Decomposition and N Cycling Changes in Redwood Forests Caused by Sudden Oak Death

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Introduction

Phytophthora ramorum is an emergent pathogen in redwood forests which causes the disease sudden oak death. Although the disease does not kill coast redwood (*Sequoia sempervirens*), extensive and rapid mortality of tanoak (*Notholithocarpus densiflorus*) has removed this important tree in much of the central and southern distribution of the redwood forest type. *Phytophthora ramorum* was first described in the 1990s and while the native range of the pathogen remains unknown, it has a narrow range of genetic variation characteristic of an exotic species (Rizzo et al. 2005). *P. ramorum* has a broad host range in California but infection leads to very different impacts to host health. Infection in tanoak leads to rapid host mortality which can occur in as little as 2 years in large diameter trees (Cobb 2010a). Sporulation rates are also highly variable among redwood forest hosts. Tanoak and California bay laurel (*Umbellularia californica*) support sporulation sufficient for emergence of disease, but sporulation can be as much as 10 times greater in bay laurel during warm spring rain events (Davidson et al. 2008, 2011). Infection in bay laurel has no known negative impacts on bay laurel health at the individual or population level (Cobb et al. 2010, Davidson et al. 2008). These differences in sporulation are important drivers of pathogen spread across the range of redwood (Meentemeyer et al. 2011). Within stands, increased prevalence of infected bay laurel and tanoak increase tanoak mortality rates but infection in bay laurel has the greatest effect on tanoak mortality commensurate with the high rates of sporulation in this species (Cobb et al. 2010). Redwood stands with high densities of bay laurel are most likely to be invaded by *P. ramorum* (Meentemeyer et al. 2008) while stands with high densities of tanoak are likely to experience the greatest ecosystem impacts (Lamsal et al. 2011, Ramage et al. 2011).

Foresters have recognized the importance of native insect pests and pathogens since the beginning of modern forestry but over the last 100 years, exotic pests and pathogens increasingly challenge the goals of ecosystem management including the maintenance of biodiversity and functional processes such as nutrient cycling (Eviner and Likens 2009, Lovett et al. 2006). Insects and pathogens can alter the chemical composition of plant material by physically damaging foliage or eliciting plant chemical defenses. These changes can result in altered rates of litter decomposition

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and nutrient release (Cobb et al. 2006). Mortality of individual trees arrests nutrient uptake and alters forest microclimate (Orwig et al. 2008) which can in turn cause increased nutrient cycling and decomposition rates (Cobb and Orwig 2008). When outbreak results in the removal of one species, a shift in forest community composition can lead to long-term changes to decomposition and nutrient cycling. Species removal can cause disproportionately large changes to an ecosystem if the removed tree has ecologically unique functions such as casting deep shade, producing especially nutrient rich, or nutrient poor litter (Cobb 2010b, Lovett et al. 2006). While it is clear that tanoak is declining in much of the range of redwood forests, the implications of tanoak removal for redwood ecosystem function are unknown (Rizzo et al. 2005).

Eradication of many exotic forest pests and pathogens is rarely an attainable goal. For *P. ramorum*, the broad host range, extensive geographic area which has been invaded, and the lack of impacts to bay laurel health suggest this pathogen is a naturalized part of many redwood forest communities. Furthermore, *P. ramorum* is expected to establish throughout the entire redwood range within the next 20 to 30 years (Meentemeyer et al. 2011). Understanding how the pathogen has altered redwood ecosystem processes is essential to assessing the costs and benefits of disease management. However, almost no published studies have reported baseline rates of ecosystem processes for redwood forests. How substantial are *P. ramorum* impacts on redwood ecosystem processes? What mechanisms are responsible for ecosystem change in these forests? We conducted a series of field studies quantifying soil N cycling, litterfall, and litter decomposition to begin addressing these questions. The objective of this paper is to report baseline rates of nutrient cycling for redwood forests and summarize the overall affects of sudden oak death on these processes.

