



Original article

Canopy gaps decrease microbial densities and disease risk for a shade-intolerant tree species

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ABSTRACT

Canopy disturbances such as windthrow events have obvious impacts on forest structure and composition aboveground, but changes in soil microbial communities and the consequences of these changes are less understood. We characterized the densities of a soil-borne pathogenic oomycete (*Pythium*) and a common saprotrophic zygomycete (*Mortierella*) in nine pairs of forest gaps created by windthrows and adjacent forest understories. We determined the levels of *Pythium* necessary to cause disease by performing pathogenicity experiments using two *Pythium* species, a range of *Pythium* densities, and two common tree species (*Acer rubrum* and *Prunus serotina*) from the study sites. Three years post-disturbance, densities of *Mortierella* remained suppressed in soil from forest gaps compared to levels in intact forest understories while varying across sites and sampling dates. *Pythium* were infrequently detected likely because of soil handling effects. Expression of disease symptoms increased with increasing inoculum density for seedlings of *P. serotina* with each *Pythium* spp. having a similar effect on this species. Conversely, *A. rubrum* appeared resistant to the two species of *Pythium*. These results suggest that *Pythium* densities at sites where they were detected are sufficient to cause disease and possibly affect establishment of susceptible species like *P. serotina*. Because early seral environments have lower loads of the saprotrophic *Mortierella*, pathogen loads may follow a similar pattern, causing susceptible species to establish more frequently in those habitats than in late-seral forests. Forest disturbances that alter the disease landscape may provide an additional mechanism for explaining succession of temperate forests in addition to the shade-tolerance paradigm.

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1. Introduction

Disturbances are important processes affecting forest community composition (e.g. Peterson and Pickett, 1995) and resource availability. For example, forest gaps are known to affect light penetration to the understory (Ritter et al., 2005), soil moisture (Ritter et al., 2005), and fine root biomass (Wilczynski and Pickett, 1993). Gaps also alter trophic interactions. For example, aboveground herbivory varies in gaps vs. outside of gaps and in some cases counters the beneficial effects of increased growth in gaps (Tripler et al., 2005; Krueger et al., 2009). It is less clear how forest disturbances alter soil microbial communities and the consequences of these changes.

Soil-borne pathogens are known to alter the growth and survival of seedlings and saplings of both temperate (e.g. Packer and Clay, 2000, 2002; Romero et al., 2007; Reinhart and Clay, 2009) and tropical tree species (Augspurger, 1984; Hood et al., 2004; Augspurger and Wilkinson, 2007). Gaps in tropical forests appear to function as recruitment sanctuaries and may provide an escape from the effects of soil-borne pathogens (Fig. 1). Gaps could affect disease dynamics in complex ways that influence both the host and pathogen. For example, the increased growth rate of plants in gaps vs. understories may allow them to shorten the period of time they are most susceptible to disease (i.e. seedling developmental stage). Individuals that rapidly transition from seedlings to juveniles are likely to experience less disease than plants spending more time as seedlings either because these later stages of development contain more lignified roots and/or have more structurally complex root architecture to compensate for the loss of root segments to disease (Augspurger, 1990).

Gaps may also alter pathogen populations either directly or indirectly. Gap environments are drier (and warmer) than understory

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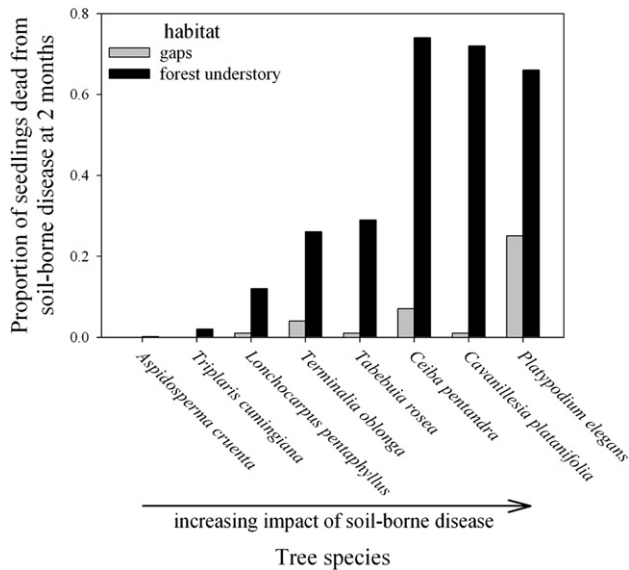


Fig. 1. Soil-borne disease of tropical tree seedlings varied with tree species identity and occurred at greater frequency for seedlings growing in forest understoreys than gaps (redrawn and modified from Augspurger, 1984).

environments (Ritter et al., 2005) which may negatively affect the plants but also has a negative effect on some pathogen populations since their density and the expression of disease symptoms are often positively correlated with soil moisture (e.g. Augspurger, 1990; Erwin and Ribeiro, 1996; van Os and van Ginkel, 2001). Gaps may also be associated with changes in other soil microbial assemblages (e.g. mycorrhizal fungi) that have the potential to suppress development of disease by affecting the pathogens directly (e.g. competing for carbon and colonization space) or by affecting host plants (e.g. increased growth rates and phosphorus) (Borowicz, 2001).

