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Rate of litter decay and litter macroinvertebrates in limed and unlimed forests of the Adirondack Mountains, USA

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ABSTRACT

Acid deposition can reduce the rate of litter decay in forests by changing environmental and substrate quality for macroinvertebrates and microbes. Terrestrial application of lime can ameliorate many of the negative effects of acid deposition, but the effects of liming on forest litter decay and fauna are poorly understood. We used reciprocal transplants of litter bags to better understand the effects of substrate calcium content and incubation context (limed plots versus unlimed plots) on rate of litter decay and abundance of litter-dwelling macroinvertebrates. Our study took place in the Adirondack Mountains (Adirondacks) of New York State, USA, a region affected by chronic acid deposition. Lime was added to randomly-selected plots at a rate of 10 Mg ha^{-1}; control plots were not limed. Leaves for high-calcium litter bags were collected under trees grown in limed plots, and leaves for low-calcium litter bags were collected in unlimed plots. High-calcium and low-calcium leaves differed in %Ca but not in %N or C:N at the beginning of our study. Leaf litter decay was faster for bags containing high-calcium leaves than for those litter bags containing low-calcium leaves, and decay was slower in limed than unlimed plots. Assemblages of litter-dwelling macroinvertebrates were markedly different between litter bags collected from limed and those collected from unlimed plots. Snails increased in abundance; whereas, millipedes and spiders decreased in abundance at limed plots following liming. Millipedes likely were important litter-eating macroinvertebrates at these sites, and the decline in millipedes may have contributed to the reduction in rate of litter decay. The liming of areas negatively affected by acid deposition may decrease rate of litter decay immediately following lime application. This was a short-term study. Understanding the long-term, as well as immediate, effects of liming is necessary to determine the advisability of lime application in regions affected by acid deposition.

1. Introduction

Anthropogenic acid deposition and the associated depletion of cations from soils have affected the chemistry and biota of ecosystems in certain regions (Driscoll et al., 2001). Recent regulations on the emission of air pollutants have led to a reduction in the deposition of sulfate and increased precipitation pH in North America (Driscoll et al., 2003) and Europe (Kopacek and Vesely, 2005; Matzner and Meiwes, 1994). These improvements have been reflected in the improved quality of surface water (Bouchard, 1997). However, the exchangeable calcium and pH of soils in areas historically affected by acid deposition have not convincingly increased (Warby et al., 2009; Wesselink et al., 1995; but see Lawrence et al., 2012), potentially prolonging the recovery of terrestrial ecosystems despite improvements to air and surface water quality.

Soil acidification can affect litter decay and mineralization of nutrients, partly by changing the quality of the habitat for soil organisms. Increasing soil acidification was associated with reduced rates of carbon mineralization in Sweden (Persson et al., 1989), and decreasing soil acidification was associated with an increase in litter decay in a Czech forest (Oulehle et al., 2011). The mechanisms by which acidification affects the breakdown of litter are complex and include shifting the microbial community from bacteria to fungi (Pennanen et al., 1998; Rousk et al., 2009) and changing the composition of the bacterial community (Persson et al., 1989). Acidification also decreases the quality of the environment for certain soil and litter macroinvertebrates, which play an important role in litter decay by fragmenting litter and increasing its availability to microbes (Coleman et al., 2004; Gießelmann et al., 2010; Wall et al., 2008). For example, snails, isopods, and certain earthworms have high calcium needs and have been negatively affected by ambient or simulated acid deposition, probably

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because it leads to leaching of calcium (Ammer and Makeschin, 1994; Kuperman, 1996; Tompson et al., 2013; Wäreborn, 1992).

The application of buffering geological substrates such as crushed limestone (liming) has been used as a mitigating strategy to improve water quality and the health of forests affected by acid deposition (Farmer, 1992). In northeastern North America, liming has frequently been used to improve the vigor of stands of sugar maple (*Acer saccharum* Marsh.) growing on base-poor soils, particularly those affected by anthropogenic acid deposition. Long-term studies have demonstrated that liming can positively affect vigor (Huggett et al., 2007; Juice et al., 2006; Wilmot et al., 1996) and net primary productivity (Gradowski and Thomas, 2008) of sugar maple trees. Liming also may affect leaf litter decay through changes in microbial or invertebrate communities. Liming shifted the microbial community from fungi to bacteria in a temperate spruce forest, opposing the shift typically observed during soil acidification (Zelles et al., 1990), and Bååth and Arnebrandt (1994) found that liming caused a change in the community of bacteria in a coniferous soil in Sweden. Terrestrial liming also has been associated with a decrease in the abundance of oribatid mites (Hågvar and Amundsen, 1981) and collembolans (Chagnon et al., 2001; Hågvar, 1984; Haimi and Mätäsniemi, 2002), two taxa that play an important role in litter decay. Conversely, liming may increase the abundance of snails and certain earthworms (Gärdenfors, 1992; Potthoff et al., 2007), and Tompson et al. (2013) found that soil liming improved growth and survival of isopods living on acidic soils.

