ELSEVIER

Soil Biology & Biochemistry 38 (2006) 972–982

Soil Biology & Biochemistry

www.elsevier.com/locate/soilbio

Impacts of herbivorous insects on decomposer communities during the early stages of primary succession in a semi-arid woodland

Aimée T. Classen [a,b,e,*], Jennie DeMarco [c], Stephen C. Hart [b,d], Thomas G. Whitham [a,b], Neil S. Cobb [b], George W. Koch [a,b]

[a] *Department of Biological Sciences, Northern Arizona University, Flagstaff, AZ 86011, USA*
[b] *Merriam-Powell Center for Environmental Research, Flagstaff, AZ 86011, USA*
[c] *Department of Environmental Science, Northern Arizona University, Flagstaff, AZ 86011, USA*
[d] *School of Forestry, Northern Arizona University, Flagstaff, AZ 86011, USA*
[e] *Environmental Sciences Divisions, Oak Ridge National Laboratory, P.O. Box 2008, Oak Ridge, TN 37831-6422, USA*

Received 9 November 2004; received in revised form 13 August 2005; accepted 19 August 2005
Available online 21 September 2005

Abstract

Changes in nutrient inputs due to aboveground herbivory may influence the litter and soil microbial community responsible for processes such as decomposition. The mesophyll-feeding scale insect (*Matsucoccus acalyptus*) found near Sunset Crater National Monument in northern Arizona, USA significantly increases piñon (*Pinus edulis*) needle litter nitrogen (N) and phosphorus (P) concentrations by 50%, as well as litter inputs to soil by 21%. Because increases in needle litter quality and quantity of this magnitude should affect the microbial communities responsible for decomposition, we tested the hypothesis that insect herbivory causes a shift in soil microbial and litter microarthropod function. Four major findings result from this research: (1) Despite increases in needle inputs due to herbivory, soil carbon (C) was 56% lower beneath scale-susceptible trees than beneath resistant trees; however, soil moisture, N, and pH were similar among treatments. (2) Microbial biomass was 80% lower in soils beneath scale-susceptible trees when compared to resistant trees in the dry season, while microbial enzyme activities were lower beneath susceptible trees in the wet season. (3) Bacterial community-level physiological profiles differed significantly between susceptible and resistant trees during the dry season but not during the wet season. (4) There was a 40% increase in Oribatida and 23% increase in Prostigmata in susceptible needle litter relative to resistant litter. Despite these changes, the magnitude of microbial biomass, activity, and community structure response to herbivory was lower than expected and appears to take a long time to develop. These results suggest that herbivores impact soils in subtle, but important ways; we suggest that while litter chemistry may strongly mediate soil fertility and microbial communities in mesic ecosystems, the influence is lower than expected in this primary succession xeric ecosystem where season mediates differences in microbial populations. Understanding how insect herbivores alter the distribution of susceptible and resistant trees and their associated decomposer communities in arid environments may lead to better prediction of how these ecosystems respond to climatic change.

Keywords: Community-level physiological profiles; Enzyme activity; Insect herbivory; Insect-susceptible and resistant trees; Litter microarthropods; Microbial biomass; Piñon-juniper woodlands; Semi-arid

1. Introduction

Insect herbivores are common in terrestrial ecosystems (Schowalter, 2000), and can have a striking impact on the landscape by reducing plant biomass (Brown, 1994; Holland et al., 1996; Kosola et al., 2001), by altering the quality of litter inputs (Chapman et al., 2003), and by changing the microclimate beneath the area they infest (Classen et al., 2005). Altered microclimate and litter inputs should directly impact the processes that microbes mediate including decomposition (Chapman et al., 2003) and nitrogen (N) mineralization (Brown, 1994). Few studies, however, have investigated how these direct effects of herbivory may indirectly affect litter and soil microbial communities (Kuske et al., 2003). Investigating how insect herbivory modifies microbial populations and their functioning will lead to a better understanding of how species interactions may alter ecosystem processes.

Insect herbivores can indirectly change soil and litter microorganism populations in a variety of ways, but three

* Corresponding author.
E-mail address: classenat@ornl.gov (A.T. Classen).

0038-0717/$ - see front matter © 2005 Elsevier Ltd. All rights reserved.
doi:10.1016/j.soilbio.2005.08.009

mechanisms stand out. First, aboveground herbivory can increase the amount of herbivore frass and carcasses that enter an ecosystem (Hollinger, 1986; Risley, 1986; Lovett and Ruesink, 1995; Christenson et al., 2002). These products can be nutrient rich and may stimulate microbial populations. Second, aboveground herbivory can increase or decrease carbon (C) allocation between above- and below-ground biomass, thus altering the amount of substrate available for microbial growth (Dyer and Bokhari, 1976; Holland et al., 1996; Ritchie et al., 1998; Kosola et al., 2001). Third, herbivory can increase or decrease the quantity and quality of litter inputs by causing changes in the chemical properties of litter produced by plants (Risley and Crossley, 1993; Uriarte, 2000; Chapman et al., 2003), by changing the amount and timing of litterfall (Risley, 1986; Chapman et al., 2003) or, over the long-term, by causing a plant community shift from nutrient-rich to nutrient-poor plant species (Long et al., 2003).

