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Response of eastern white pine and associated foliar, blister rust, canker and root rot pathogens to climate change

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ABSTRACT

Climate model predictions for the northeastern U.S. forecast a warmer and wetter climate, which favors the survival, reproduction and dispersal of foliar diseases of eastern white pine, collectively called White Pine Needle Damage (WPND). Foliar diseases cause defoliation of white pine, leading to growth reductions, canopy dieback and predisposing trees to other pathogens and insects. This situation is very similar to other conifer foliar diseases, such as Dothistroma needle blight (DNB) in British Columbia and Swiss needle cast (SNC) in Oregon, where the climate is also becoming warmer and wetter. The purpose of this review is to summarize recent WPND findings of the impact climate change, particularly increased spring precipitation and annual warming has on the emergence of this disease complex. These findings will then be related to what is currently known about climatic factors affecting DNB and SNC and their role as native foliar pathogens affecting their natural forest ecosystems. We also discuss other eastern white pine diseases such as blister rust, cankers, and root rots in relation to climate change.

1. Introduction

As the climate continues to change, researchers remain focused on understanding how these variations in environmental conditions influence pathogen migration, incidence, and severity (Garrett et al., 2006). This task is particularly complex in natural forest settings due to the long-lived nature of trees and the relatively short generation time of pathogens, thus providing pathogens the ability of a faster genetic response and quicker adaptability to new climate conditions (Brasier, 2001; Sturrock et al., 2011; Burdon et al., 2012; Gray et al., 2013). Changes in climate have been shown to directly affect forest pathogens' ability to persist in an ecosystem through: increased growth, increased rates of dispersal, expanded geographic ranges, and increased overwintering survival (Dukes et al., 2009).

Over the past decade, eastern white pine (*Pinus strobus* L.) has been suffering from a severe and destructive needle blight outbreak in northeastern North America which has been caused by recent shifts in the regions climate (Munck et al., 2011; Wyka et al., 2017a). Many foliar pathogens causing needle diseases are sensitive to precipitation and humidity and exhibit increased rates of reproduction, spread, and infection under moist conditions (Sturrock et al., 2011; Harvell et al., 2002). The favorable effects of warming temperatures, for foliar species such as *Mycosphaerella pini* (Rostr.) could be offset by the negative effect of decreased summer precipitation, resulting in an overall decrease of the pathogen population over time (Desprez-Loustau et al., 2007). Dry summers are predicted to occur in the northeastern region of the United States (Campbell et al., 2011), leading to drought stress which could predispose trees to *Caliciopsis pinea* and *Diplodia sapinea*, two of the more damaging forest pathogens in the region. Although, drier summers have little effect on the spread and survivability of WPND as this emergent disease complex is favored by spring/early summer precipitation, which is expected to increase in this region (Campbell et al., 2011).

The impacts of climate change on forested ecosystems are already being felt at a greater frequency and the severity of biotic attacks and climate extremes—*as well as interactions between biotic and climate stressors*—have contributed to increased tree mortality rates worldwide (McDowell et al., 2011; Woods et al., 2017). Defoliation by pathogens and environmental stress can limit a tree's ability to take up water and nutrients, which can affect forest productivity and carbon stocks (Hicke et al., 2012). Much recent attention has focused on the interaction between drought and disease on tree health given the many regions of the world predicted to experience hotter and drier future conditions. However, in some areas, including the northeastern U.S., climate

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change forecasts predict a wetter and warmer climate (Hayhoe et al., 2007), which will most certainly favor foliar pathogens, as has been recently documented for WPND in the Northeast (Wyka et al., 2017a,b), Dothistroma needle blight (DNB) in British Columbia (Woods et al., 2016), and Swiss needle cast (SNC) in parts of Oregon (Agne et al., 2018). Despite the complexity of understanding climate-pathogen interactions, it is still prudent to continue to investigate potential disease risks in forest ecosystems that are experiencing increases in both temperature and precipitation. This is especially true when the affected host, eastern white pine, is not only an essential economic lumber resource but a crucial ecological component of the forests of northeastern United States and eastern Canada.

2. Climate change in the natural range of eastern white pine

2.1. What are the future climate predictions for this region?

Climate change projections for the northeastern USA include increases in both temperature and precipitation, resulting in an overall warmer and wetter climate for the region (Hayhoe et al., 2007). A continuing trend towards warmer and wetter condition could be supported by long-term measurements at the Hubbard Brook Experimental Forest in New Hampshire, which show increased temperature and precipitation (Campbell et al., 2011). In addition, the northeastern U.S. has experienced above average precipitation and average to above average temperatures from 2003 to 2014, including six years that were in the top 10% for precipitation (with 2011 being the wettest on record), and four years in the top 10% for temperature (NOAA, National Climatic Data Center, 2015). While this data represents annual precipitations, seasonal weather data analyses predict increases in precipitation in every season but summer (Campbell et al., 2011). Increases in temperature are expected to lengthen the growing season, and thus, the length of time that foliar pathogens can be active. Drier and hotter summers could result in water deficits that would lead to the development of drought stress in plants (Hayhoe et al., 2007). Increases in temperature are also expected within winter months, which will likely improve overwintering survival of forest pathogens. However, previous research of foliar diseases of conifer forests indicates that increased spring precipitation is the most influential climatic factor favoring reproduction and dispersal of foliar pathogens and thus disease severity such as Dothistroma needle blight (DNB) (Woods et al., 2016), Swiss needle cast (SNC) (Manter et al., 2005), and white pine needle damage (WPND) (Wyka et al., 2017a).

