the summer. Rainfall during El Niño years can be four to ten times higher than average (Holmgren et al. 2001). Halpert and Ropelewski (1992) also found warmer than normal temperatures associated with seven out of nine warm phase ENSOs dating back to 1950 over the period of October to September across the Northern Hemisphere.

Relationships between vector-borne human diseases and El Niño events are well documented (Nicholls 1993; Hales et al. 1999; Maelzer et al. 1999; Shaman and Lipsitch 2013). The potential for using retrospective climate fingerprint studies to assess the impacts of global climate variability on plant pathogens is more limited primarily due to the lack of long-term

series of population or disease variables in a standardized manner (Scherm 2004). Links have been made, however, in agricultural settings between ENSO and (i) wheat rusts in China and the United States (Scherm and Yang 1995), (ii) soybean rust in Brazil (Del Ponte et al. 2010), (iii) Fusarium head blight epidemics in wheat in Brazil and the United States (Del Ponte et al. 2009; Kriss et al. 2012) and (iv) other crops (Magrin et al. 2007). There have been few attempts to link forest disease behaviour and ENSO-related climate variability although Rizzo et al. (2005) suggested that increased precipitation associated with El Niño could influence the establishment and spread of *Phytophthora ramorum*. If a climate fingerprint was to be found linking a forest pathogen to global climate variability one of the best candidates would be DNB given its global distribution (Barnes et al. 2014), known rapid response to favourable weather conditions (Peterson 1973) and worldwide recognition as a major disease of pines over the past six decades (Bradshaw 2004).

Dothistroma was considered a benign pine needle pathogen, distributed widely in the temperate zones of North America and Europe prior to the end of the 1940s (Gibson 1972). Since then, a review of the *Dothistroma* literature dating as far back as the 1950s suggests that more severe *Dothistroma* outbreaks over the subsequent decades may have been triggered by more conducive weather although increased planting of susceptible hosts in areas suitable for DNB has also taken place. Given the pathogens' strong link to weather and the large influence that ENSO has on global weather, it seems possible that an increase in *Dothistroma* outbreaks could be associated with strong El Niño events.

In his review of DNB in *P. radiata*, Gibson (1972) referred to the first recognition of *Dothistroma septosporum* as a serious pathogen in Africa occurring in 1957, and the same year the first strong El Niño was noted in the period of time that ENSO events have been tracked, 1950–2014 (Fig. 1). Gibson (1972) believed that the rapid disease expansion in central Africa in the late 1950s was not the result of a recent introduction of the pathogen which evidence suggested was probably there since the early 1940s. El Niño events are known to bring above normal precipitation (Ropelewski and Halpert 1987) and below normal temperatures (Halpert and Ropelewski 1992) to that region.

The strong El Niño of 1965–1966 (Fig. 1) coincided with global recognition of DNB as an emerging disease concern in British Columbia, Canada (Parker and Collis 1966), the US Mid-West (Peterson 1967), East Africa (Gibson 1972), France (Lanier et al. 1976), New Zealand (Gibson 1972) as well as Chile (Dubin and Staley 1966). In each of these cases, there is evidence of the pathogen being present years before the disease increased in severity suggesting the outbreaks were the result of environmental circumstances that favoured the pathogen's build-up and spread.

Few notable records of *Dothistroma* co-occur with the strong El Niño of 1972–1973, a possible exception being France (Fabre et al. 2012). The relationship between ENSO-related precipitation patterns can vary from episode to episode in some regions. In the western United States the 1976 El Niño, for example, brought extremely dry conditions, while the 1982–1983 El Niño was exceptionally wet (Ropelewski and Halpert 1987).