Study design

We quantified litterfall dynamics in two second-growth redwood forests in Sonoma and Marin Counties, Jack London State Park and the Marin Municipal Water District respectively. At each site, 30 circular 500 m^2 plots were established in 2002 to study the influence of community composition on pathogen establishment and disease progression (Maloney et al. 2005). We selected a subset of 15 plots at each site which spanned a range of tanoak biomass and pathogen prevalence. We examined plots across a range of disease impacts with the expectation that increasing mortality will lead to greater impacts to ecosystem processes. Litter traps were collected every 6 to 12 weeks from 2007 to 2009. Soil N cycling was quantified *in situ* using open-top, intact soil cores with incubation periods of 10 to 18 weeks. We made an additional measurement of species effects on soil N cycling at the Jack London site by collecting soils directly beneath individual redwood, tanoak, bay laurel, and *P. ramorum* killed tanoak. These soils were collected outside of our permanent study plots from the top 20 cm from eight locations at cardinal directions around each tree. All soils were returned to the laboratory on ice, sieved to pass a 2 mm mesh screen and extracted with 1N KCL within 48 hours of collection. Litter decomposition of redwood, bay laurel, and tanoak litter was measured over 2 years with 1 mm mesh bags.

Results

Litterfall amounts were variable across seasons and among species. Monthly amounts of tanoak and bay laurel litterfall tended to peak in midsummer while redwood litterfall was greatest in late fall and early winter. Tanoak litterfall was the most consistent across seasons but reached the maximum (~100 kg ha^{-1} $month^{-1}$) in May and June. Bay laurel litterfall peaked at ~50 kg ha^{-1} in August. Redwood contributes the greatest mass to litterfall in these forests with maximum amounts of ~800 kg ha^{-1} in December. Cumulative tanoak mortality was associated with lower tanoak litterfall mass.

Soil N cycling rates were within the range of other coniferous forests (*fig. 1*) and N pools and N mineralization were frequently dominated by NO_3-N. Mineralization rates in the field were an order of magnitude higher than rates measured in the laboratory (*fig. 1*) which may be a function of moisture availability. The open-top cores used in field incubations allow moisture to reach microbes and maintain mineralization processes while in the laboratory, we used field moist soils and did not add any additional water.

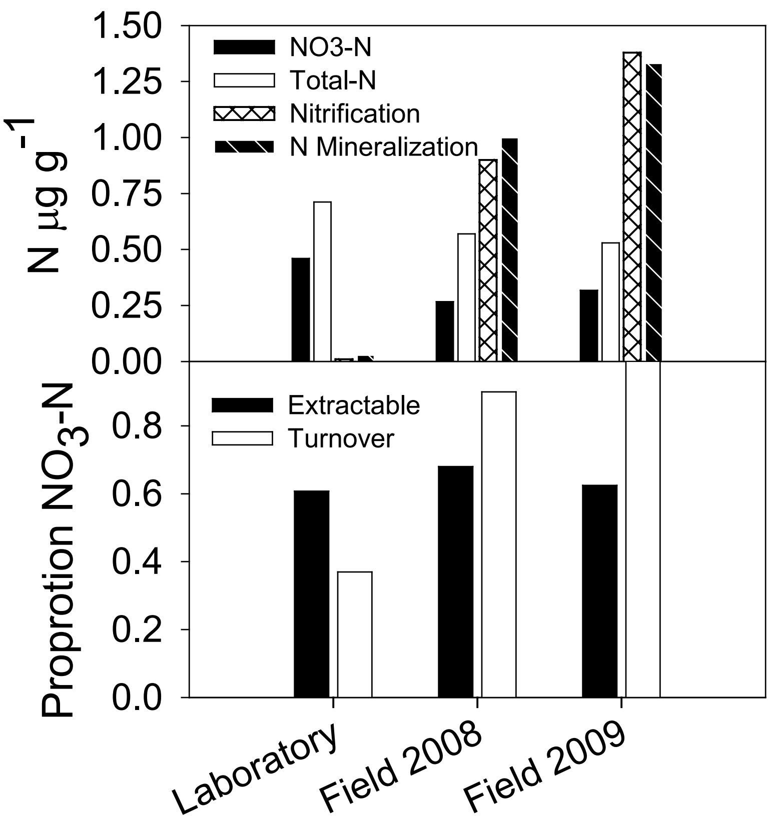

Figure 1—Extractable N and N turnover rates (top) and the proportion of NO_3-N in extractable N and N turnover (Bottom). Data are from a 5-week measurement of field-moist soils conducted in the laboratory at 22 °C (laboratory) and average rates (µg N g^{-1} soil d^{-1}) or amounts (µg N g^{-1} soil) from 2 years of measurements in the field. All data are means.

