ACTA OECOLOGICA 33 (2008) 222–230

available at www.sciencedirect.com

ScienceDirect

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

ELSEVIER

ACTA OECOLOGICA
INTERNATIONAL JOURNAL OF ECOLOGY

Original article

Ecosystem and decomposer effects on litter dynamics along an old field to old-growth forest successional gradient

Paul M. Mayer

US Environmental Protection Agency, Office of Research and Development,
National Risk Management Research Laboratory, Ada, OK 74820, USA

ARTICLE INFO

Article history:
Received 2 November 2006
Accepted 23 November 2007
Published online 9 January 2008

Keywords:
Carbon
C:N
Decomposition
Ecosystem
Litter
Macro-detritivore
Nitrogen
Old-growth forest
Old field
Succession

ABSTRACT

Identifying the biotic (e.g. decomposers, vegetation) and abiotic (e.g. temperature, moisture) mechanisms controlling litter decomposition is key to understanding ecosystem function, especially where variation in ecosystem structure due to successional processes may alter the strength of these mechanisms. To identify these controls and feedbacks, I measured mass loss and N flux in herbaceous, leaf, and wood litter along a successional gradient of ecosystem types (old field, transition forest, old-growth forest) while manipulating detritivore access to litter. Ecosystem type, litter type, and decomposers contributed directly and interactively to decomposition. Litter mass loss and N accumulation was higher while litter C:N remained lower in old-growth forests than in either old fields or transition forest. Old-growth forests influenced litter dynamics via microclimate (coolest and wettest) but also, apparently, through a decomposer community adapted to consuming the large standing stocks of leaf litter, as indicated by rapid leaf litter loss. In all ecosystem types, mass loss of herbaceous litter was greater than leaf litter which, in turn was greater than wood. However, net N loss from wood litter was faster than expected, suggesting localized N flux effects of wood litter. Restricting detritivore access to litter reduced litter mass loss and slowed the accumulation of N in litter, suggesting that macro-detritivores affect both physical and chemical characteristics of litter through selective grazing. These data suggest that the distinctive litter loss rates and efficient N cycling observed in old-growth forest ecosystems are not likely to be realized soon after old fields are restored to forested ecosystems.

1. Introduction

Identifying the mechanisms controlling decomposition is key to understanding ecosystem function. Controls on litter decomposition include abiotic and biotic factors such as temperature, moisture, and pH (Coûteaux et al., 1995; Murphy et al., 1998), litter quality (Cornelissen, 1996; Aerts, 1997), soil nutrient availability (Hobbie and Vitousek, 2000), and the abundance and diversity of the decomposer community (Seastedt, 1984; Blair et al., 1990). For example, litter quality (e.g. C:N and lignin content) varies among ecosystems depending upon soil and nutrient availability as well as plant community composition which, in turn, is dictated by successional stage (Fisk et al., 2002). Detritivores respond to litter quality by selectively consuming litter with nutrient concentrations (e.g. C:N) that satisfy their stoichiometric requirements

---

E-mail address: mayer.paul@epa.gov

1146-609X/$ – see front matter © 2007 Published by Elsevier Masson SAS.
doi:10.1016/j.actao.2007.11.001

(Hessen et al., 2004). Likewise, plant community composition may strongly but indirectly affect decomposition by influencing the macro-detritivore community structure and/or feeding patterns (Mayer et al., 2005). Conversely, litter biomass may affect plant production and community composition by serving as a nutrient pool or by inhibiting seedling growth (Foster and Gross, 1998; Mack and D'Antonio, 2003). In addition, variation in ecosystem structure due to successional processes is likely to alter the importance and interaction of these mechanisms (Köchy and Wilson, 1997; Shaw and Harte, 2001; Herman et al., 2003). Ecosystem type is known to influence decomposition via microclimate effects (Coûteaux et al., 1995; Köchy and Wilson, 1997; Shaw and Harte, 2001), litter production (Cebrian, 1999; Cebrian and Lartigue, 2004), and decomposer diversity (Seastedt, 1984; Mikola and Setälä, 1998; Hättenschwiler et al., 2005).

To distinguish among these factors and feedbacks, I studied litter dynamics along a successional gradient, measuring the interactive effects of ecosystem type (old field, transition forest, old-growth forest), litter type (herbaceous, leaf, wood) and decomposers (open vs restricted access litter bags) on litter mass loss and N flux. My objective was to quantify the effects of and the interactions among ecosystem type, litter type, and decomposers.

