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Impacts of White Pine Needle Damage on seasonal litterfall dynamics and wood growth of eastern white pine (*Pinus strobus*) in northern New England☆

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ABSTRACT

White Pine Needle Damage (WPND) is a complex of foliar fungal pathogens that have established as a chronic disease impacting eastern white pine (*Pinus strobus* L.) stands in the northeastern United States. With long-term ecological and economic impacts in mind, it is critical to quantify the negative effects of this disease on tree and forest health in order to make informed management decisions. We measured litterfall to determine the timing and magnitude of WPND-induced defoliation across four study sites in the northeastern US between 2014–2016. We measured N concentrations of needles cast throughout the 2014 growing season to estimate total litter N flux resulting from WPND. Additionally, to quantify growth declines we measured annual basal area increment (BAI) from six symptomatic study sites in the infected region. We found that WPND-induced defoliation in the months of June and July accounted for 47% of the total annual litterfall across the study sites, often exceeding normal needle senescence in October. Foliar %N in June and July was 0.78 and 0.84% respectively, significantly higher than October concentrations of 0.40%, suggesting incomplete resorption of N during the summer months. Untimely summer defoliations resulted in a mean estimated N loss of 0.92 $g\,N\,m^{-2}\,yr^{-1}$, representing 63% of the total growing season N input from foliage. Growth of symptomatic trees at all sites was reduced following outbreaks of WPND initiating between 2007–2009. Severely infected trees reduced BAI 25–73% compared to pre-outbreak years. Our results show that WPND-induced defoliation significantly alters litterfall and N dynamics of affected stands, and suggest that subsequent N limitation in addition to reduced foliar area greatly reduces annual wood growth within infected stands.

1. Introduction

White Pine Needle Damage (WPND) is a disease complex caused by several pathogenic ascomycete fungi presumed to be native to the northeastern United States (Broders et al., 2015; Munck et al., 2012, Costanza et al. 2018 *this issue,* Wyka et al. 2018 *this issue*). Four species of fungi, *Lecanosticta acicola* Thümen, *Lophophacidium dooksii* Corlett and Shoemaker, *Bifusella linearis* Peck, and *Septorioides strobi* Wyka and Broders, are now commonly found on the mature needles of eastern white pine (*Pinus strobus* L) within the northeastern part of its range. These fungi are known to occur independently or concurrently on trees within infected stands (Wyka et al., 2017a). In recent years, outbreaks of these foliar pathogens have caused untimely needle casting during the summer months, resulting in thinned crowns and the dieback of lower branches within the crown. Changes in the regional climate in recent decades, specifically a trend of warmer and wetter springs, may be a driver of contemporary fungal disease outbreaks and are strong predictors of annual WPND outbreak severity (Wyka et al., 2017a, 2018). The dispersal and growth of primary pathogens such as those associated with WPND are thought to be enhanced during wet periods due to the increased availability of water and humidity conducive to fungal growth and reproduction (Kolb et al., 2016). Projections from atmosphere-ocean general circulation models of the northeastern US suggest that both annual temperature and precipitation will continue to increase through the end of the century (Hayhoe et al., 2007). The development of fruiting bodies and spore dispersal of WPND fungi are

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most sensitive to early growing season precipitation in the months of May, June, and July (Wyka et al., 2017a). Within the past decade the northeast US has experienced the wettest (2006) and second wettest (2009) summer on record, while 2011 was the wettest year (annually) since 1895 (Kunkel et al., 2013). Given the recent trends in regional climate and the unprecedented outbreaks of fungal pathogens associated with this disease complex, it is critical to quantify the negative effects of this disease on tree and forest health in order to make informed management decisions.

Needle blight diseases on white pine have been observed and studied since 1908 (Clinton, 1908; Faull, 1920), however exact causal agents went unidentified until much later and in some cases pathogenic symptoms may have been attributed to ozone damage (Dreisbach, 1989). The white pine needle pathogen *L. dooksii* has been previously reported as being widespread throughout the northeastern US, but with low incidence rates on infected trees (Baldwin, 1954; Merrill et al., 1996). It is possible that several or all the fungal pathogens associated with WPND have been historically present in the region, but recent favorable weather has facilitated the rapid spread of the current epidemic. While outbreaks of WPND were first reported in Maine in 2006 (Munck et al., 2012), the year 2010 is often cited as the first time widespread defoliation was observed throughout the northeastern US (Broders et al., 2015; Munck et al., 2012). Presently, chronic outbreaks continue to occur in the region as WPND fungi are established and active throughout white pine stands. Among New England pine stands sampled for needle pathogens between 2011–2014, only 7% were found to be asymptomatic for fungi associated with WPND (Wyka et al., 2017a). To date, mortality associated with WPND is low and typically observed in conjunction with other biotic and abiotic stressors. Infected trees that are in intermediate or overtopped crown positions tend to succumb more rapidly than dominant and emergent individuals, in part due to the rain-splash dispersed nature of the pathogens. The asexual spores carried by rain droplets disperse predominantly downward through crowns (Wyka et al., 2017b), thus the lower portions of crowns and presumably understory trees receive the highest amounts of inoculum.