The 1982–1983 El Niño, the second strongest to date (Cai et al. 2014) again appeared to coincide with reports of DNB in BC, Canada (Unger and Humphreys 1984), southern Japan (Suto 1990), southern India (Ivory 1994) and areas of Europe (Fabre et al. 2012) (Fig. 1). While monitoring DNB behaviour in Serbia over a 7-year period from 1978 to 1985, Karadžić

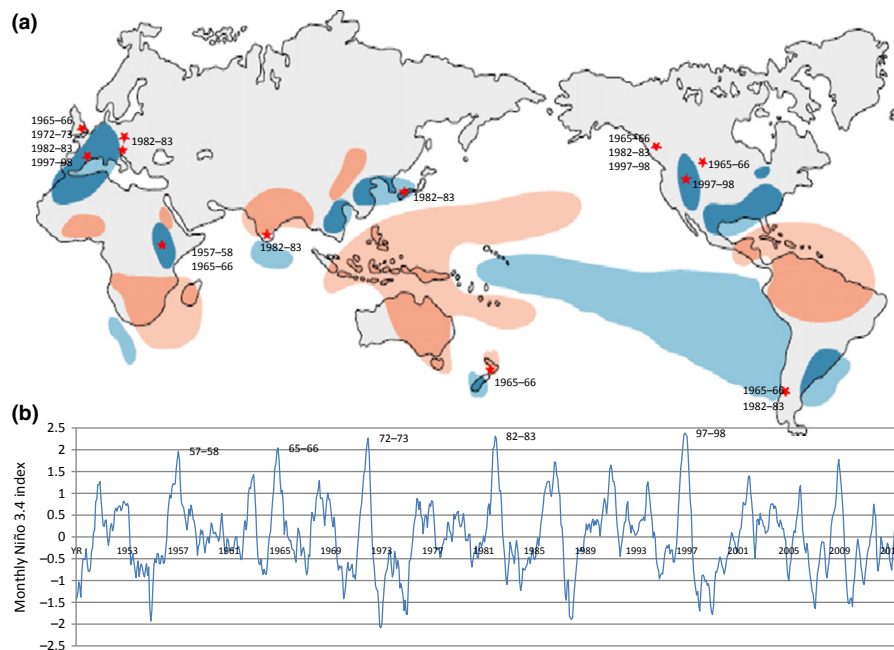


Fig. 1. (a) Regions showing increased precipitation (blue) and drier conditions (orange) during El Niño events* and the dates of documented *Dothistroma* needle blight outbreaks and their general locations (red stars) that appear to coincide with the timing of strong El Niños. (b) Monthly Niño-3.4 Oceanic Niño Index (ONI) values for the period 1950–2014 with very strong El Niño events (those ≥ 2.0) identified with the 2-year period on which they occurred (http://www.cpc.noaa.gov/products/analysis_monitoring/ensostuff/ensoyears.shtml). *Modified with permission from Allan et al. (1996) and Holmgren et al. (2001).

(1989) observed the possible influence of this very strong El Niño with the critical period of infection extending to mid-August in 1983. In Karadzić's study, conidia were found to be dispersed during wet periods, similar to the findings of others (Gadgil 1967; Peterson 1967), but the longest dispersal period occurred during 1983 (Karadzić 1989).

The most compelling concurrence between the timing of strong El Niño events and global DNB events occurred in the late 1990s. The initiation of the DNB outbreak in north-west BC, Canada (Woods et al. 2005), coincided with the very strong El Niño of 1997/1998 (Cai et al. 2014). The summer of 1997 was one of the wettest over a 50-year weather record in north-west BC (Woods et al. 2005). Similarly, in the East Anglia area of the UK, a peak in mean temperature and precipitation during the growing season of 1997 was implicated in the initiation of a severe DNB outbreak in several pine species (Archibald and Brown 2007). Meteorological data from East Anglia suggests that since the late 1990s, climatic conditions have become increasingly favourable for DNB with mean annual maximum temperatures and rainfall accumulations having increased by 0.9°C and 0.3 mm, respectively (Brown et al. 2003; Archibald and Brown 2007). Similar patterns of DNB emergence in the late 1990s and early 2000s have taken place in Montana USA (Taylor and Walla 1999), France (Fabre et al. 2012) and Eastern Europe (Dvorak et al. 2012).