A key question to be resolved is whether forest disturbances alter pathogen pressure and affect tree recruitment. A recent study reported that shade-tolerance rankings of seedlings of 21 tropical tree species were negatively correlated with their susceptibility to soil-borne diseases (McCarthy-Neumann and Kobe, 2008). This corresponds with patterns of succession and foliar defenses to herbivores (Cates and Orrians, 1975). Other results from tropical systems indicate that seedlings experience less disease in gaps than intact forest (e.g. Augspurger, 1984) and that gap specialists are more susceptible to soil-borne disease (McCarthy-Neumann and Kobe, 2008). In total, these results suggest that generalizations about shade tolerance and tropical forest succession may actually be the synergistic result of physiological shade tolerance, positive relationship between shade tolerance and resistance to enemies, and variation in enemy pressure by habitat type.

Synergistic effects of shade tolerance, enemy resistance, and habitat type driven enemy pressure may also affect recruitment in temperate forests. For example, (O'Hanlon-Manners and Kotanen, 2004) reported that the pathogenic activity of soil-borne pathogens on *Betula papyrifera* seeds was greater in the understory than in gaps. The authors proposed that susceptibility of *B. papyrifera* seeds, a species traditionally classified as shade intolerant, to soil-borne pathogens may exclude it from understory environments rather than physiological limits associated with low-light availability. Trade-offs may exist between life history and physiological traits correlated with pathogen susceptibility (McCarthy-Neumann and Kobe, 2008 but see O'Hanlon-Manners and Kotanen, 2006) such that shade-tolerance classifications may be indirect indicators of disease susceptibility. In another study on seed diseases, O'Hanlon-Manners and Kotanen

(2006) included three congeneric (or closely related) pairs of shade-tolerant and shade-intolerant taxa. They found that seed diseases did not vary between gaps and understoreys and that only in one of three congeneric pairs did the shade-intolerant species experience greater disease than the shade-tolerant species. Others have suggested that related variation in survival and recruitment patterns used to test the Janzen–Connell hypothesis, potentially related to the effects of soil-borne disease (e.g. Packer and Clay, 2000), are not typical in temperate systems (Hyatt et al., 2003). Thus, further research in temperate forests is necessary to determine if there are general patterns and to specifically determine if habitats vary in the density of key soil pathogens, if this variation is ecologically significant (i.e. affects disease dynamics), and how potential host species vary in susceptibility.

In this study we estimated the density of a common soil-borne pathogenic oomycete (*Pythium*) and a common saprophytic zygomycete (*Mortierella*) in paired plots of forest windthrows (i.e. gaps) vs. adjacent intact forests in the Allegheny Plateau. *Pythium* species often have a wide host range, can severely reduce plant fitness, and can survive as saprophytes in the soil (Burdon, 1987; Jarosz and Davelos, 1995). Although much is known about *Pythium* densities and their density-dependent disease dynamics in agricultural systems (e.g. Burdon and Chilvers, 1975; Mitchell, 1975; Ingram and Cook, 1990), considerably less is known about their densities in natural plant communities and the relationship between their density, how it varies with habitat, and how density affects disease. We quantified the effects of a range of densities of two *Pythium* species on seedling performance of two dominant temperate tree species (Morin et al., 2006) that are known to differ greatly in their shade tolerance: *Prunus serotina* (shade intolerant) and *Acer rubrum* (shade tolerant) (Burns and Honkala, 1990). In line with results from other studies, we predict that pathogen density will be greatest in intact forests (e.g. Augspurger, 1984) and that the shade-intolerant species (*P. serotina*) will be most susceptible to disease (McCarthy-Neumann and Kobe, 2008).

2. Materials and methods

2.1. Study system and soil sampling

A severe thunderstorm created >200 forest windthrow gaps across the Allegheny Plateau region of northwestern Pennsylvania, USA in Jul-2003 (Evans et al., 2007). Alejandro Royo and colleagues identified 17 sites with pairs of gaps and intact forest for a series of studies. From these 17 sites, we randomly selected nine sites for our study. Each of the selected sites contained a forest gap ranging in size from 0.1 to 4 ha with mean of 1.26 ± 0.47 ha ($\pm 1SE$) and a mean reduction in standing trees of $54.6 \pm 5.35\%$ (see panoramas in the Online Resource for examples of sampled windthrows). *P. serotina* and *A. rubrum* are two dominant tree species in this region (Morin et al., 2006).

We collected soil samples from the nine replicate pairs of forest gaps and adjacent intact forests in 2006, three years post-disturbance, during 19–20-Jun-2006 and 20–21-Aug-2006 (e.g. 3 composite soil samples \times 2 habitat types [gaps vs. intact forest] \times 9 sites \times 2 sampling dates). During the June sampling period, one nearby gap was mistakenly sampled instead of the intended gap (gap reference 850b instead of 850). At each site and date, we collected three composite soil samples inside and outside each gap. Each composite sample consisted of five haphazardly selected soil cores (2.2 cm diameter core and 0 to –10 cm sampling depth). A total of 108 soil samples were collected during the two sampling periods. Each composite sample was homogenized and air dried for 1 week and stored at room temperature.

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