Forest Ecology and Management 302 (2013) 354–362

Contents lists available at SciVerse ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Belowground herbivory in red pine stands initiates a cascade that increases abundance of Lyme disease vectors

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ARTICLE INFO

Article history:
Received 10 January 2013
Received in revised form 12 March 2013
Accepted 17 March 2013
Available online 1 May 2013

Keywords:
Borrelia burgdorferi
Environmental precursor
Human disease
Pinus resinosa
Red pine pocket decline
Root herbivory

ABSTRACT

There is increasing recognition that infectious disease patterns are often driven by complex underlying ecological processes. In red pine plantations in the Great Lakes region of North America, feeding by rhizophagous insects triggers a cascade that ultimately results in higher densities of blacklegged ticks, *Ixodes scapularis*, which are the primary vector of the Lyme disease pathogen *Borrelia burgdorferi*. We sampled 31 plantations in Wisconsin, USA, that were diseased or asymptomatic for a previously described tree mortality syndrome that originates with root infestation. Understory vegetation was greater in diseased stands, as were the proportion of samples containing ticks and the number of ticks per sample. Infection rates with *B. burgdorferi* were consistent. Tick densities were identical between declining and healthy portions of symptomatic stands, suggesting stand-level factors are responsible, consistent with mammal movement. These results suggest that forest management practices that affect the dynamics of belowground food webs may have implications for human health.

1. Introduction

Complex ecological processes can yield outcomes that extend beyond the perceived boundaries of the system. For example, deforestation, invasive species, and suburban landscape design can increase the abundance of vectors of human disease pathogens (Frank et al., 1998; Vittor et al., 2009; Swei et al., 2011; Lehmer et al., 2012), bark beetle outbreaks released by warm temperatures can threaten grizzly bear populations by reducing their overwintering food source of whitebark pine cones (Koteen, 2002; Logan et al., 2010), and insect defoliation can alter stream hydrology (Townsend et al., 2004). Unfortunately, our ability to predict such far-reaching outcomes is limited, and their recognition is often *post hoc*. However, there are several commonalities among these examples, including interactions that operate across multiple spatiotemporal scales, thresholds that normally constrain the system within a stable range, and intermittent external drivers that release endogenous positive feedbacks after a critical threshold is exceeded, and thereby alter emergent properties of the system (Peters et al., 2004; Raffa et al., 2008).

Our study focused on a form of habitat conversion – growing conifers in extensive plantations – which is prevalent worldwide. Plantations provide substantial benefits, such as facilitating rapid tree growth, simplifying operational activities, alleviating demands on natural ecosystems, providing employment and economic benefits to rural communities, serving as islands of improved biodiversity in agricultural landscapes, and contributing to carbon sequestration (Gerrand et al., 2003). However, plantations are commonly even-aged monocultures of relatively narrow genetic stock, and are often planted in locations selected for economic rather than ecological factors, both of which can increase susceptibility to damage by insects and pathogens. In contrast, natural forests are more heterogeneous and tend to harbor more numerous and diverse predator communities, which confronts herbivores with difficult challenges in locating and colonizing suitable host trees (Jactel et al., 2002; Jakel and Roth, 2004).

In the Great Lakes region of North America, red pine (*Pinus resinosa* Aiton) is widely grown because of its rapid growth, high uniformity, and ability to grow on marginal soils. Many mature plantations in Wisconsin, USA, are experiencing a syndrome known as 'Red Pine Pocket Decline', which is initiated by native

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http://dx.doi.org/10.1016/j.foreco.2013.03.017

root-feeding beetles and their fungal symbionts (Klepzig et al., 1991; Erbilgin and Raffa, 2003; Aukema et al., 2010). Adult *Hylobius radicis* Buchanan, *Hylastes porculus* Erichson, and *Dendroctonus valens* LeConte oviposit in the roots, soil, or basal stem. The larvae partition the resource, developing in the root collar, lateral roots, and basal stem/root collar, respectively. These beetles vector moderately phytopathogenic *Leptographium* spp. fungi into roots (Klepzig et al., 1995). Infection by this insect–fungal complex does not typically kill mature red pine trees, but the resulting stress impairs tree defenses against lethal stem-colonizing bark beetle–fungal complexes (Klepzig et al., 1996; Zhu et al., 2008). *Leptographium* readily grow through a lattice-like system of root grafts below red pine plantations, preceding noticeable above-ground symptoms by 6–8 m (Erbilgin and Raffa, 2003). The resulting gaps expand relatively uniformly and indefinitely, at the rate of several rows of trees per year. As gaps expand, they are colonized by shrubs, forbs, and early-successional woody angiosperms (Aukema et al., 2010) (Fig. 1A).