Based on a previous study at this site showing that macro-detritivores affect herbaceous litter decomposition in old fields (Mayer et al., 2005), I hypothesized that macro-detritivores would accelerate mass loss and N flux of all litter types in all ecosystem types (Hättenschwiler et al., 1999; González and Seastedt, 2001), by preferentially consuming litter with low C:N (Melillo et al., 1982) and litter collected *in situ* (Hunt et al., 1988). I expected that litter dynamics would reflect the gradient of ecosystem succession (Fisk et al., 2002; Xuluc-Tolosa et al., 2003; Vasconcelos and Laurance, 2005), and hypothesized that mass loss and N flux would increase with successional stage (i.e. rates in old field < transition forest < old-growth forest). Finally, I expected litter dynamics to be influenced by strong interactions among ecosystem type, litter type, and decomposers, but that the strength of these interactions would vary by successional stage (Wardle et al., 2004a,b) due to microclimate effects (i.e. temperature and moisture). Thus, I hypothesized that mass loss and N flux rates would be greatest in the warmest, wettest successional stage, especially where macro-detritivores were present (González and Seastedt, 2001).

2. Study site and methods

This study was conducted near Ada, Oklahoma, USA, at the Center for Subsurface Ecological and Assessment Research (CSEAR) site, in the cross timbers, a mosaic of mixed grasslands and oak-dominated forest (Hoagland et al., 1999). CSEAR encompasses ca. 45 ha covering a successional gradient of old fields on which cultivation was abandoned in about 1950, second-growth forest in various stages of succession, and old-growth fragments of oak (*Quercus*), hickory (*Carya*), and elm (*Ulmus*). Cattle grazed on the site until 1998.

Four 10 × 10-m plots were selected in each of the three successional zones (12 plots): (1) old-fields, (2) transition forests, and (3) old-growth forests. Plots were dispersed throughout CSEAR and spaced $\geq$50 m apart. Plots in transition forests were located at the edge of a natural invasion front leading from old-growth forests into old fields. Based on aerial photos, only 6% of CSEAR was forested in 1969 and 27% forested by 2000. The increase in forested area was a function of woody invasion into old fields. Thus, old field and transition forests plots were of the same age since abandonment of cultivation but differed by the speed of woody invasion, apparently due to proximity to a seed source from the old-growth forest.

Old-growth forest plots were located in the centers of mature forest fragments intact since at least 1938 based on aerial photos. Based on tree ring counts, average age of trees in transition forests was (mean ± 1SE); 16.5 ± 1.5 years ($n = 8$), whereas old-growth forest trees were older (75.1 ± 8.8 years; $n = 7$; $t = 7.07$, $P < 0.001$). Barring cultivation, grazing, or invasion by eastern red cedar (*Juniperus virginiana*; Briggs et al., 2002; Horncastle et al., 2005), transition forests and old fields would eventually succeed to mixed-deciduous forests of oak, hickory, and elm (Hoagland et al., 1999). Therefore, plot types represented a successional range of ecosystem types in this region and a chronosequence of growth from old field to old-growth forest.

Common herbaceous plants in old fields include *Ambrosia psilostachya*, *Andropogon virginicus*, *Aristida oligantha*, *Aster ericoides*, and *Festuca arundinacea* (Tunnell et al., 2004). Post oak (*Q. stellata*) and winged elm (*Ulmus alata*) were the most common trees in both forest types, comprising 89% and 61% of overstory trees in old-growth and transition forests, respectively. All plots were located in well-drained, sandy loam soils of the Chigley (Ultic Paleustalfs) and Durant (Vertic Argiustolls) soil series (US Department of Agriculture, 1973).

I used litter bags to quantify decomposition among ecosystem types, adding one of three types of litter to bags, either (1) mixed herbaceous biomass from old-fields, (2) senesced (but not abscised) *Quercus* leaves collected from trees in old-growth forest fragments, or (3) commercially available, untreated bark and wood chips (Ozark Wood International, Inc., Pineville, MO, USA), approx. 1 × 1–10 cm in size, of *Carya* spp., a genus common to the area. Similar volumes of litter were placed inside bags but mass of wood differed from herbaceous and leaf litter ($P < 0.001$) due to the density of wood; (mean grams ± 1SE) 6.9 ± 0.04, 7.1 ± 0.02, and 40.1 ± 0.2 for herbaceous, leaf, and wood litter, respectively.

I manipulated detritivore access to litter following Mayer et al. (2005), using fine-mesh (0.3 mm) nylon bags to excluded macro-detritivores (e.g. Arthropoda, Isopoda, Gastropoda, Annelida) and using coarse-mesh (6.3 mm) nylon bags to allow macro-detritivore access to litter.

In May 1999, 36 litter bags were placed randomly on the ground surface in each of the 12 plots ($N = 432$) in a complete factorial design where mesh size (fine and coarse) was crossed with litter type (herbaceous, leaf, and wood) with 6 replicates in each plot. Initial litter C:N ratios were (mean ± 1SE) 73.5 ± 2.5, 65.4 ± 1.3, and 98.6 ± 5.5 for herbaceous, leaf, and wood litter, respectively. One bag from each combination of mesh size and litter type was retrieved from each plot in random order every 2 months until May 2000 (6 collections). Thirty-five litter bags were excluded from the experiment because of loss, damage by animals, or contamination with