Despite the low levels of observed mortality, pest and pathogen defoliations occurring mid-growing season are known to have significant impacts on tree growth and physiological processes among conifer species. Marked reductions in wood growth resulting from defoliation have been documented in several other *Pinus* species including *P. pinaster* Aiton in response to processionary moth (*Thaumetopoea pityocampa* Denis and Schifferüller) herbivory (Jacquet et al., 2013, 2012; Puri et al., 2015), Scleroderris canker (*Gremmeniella abietina* M. Sars) on *P. silvestris* L. (Oliva et al., 2016; Sudachkova et al., 2015), P. *taeda* L. (Lashomb et al., 1978; Weise et al., 2016) attacked by Nantucket pine tip moth (*Rhyacionia frustrana* Scudder *in* Comstock), and *P. radiata* D. Don defoliated by ascomycete fungal pathogens Mycosphaerella *cryptica* (Cooke) Hansf. and *M. nubilosa* (Cooke) Hansf. (Carnegie and Ades, 2003; May and Carlyle, 2003). Unlike many broadleaf tree species, conifers are not able to produce a new flush of foliage following a mid-season defoliation event. Additionally, white pine fascicles (needle clusters) of the current year elongate over several months between May and August, thus are only partially developed upon WPND-induced defoliations of previous-year needles. As a result, infected trees generally bear thinned crowns with greatly diminished amounts of mature foliage. Early leaf drop due to pests and pathogens is also known to significantly alter the recycling of nitrogen (N) within trees, such that infected stands redistribute a greater proportion of N to the forest floor in lieu of resorption into storage tissues ahead of natural senescence (Lovett et al., 2002). As N is closely linked to photosynthetic capacity (Evans, 1989), a large loss of organic N from foliage mid-growing season can modify carbon assimilation rates and N uptake demand. Forest managers in the region are concerned about the impacts of WPND on wood growth and the potential for tree mortality in diseased stands. Therefore, information regarding the impact WPND is having on tree health and physiology will aid us in understanding the consequences of this emerging disease complex and allow us to make better predictions concerning the future of WPND-infected white pine stands. The first purpose of this study was to quantify the magnitude, temporal distribution, and foliar N concentration of litter cast due to defoliation by WPND across sites in New Hampshire and Maine. In turn, due to significant losses of mature foliage during the growing season, we hypothesize that gross seasonal carbon assimilation rates will be reduced, resulting in a reduction of carbon allocated to wood growth throughout infected stands in the northeastern US.

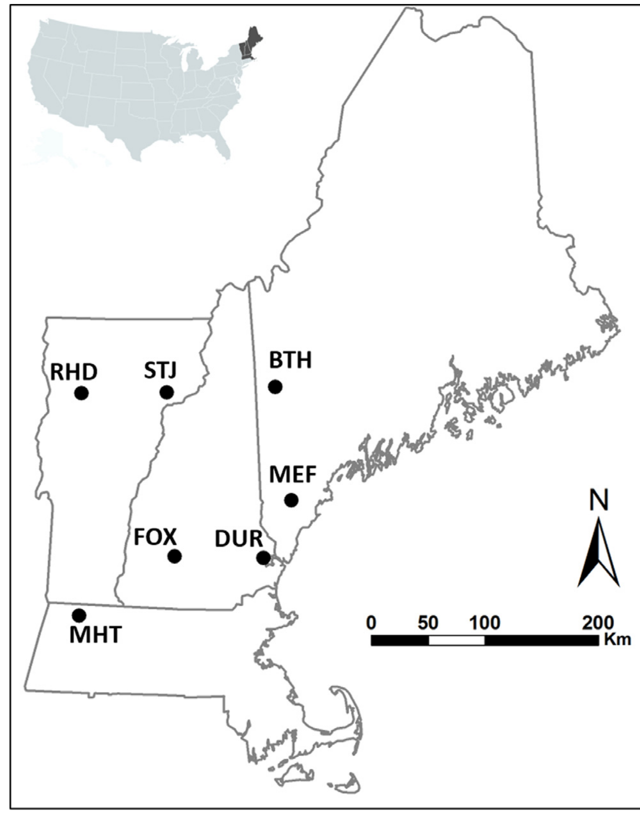

Fig. 1. Map of the New England states showing the location of the eight US Forest Service White Pine Needle Damage (WPND) monitoring sites assessed in this study. All sites except for DUR were sampled for tree ring analysis. Sites DUR, FOX, MEF, and BTH were sampled for litterfall during the 2014–2016 growing seasons.

2. Materials and methods

2.1. Study sites

We studied tree growth rings at six white pine dominated stands located in Maine, New Hampshire, Vermont, and Massachusetts. Litter fall was sampled on a subset of three sites in Maine and New Hampshire, plus an additional location in Durham, New Hampshire where only litterfall collection was conducted because the stand was initially identified as asymptomatic for WPND during an initial survey in 2012 (Fig. 1, Table 1). The study area includes several biophysical regions (Krohn et al., 1999; Sperduto and Nichols, 2004; Thompson, 2002) and spans four USDA cold-hardiness zones (USDA, 2012). The climate within this region is characterized by a humid continental climate, with cold winters, moderately warm summers, and a relatively even distribution of rainfall throughout the year. These sites also include a range of silvicultural management strategies and land use histories. The plots at Mohawk Trail Reserve in Charlemont, MA (MHT) are within an unmanaged white pine stand regarded as old-growth forest, with several of the largest known pines in the state. The study