While the importance of belowground interactions on aboveground processes is becoming increasingly appreciated (Masters et al., 1993; van der Putten et al., 2009), there is a paucity of data

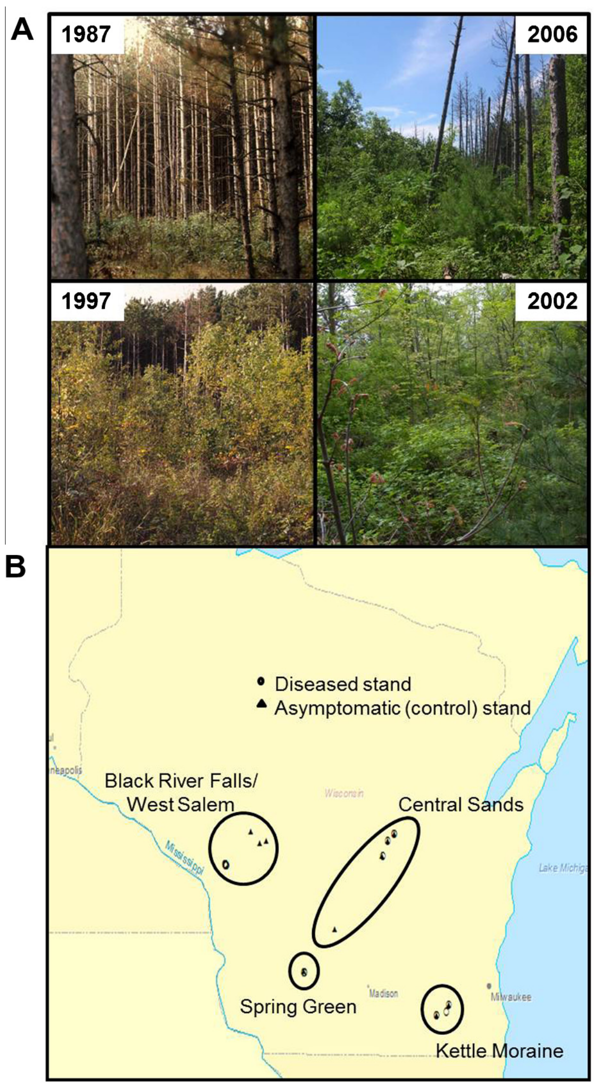

Fig. 1. (A) Gap formation over 20 years caused by interactions among root herbivores, root pathogens, and bark beetles responding to resulting decline in tree defenses. (B) Location of Wisconsin study sites sampled for ticks in 2008 and 2009. Sites were grouped by soil type.

regarding their influence on human disease dynamics (Manangan et al., 2007). We used an established ecological research system to examine the intersection of belowground herbivory, plant pathology, aboveground forest ecology, and human epidemiology. Lyme disease is an inflammatory neurological and rheumatoid condition caused by the bacterial pathogen *Borrelia burgdorferi*, which is vectored by the blacklegged tick, *Ixodes scapularis* Say. This tick has a 2-year life cycle (Yuval and Spielman, 1990) and wide host range (Keirans et al., 1996). In the southern area of the Great Lakes region, abundance of larvae peaks in June and August, nymphs peak in June, and adults peak in October. Populations and distributions of *I. scapularis* are increasing across the Midwest, which is the second largest epicenter of Lyme disease incidence in North America (Diuk-Wasser et al., 2010). Reported cases in Wisconsin have risen 6-fold in the last 20 years (Diep Hoang Johnson, WI Dept. of Health Services, pers. comm.), and areas considered at risk are expanding (Estrada-Peña, 2002; Caporale et al., 2005; Diuk-Wasser et al., 2006). Disease incidences of other pathogens vectored by *I. scapularis*, including *Anaplasma phagocytophilum*, *Babesia microti*, and Powassan virus, are also increasing rapidly in the Great Lakes region of North America. Understanding the impact of environmental precursors to tick-borne disease incidence can provide useful insights about emerging and future health risks.

We sampled ticks across red pine sites in central and southern Wisconsin, and report their spatiotemporal variation during two consecutive years. We tested whether habitat changes caused by interactions between below- and aboveground insect herbivores and their symbionts affected the abundance, distribution, and infection rates of *I. scapularis*. We hypothesized that *I. scapularis* population densities would be higher in diseased than asymptomatic stands, owing to the increases in vegetation types conducive to *I. scapularis* and their mammalian hosts. We also hypothesized that *I. scapularis* population densities would be higher in diseased than nonsymptomatic portions of diseased stands, which were located outside the edge of tree mortality. Finally, we hypothesized that *B. burgdorferi* and *A. phagocytophilum* nymphal infection rates would not differ between diseased and asymptomatic stands.

2. Materials and methods

2.1. Study locations and descriptions

Thirty-one mature *P. resinosa* plantations (Table 1), previously studied for their condition and abundance of insects and pathogens causing Red Pine Pocket Decline (Klepzig et al., 1991; Erbilgin and Raffa, 2003; Aukema et al., 2010), were sampled along a transect from west-central to southeastern Wisconsin (Fig. 1B). These stands overlaid regions with known or anecdotal *Ixodes* and *Borrelia* incidence. Stands were either symptomatic of Red Pine Pocket Decline (hereafter called diseased) ($n = 21$) or healthy, asymptomatic control stands ($n = 10$). Soils were generally sandy with suboptimal nutrition for *P. resinosa* (Appendix A).

2.2. Tick sampling

We sampled ticks in June and August 2008, and June, August, and October 2009. All stands were sampled within 3 consecutive days on each occasion. In diseased stands, *I. scapularis* were sampled along the edge of tree mortality ("inside" ring) and 10 m outside the edge in apparently healthy forest ("outside" ring). In asymptomatic control stands, the inside ring was 25 m outside a permanently marked central point, and the outside ring was 35 m from the central point. *Ixodes scapularis* were sampled using a standard white flannel sheet dragging technique. Each sheet was