Studies of the effect of liming on rate of litter decay have yielded mixed results, with some studies finding that liming enhanced decomposition, at least at certain doses (Marschner and Wilcynski, 1991; Geissen and Brűmmer, 1999), and others finding no effect (Bååth et al., 1980; Smolander et al., 1996). Liming has generally led to an increase in microbial activity and CO_2 evolution (Bååth and Arnebrandt, 1994; Kreutzer, 1995), but this effect has varied with soil C:N ratio (Persson et al., 1990/1991) and soil type (Neale et al., 1997). Thus, the response of litter decay to liming seems to vary among forests and may be dependent on the response by the ambient biological community. Additionally, most studies of the effects of liming on litter decay, like most studies of the effect of liming on forest biota, have been conducted in coniferous forests of Europe. The applicability of those results to deciduous forests of North America is unclear.

We aimed to better understand the complex influence of liming on rates of litter decay and macro-invertebrate abundance in a forest affected by acid deposition. We used reciprocal litter transplants to discern the influence of substrate and incubation environment on leaf-litter decay at limed and unlimed plots over two years immediately following the application of lime to a forest in the Adirondack Park, New York State, USA. We used litter-packs with apertures large enough to allow entry by macroinvertebrates and extracted macroinvertebrates from bags to better understand the role of macroinvertebrate decomposers in any observed effects.

2. Materials and methods

2.1. Site description

The study was conducted at four sites near the Hamlet of Old Forge, Herkimer County, within the Adirondack Park (Adirondacks) in northeastern New York State (43°44′N and 74°58′W). The Adirondack Park is an approximately 2.5-million-ha reserve with mixed public and private lands. The Adirondacks receive a great deal of acidic deposition and have been strongly affected due to a generally base-poor geology (Jenkins et al., 2007). Our sites were set within property managed by a local municipality, the Town of Webb, for multiple uses, including timber extraction, snowmobile traffic, and gravel mining. Timber was most recently harvested from all sites in the 1970s (S. Bick, Northeast Forests, LLC, pers. comm.). Each site included a stream, and sites were separated by ⩾200 m. Common tree species in this forest included American beech (*Fagus grandifolia* Ehrh.), red maple (*Acer rubrum* L.), yellow birch (*Betula alleghaniensis* Britton), and white spruce (*Picea glauca* [Moench] Voss). Soils were spodosols and had low buffering capacity (Kuhl et al., 1975). The pH of the soil O horizon at our sites was 3.65 ± 0.09 units prior to liming (R. April, Colgate Geology, pers. comm.).

2.2. Incubation context

At each site we established two 0.16-ha circular plots separated by 50 m, such that one plot was on either side of the stream at the site. One plot from each site was randomly selected to receive lime. Agricultural-grade crushed limestone (CON-LIME, Bellefonte, Pennsylvania, ⩾93% $CaCO_3$) was spread by hand and shoulder-mounted spreaders at these plots at a target rate of 10 Mg ha^{-1} over three equal applications in September 2005, April 2006, and September 2006. Multiple applications were used to moderate the severity of the changes accompanying addition of lime and to allow lime to become gradually incorporated into the litter layer. Collection pans placed at each limed site indicated a rate of application not significantly different than the target rate (7.8 ± 5.2 Mg ha^{-1}). In autumn 2006, the pH of the soil O horizon was 6.48 ± 0.27 at limed plots (R. April, Colgate Geology, pers. comm.).

2.3. Litter-bag experiment

Rate of litter decay was estimated using the litter bag method (Falconer et al., 1933). We used a reciprocal transfer protocol, where both high-calcium and low-calcium substrates were placed at both limed and unlimed incubation plots. High-calcium leaves were collected from near the center of limed plots and low-calcium leaves were collected near the center of unlimed plots in October 2006. In both cases, falling leaves were captured using raised netting to minimize colonization by soil organisms. Litter was returned to the lab, separated by species, and air dried. A subsample of leaves collected from each site was analyzed for initial litter chemistry. Leaves were processed in a Wiley Mill (#40 screen, Thomas Scientific, Swedesboro, NJ, USA), analyzed for initial calcium content using inductively coupled plasma atomic emission spectroscopy (PerkinElmer Life and Analytical Sciences, Inc., Waltham, Massachusetts, USA) following wet digestion (Parkinson and Allen, 1975). Apple leaves were used as a standard (National Institute of Standards and Technology No. 1515). Initial %N, %C, and C:N were determined using a Costech Elemental Analyzer (Valencia, California). Species within litter bags were analyzed together for %N, %C, and C:N.

Litter bags were constructed using nylon mesh bags with an inside diameter of approximately 20 cm and aperture size of ⩽10 mm, depending on the direction of tension. Each litter bag included 1.50 g (to the nearest 0.01 g, air-dried mass) of each of the three most common species at our sites: red maple, American beach, and yellow birch. A set of litter bags consisted of 10 bags: one high-calcium bag and one low-calcium bag for each of five collection dates: 4 May 2007 (t1), 16 July 2007 (t2), 13 November 2007 (t3), 2 July 2008 (t4), and 14 October 2008 (t5). A set of litter bags was placed at five random points within each of our eight plots for a total of 400 litter bags. Thus, our experimental design was a two-way crossed design with repeated measures. Each plot was considered a sample unit, and points within a plot were considered subsamples. Sites were used as a blocking factor to control