Litter decomposition was most rapid in bay laurel, slowest in redwood, and intermediate for tanoak. Litter decomposition rates were very low during summer months and increased during the wet season between October and May. Bay laurel consistently had the lowest mass remaining and was about 15 percent lower than tanoak and 30 lower than redwood.

Discussion

Phytophthora ramorum and the subsequent disease sudden oak death have impacted redwood forests throughout the central and southern range of this forest type (Meentemeyer et al. 2008, Ramage et al. 2011, Rizzo et al. 2005). In our study sites, tanoak mortality decreased tanoak litterfall mass and increased the availability of NO_3-N. Changes to NO_3-N availability were modest, but tanoak litterfall is rapidly reduced by disease. Tanoak rapidly develops basal sprouts following mortality of above ground biomass (Cobb et al. 2010, Ramage et al. 2011) which maintains tanoak as part of redwood forest litterfall even after substantial mortality has occurred. Although tanoak will remain as a component of redwood litterfall for several years following disease outbreak, the amounts of litterfall from tanoak will be much lower relative to redwood forests not invaded by *P. ramorum*.

Changes in species composition are likely to have the most long-lasting and the greatest magnitude of effect on ecosystem processes following the emergence of sudden oak death within stands. Although bay laurel accounts for a relatively small proportion of litterfall in redwood ecosystems, it has the highest N concentration of all species in these forests. Redwood has the lowest N concentration and tanoak was intermediate between the two species. These patterns suggest that redwood forest litter decomposition rates will either increase or decrease depending on whether bay laurel, redwood, or other species are able to exploit resources made available by tanoak mortality. Species shifts have been responsible for pronounced and long-lasting ecosystem changes following other major outbreaks (Cobb 2010b, Paillet 2002) which highlights the importance of understanding changes in species composition following outbreak of sudden oak death (e.g., Cobb et al. 2010, Maloney et al. 2006, Ramage et al. 2011). It is unclear how species composition will change over longer time scales in *P. ramorum* invaded redwood forests. However, shifts in species composition will likely have the greatest magnitude and longest-lasting impacts on the ecosystem processes focused on by this study.

Identifying management goals is the most important step to assessing the need for disease management in redwood forests. While redwood is not directly threatened by *P. ramorum* (infection does not cause mortality in redwood), increased fire impacts and fire severity in some *P. ramorum* invaded forests may justify fuel reduction treatments (see Metz et al. 2011). Preemptive management is also likely to be most effective in retaining overstory tanoak and the unique flora and fauna associated with this tree (Cobb 2010a). For disease treatments to be effective in retaining overstory tanoak it will often be necessary to remove bay laurel and reduce the overall density of tanoak such as through the removal of small tanoak stems. Treatments will be most effective when they are designed or associated with management to increase the growth of redwood which may in turn lead to suppression of regeneration from sporulation supporting species like bay laurel and tanoak. Preventative treatments would be similar to many current silvicultural prescriptions to reduce tanoak competition with redwood but would require modifications that intentionally retain and protect individual tanoak with high-biodiversity value. By shifting species composition to a greater dominance of redwood, ecosystem processes will also reflect characteristics typical of redwood ecosystems; specifically, slower litter decomposition rates, increased above ground biomass, and possibly increased soil C storage. However, the metric of success for these treatments should be based on their effectiveness in retaining unique biodiversity associated with tanoak. Lack of action is likely to increase the importance of bay laurel in many stands and this will shift ecosystem processes towards overall rates of N cycling, litter decomposition, and above ground biomass dynamics that reflect the autecology of bay laurel. For the individual manager facing the emergence of sudden oak death, the costs of these disease impacts must be weighted in the light of their overall goals to determine appropriate management actions.

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