Temporal and spatial scales are critical in any attempt to link climatic variability with biologically important effects (Scherm and Yang 1995). In the case of DNB, there is a century long record of disease occurrence on a global scale (Morelet 1980; Welsh et al. 2009) and a driving force behind the critical environmental factors for disease development in the El Niño phenomenon (Fig. 2). To make a definitive link between DNB outbreaks and strong El Niño events on a global basis, a standardized record of damage, in a common host, under similar management regimes over multiple decades would be required and those conditions do not exist. We have presented a compelling series of coincidences between past strong El Niño events and DNB outbreaks over the past sixty years. Variability in the timing of disease response to weather events and variability associated with El Niño events themselves both reduce precision, still four of the past five strong El Niño events appear to have coincided with reports of increased DNB activity on an intercontinental scale.

Recent observations of increased disease severity are coming from areas of the Northern Hemisphere where the disease has hitherto been absent (Jankovský et al. 2004; Bednářová et al. 2006; Barnes et al. 2008; Drenkhan and Hanso 2009; Lilja et al. 2011; Solheim and Vuorinen 2011) or has been known for decades as a minor pest (Brown et al. 2003; Woods et al. 2005). Since the late 1990s, the severity of DNB in the UK (Brown et al. 2003), France (Fabre et al. 2012) and north-west BC, Canada, has fluctuated but has not dropped below pre-1997 levels. Earlier DNB outbreaks developed then collapsed when less favourable climatic conditions returned (Woods et al. 2005).

It has been suggested that ENSO and the associated elevated climate extremes could serve as an analogue for assessing the impacts of long-term climate change (Coakley et al. 1999). Based on analysis of fossil corals which have been used to date ENSO events for the last millennium in the tropical Pacific, the late twentieth century represented the warmest, wettest period in the past 1000 years (Cobb et al. 2003). Perhaps any possible link to ENSO as a trigger for DNB epidemics may be being superseded by a larger climatic trend.

4.2 Global climate change

The Earth has been in radiative imbalance, with more energy from the sun entering than exiting the top of the atmosphere, since at least about 1970 (Hansen et al. 2005). It is virtually certain that the Earth has gained substantial energy from 1971 to 2010, and in the Northern Hemisphere, 1983–2012 was likely the warmest 30-year period of the last 1400 years (Stocker et al. 2013). The greatest increases in temperature associated with climate change are occurring in overnight minimums. Across the continental US, record high temperatures have exceeded record low temperatures by a ratio of 2:1 over the period of 1950–2009 largely due to a small number of record low temperatures. This means that much of the warming

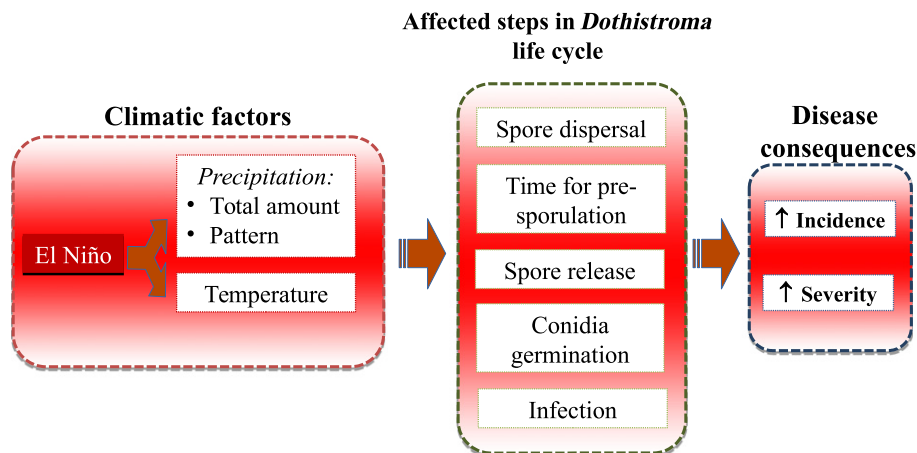


Fig. 2. The potential influence of the El Niño phenomenon on the life cycle of *Dothistroma* needle blight and resulting disease consequences.