2.2. How might climatic changes affect foliar, blister rust, root, and stem canker pathogens?

Shifting environmental conditions can lead to interacting stresses that may predispose eastern white pine to decline (Manion, 1981). These changes may result in increased exposure to abiotic stresses that directly impact white pine, such as drought, cold/freeze injury and airborne pollutants (Benoit et al., 1982; McLaughlin et al., 1982). Weakened trees are more susceptible to attack from opportunistic fungal pathogens, of which there are many associated with eastern white pine in the northeast (Hepting, 1971; Sinclair and Lyon, 2005). Shifting climate patterns may favor the pathogens of eastern white pine, by increasing the time that specific environmental conditions (e.g. a temperature and humidity range, duration of free moisture on the surface of tissues, etc.) that are necessary for spore production and dispersal exist. For example, increases in precipitation from May through July in the northeast are resulting in increased levels of spore production and dispersal of foliar pathogens when eastern white pines are most susceptible to infection (Wyka et al., 2017b). While drought is often associated with forest declines (Allen et al., 2010), the chronic effects of needle blight on eastern white pine due to increased early season precipitation may prove to be the most important climate-induced shift.

Eastern white pine needle damage (WPND) has become a serious issue throughout the range of white pine over the past decade, with four fungal pathogens identified as having a significant role in the epidemic (Broders et al., 2015; Wyka and Broders, 2016). Foliar diseases are rarely lethal to forest and landscape trees, but they create a chronic and compounding stress as needles are killed (Hansen and Lewis, 1997). The repeated defoliation of conifers can result in reduced photosynthetic capacity, decreased growth rates, increased susceptibility to environmental stresses and fewer resources to combat opportunistic insect pests and fungal pathogens (Maguire et al., 2002). Opportunistic pathogens considered to be secondary in importance to white pine, such as *Lophodermium* spp. and *Diplodia sapinea* (Fr.) Fuckel, may benefit from weakened and stressed trees and could become more prominent members of the needle blight complex.

Increased precipitation and high humidity is also expected to favor sporulation and spore dispersal of *Cronartium ribicola* J.C. Fisch., Hedwigia: 182 (1872), the causal agent of white pine blister rust (WPBR) (Dukes et al., 2009). In the Northern Rockies, where WPBR has caused devastating mortality to native pines, wave years of blister rust have been associated with maritime weather conditions favorable to reproduction of the pathogen in the northwestern portions of the region (Geils et al., 2010; Mielke, 1943; Smith and Hoffman, 2000). In contrast to the Intermountain West, although WPBR is widespread and chronic in the Northeast, the disease incidence is limited to < 10% of trees affected in stands where it occurs (Lombard and Bofinger, 1999; Ostrofsky et al., 1988). The relatively low WPBR incidence in the Northeast, has been attributed to the effective program to eradicate the alternate host: *Ribes* spp. (Benedict, 1981; Geils et al., 2010; Ostrofsky et al., 1988). In Maine, Ostrofsky et al. (Ostrofsky et al., 1988) investigated WPBR incidence across WPBR hazard zones developed by Charlton (Charlton, 1963) for the Northeast based on climatic conditions favorable to the reproduction and dispersal of the pathogen. Contrary to expectations, WPBR incidence was not related to hazard zones. White pine blister rust incidence was related to past *Ribes* eradication efforts, and thus, the authors concluded that the *Ribes* eradication program was effective in controlling WPBR in Maine (Ostrofsky et al., 1988).

Root, butt and trunk rot fungi of eastern white pine are abundant and yet often overlooked because symptoms and signs of infection are cryptic or confused with other stresses. *Armillaria ostoyae* (Romagn.) and *A. mellea* (Vahl), regarded as two of the most virulent species of *Armillaria* (Morrison, 2004), were the most commonly isolated species from declining and dead white pines in Massachusetts (Brazee and Wick, 2011). Further, the incidence of *Armillaria* was significantly higher on white pines in the suppressed and intermediate crown classes, illustrating the preference of the fungus for low vigor trees. *Armillaria* has been reported to be particularly virulent to regenerating white pines when large inoculum reservoirs, such as hardwoods stumps, are present nearby (Hepting, 1971). In managed stands of white pine, serious losses of merchantable timber have been reported due to *Armillaria* (Silverborg and Gilbertson, 1962). Additional root and butt rot pathogens that regularly attack eastern white pine include *Phaeolus schweinitzii* (Fr.) and *Heterobasidion irregulare* (Garbelotto & Otrosina). White pines in both natural stands and plantations are affected, but especially trees growing in dense, low vigor plantations (Spaulding, 1952) and those where thinning operations have facilitated spread of *H. irregulare* (Hepting, 1971). By far, the most important trunk rot pathogen of white pine is *Porodaedalea pini s.l.* (Brot.) (Wendel and Smith, 1990). While fruiting bodies are generally uncommon and mostly observed on trees over 100-years-old (White, 1953; Silverborg and Gilbertson, 1962), young trees in natural and managed stands can also be infected (Hepting, 1971). A study of trunk rot pathogens of white pine in eastern Canada revealed that among the 13 wood-decaying pathogens that were isolated, *P. pini s.l.* accounted for 90% of the volume loss present (White, 1953). Additional investigation on trunk rot