Here, we examine how aboveground insect herbivory by the piñon needle scale (*Matsucoccus acalyptus*) seasonally alters soil and litter microbial communities beneath piñon pines (*Pinus edulis*) near Sunset Crater National Monument in northern Arizona, USA. This is an ideal system to examine this question for several reasons. First, Sunset Crater is dominated by piñon-juniper woodland, the third largest vegetation type in the US (West, 1984). The isolation of the dominant trees on this sparsely vegetated landscape provides an opportunity to examine the effects of herbivory with reduced interference from other plants and the effects of tree development on the soil environment. Second, there has been long-term monitoring and experimental removal for 16 years of the needle scale that chronically infest approximately 90% of the reproductively immature piñons (<60 years) at Sunset Crater (DelVecchio et al., 1993; Cobb and Whitham, 1998). Some trees at Sunset Crater are naturally resistant to the scale insect (hereafter ‘resistant’), with scale populations never exceeding 0.1% of the populations found on susceptible trees. Other trees are naturally susceptible to the scale insect (hereafter ‘susceptible’), and some trees have had scale insects manually removed for the past 16 years (hereafter ‘removed’). Comparing scale-susceptible trees to scale-removed trees enables us to examine the short-term effects of herbivory (< 16 years), while comparing scale-susceptible trees to scale-resistant trees enables us to examine the long-term effects of herbivory (up to 60 years). Third, previous research at Sunset Crater has shown that scale herbivory reduces tree ring growth by 35% (Trotter et al., 2002) and increases needle litter N by 46%, litter phosphorus (P) concentrations by 55%, and needle litter inputs by 21%, while having no effect on needle litter lignin or condensed tannin concentrations relative to resistant trees (Table 1; Chapman et al., 2003). Increases in needle litter chemical quality of this magnitude should alter microbial populations and communities beneath susceptible trees. Fourth, DelVecchio et al. (1993); Gehring et al. (1997) have found that resistant trees have greater mycorrhizal colonization and increased root biomass compared to susceptible trees. An increase in mycorrhizae and root biomass beneath resistant trees would lead to a greater amount of soil C being shunted belowground, thus potentially increasing microbial populations by increasing C availability to decomposers (Wardle et al., 2002). Finally, insect populations are expected to expand their range into previously uninhabited forests with global climatic change (Dale et al., 2001). Range expansions should be expected in arid climates first because plant populations in these ecosystems are often functioning at their physiological extremes and these ecosystems are, therefore, less buffered to insect expansions. Understanding how insect herbivores alter seasonal decomposer communities in arid environments may lead to models that better predict how ecosystems will respond to future climatic change.

Table 1
Needle litter chemistry needle litter inputs and fine root production

	Susceptible	Resistant	Removed
C:N[a]	64.2a	99.9b	106.2b
Phosphorus (g kg^{-1})[a]	1.7a	1.1b	1.1b
Nitrogen (g kg^{-1})[a]	7.9a	5.4b	5.0b
Lignin (%)[a]	18.2a	19.1a	17.2a
Lignin:Nitrogen[a]	23.9a	35.5b	36.0b
Tannin (g kg^{-1})[a]	51.3a	49.8a	50.3a
Needle inputs (g m^{-2} yr^{-1})[a]	90.6a	75.1b	76.0b

Within rows, contrasting letters denote significant differences among treatments (scale-susceptible, resistant, and scale-removed trees).
[a] Data from Chapman et al. (2003).

In this paper, we ask three explicit questions about the impact of insect herbivory on decomposer communities: (1) Does aboveground insect herbivory affect soil and litter microorganisms? (2) How does season mediate the effects of herbivores on soil microorganisms? (3) Do herbivore effects on microorganisms take a long time to develop?

2. Materials and methods

2.1. Site description

This project was conducted near Sunset Crater National Monument on the Colorado Plateau in northern Arizona (35°22′N, 111°33′W) during the summer of 2002. Sunset Crater erupted in 1064 AD, covering 800 km^2 of the landscape with a thick layer of ash and cinders (Hooten et al., 2001). Soils at the site are classified in the Soil Taxonomic family Typic Ustorthents. Sunset Crater is a nutrient-limited and dry piñon-juniper woodland (Cobb et al., 1997; Swaty et al., 1998). Piñons are the dominant woody plant at our study site followed by one-seed juniper (*Juniperus monosperma*) and apache plume (*Fallugia paradoxa*). The vegetation at this study site is widely spaced with inter-crown areas that are mostly vegetation free.

2.2. Experimental design

For the past 16 years, scale infestation has been prevented on a group of trees by annually removing egg masses found at the base of susceptible trees (Trotter et al., 2002). In total, we had four treatment categories: scale-susceptible, scale-resistant,