is taking place at night when temperatures are dipping less often to record lows (Meehl et al. 2009). Similar increases in overnight minimum temperatures have been observed in the UK and northern Europe (<http://www.metoffice.gov.uk/media/pdf/t/r/UK.pdf>). Averaged over the mid-latitude land areas of the Northern Hemisphere, precipitation has increased since 1901 (medium confidence before and high confidence after 1951) (Wentz et al. 2007; Stocker et al. 2013) and extreme precipitation events are projected to become more common in the future (Allan and Soden 2008). Indeed, the frequency of ENSO-related extremes has increased and this has been linked to climate change (Cai et al. 2014).

Support for an increase in temperature being partly responsible for the expansion of DNB in the Northern Hemisphere can be found in Eastern Europe and Scandinavian countries (Drenkhan et al. 2013). In detailed experiments conducted over a series of years, Karadžić (1989) found that *Dothistroma* conidia were released during wet periods typically from the end of March but in some years even earlier. The fact that spores could be released in March in a temperate climate such as Serbia's implies that forecast increases in temperature over the coming century (Stocker et al. 2013) could potentially release *Dothistroma* from previously limiting environmental constraints. The recent expansion of DNB in northern Europe (Bednářová et al. 2006; Barnes et al. 2008; Solheim and Vuorinen 2011; Drenkhan et al. 2013) suggests that perhaps the limiting environmental barriers have already been breached. Still, to say that warming in general would be beneficial for DNB would be an oversimplification. Desprez-Loustau et al. (2007) hypothesized that the favourable effect of warming for DNB could be counterbalanced by the negative effect of a decrease in summer rainfall, leading to a stable or decreased impact of these pathogens by the end of the century in some regions.

5 Conclusion

The growing number of reports of DNB in new countries and novel hosts of *Dothistroma* in the northern latitudes suggest an increasingly favourable climate for the pathogen. While the projected future climatic conditions in the Northern Hemisphere appear to be increasingly favourable for the disease other parts of the world may see an opposite trend. Using a climatic niche model, Watt et al. (2011a) showed that future climate scenarios resulted in a reduced projected range of DNB in some areas especially in the Southern Hemisphere. We need to be cautious about drawing too many conclusions. It is unclear what proportion of the new DNB reports are the result of increased inspection efforts and which are a result of expansion to new locations and hosts. We know that *Dothistroma* was present in Russia at latitudes similar to Norway and Sweden over 100 years ago (Doroguine 1911). It is possible that the pathogen was present in the latter countries then and that the warming climate has allowed disease to develop to a stage where it is more easily detectable. It remains to be seen whether the disease continues to progress to the stage where it causes losses similar to those observed in the Southern Hemisphere, UK and British Columbia.

At the time of his review of DNB, Gibson (1972) warned that it would be unwise to assume, based on the detailed studies and state of knowledge at the time, that enough was known about the effects of the environment on the pathogen to confidently define those conditions likely to lead to high incidence of the disease. Over the past four decades, we have learned considerably more about the effects of the environment on the infection process, symptom development, sporulation and spread of *Dothistroma* (Peterson 1973; Gadgil 1974, 1977; Watt et al. 2009), but we have also come to recognize that the environment itself is changing (Stocker et al. 2013). We must use caution when making predictions regarding how the disease will react in the future. Advanced climatic forecasts (e.g. ENSO) have been successfully used to provide early warning of epidemics of agricultural diseases (Del Ponte et al. 2010; Garrett et al. 2013). Further research is required to be able to predict DNB outbreaks and establish preventative measures and control programs including timely spray in areas where deemed appropriate. Informed tree species selection and a greater reliance on species diversity in managed forests would be wise.

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