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Site of leaf origin affects how mixed litter decomposes

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Abstract

Recent studies have demonstrated that mass loss, nutrient dynamics, and decomposer associations in leaf litter from a given plant species can differ when leaves of that species decay alone compared to when they decay mixed with other species' leaves. Results of litter-mix experiments have been variable, however, making predictions of decomposition in mixtures difficult. It is not known, for example, whether interactions among litter types in litter mixes are similar across sites, even for litter mixtures containing the same plant species. To address this issue, we used reciprocal transplants of litter in compartmentalized litterbags to study decomposition of equal-mass litter mixtures of sugar maple (*Acer saccharum* Marshall) and red oak (*Quercus rubra* L.) at four forest sites in northwestern Connecticut. These species differ significantly in litter quality. Red oak always has higher lignin concentrations than maple, and here C:N is lower in oak leaves and litter, a pattern often observed when oak coexists with maple. Overall, we observed less mass loss and lower N accumulation in sugar maple and red oak litter mixtures than we predicted from observed dynamics in single-species litterbags. Whether these differences were significant or not depended on the site of origin of the leaves ($P<0.02$), but there was no significant interaction between sites of decay and the differences in observed and predicted decomposition ($P>0.2$) . Mixing of leaf litter types could have significant impacts on nutrient cycling in forests, but the extent of the impacts can vary among sites and depends on the origin of mixed leaves even when the species composition of mixes is constant.

Keywords: *Acer saccharum*; *Quercus rubra*; Decomposition; Litter-mix experiments; Site quality; Litter quality; Mixed-species litter; Litterbags; Reciprocal transplants

1. Introduction

Plant litter decomposition is critical for nutrient cycling and productivity in terrestrial ecosystems. Because leaves from multiple plant species intermix in diverse systems, the decomposition literature has recently begun to examine the dynamics of decay in litter mixtures (reviewed by Gartner and Cardon, 2004). This research has shown that adjacent litter of different species often interacts during decomposition such that mass loss and nutrient dynamics are altered from values predicted based on decomposition of single-species leaf litter alone. Results of litter-mix experiments, however, can be contradictory, making prediction of effects of mixing on decomposition difficult. It is not yet clear whether interactions among litter types in litter mixes are similar across sites—even for the same mixtures of species. Here, we begin to address this question by examining decomposition dynamics in mixtures of sugar maple and red oak litter using reciprocal transplantation and field incubation of litterbags containing sugar maple and/or red oak leaf litter collected from four forest sites in northwestern Connecticut.

The properties of soils can influence decomposition of leaf litter indirectly through their influence on the characteristics of the leaf litter entering the ecosystem (Carreiro et al., 1999; Hattenschwiler and Vitousek, 2000), and directly by altering the microclimate or nutrient environment in which litter decomposition occurs. For example, soil nutrient availability can influence decomposer biomass

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(Schaefer and Schauermann, 1990; Raubuch and Beese, 1995) and microbial activity (Rastin et al., 1990). Such soil-related properties have been shown to be important for decay of single species, with leaf litter decay often faster on more nutrient-rich sites (Swift et al., 1979; Prescott, 1996), though not all litter types respond similarly to soil nutrients (Vesterdal, 1999). Both soil properties and the presence of other plant species can influence litter decomposition. Thus, interactions among adjacent litter types in mixtures may be influenced indirectly or directly by soil-driven chemical, physical, and biological changes within and around litter mixtures.

To begin separating the influence of leaf quality from the influence of surrounding litter and soil characteristics on interactions among leaves in decomposing litter mixes, it is important to identify plant species that differ in initial litter quality and that co-occur on a variety of soil types. Red oak (*Quercus rubra* L.) and sugar maple (*Acer saccharum* Marshall) are very common, economically important deciduous tree species that co-occur throughout eastern deciduous forests. They have been reported to have very different litter quality, with sugar maple having much lower lignin concentrations than red oak (McClaugherty et al., 1985; Ferrari, 1999). Nitrogen concentrations are often higher in sugar maple than in red oak litter (Boerner and Rebbeck, 1995; Heckman and Kluchinski, 1995; Wedderburn and Carter, 1999), but this pattern is not universal (Cote and Fyles, 1994; Hansen, 1999). In northwestern Connecticut, within only a few kilometers, these species can be found together on both calcareous and acidic soils where forest composition and soil nutrient availability are distinct and have been well documented (van Breeman et al., 1997; Finzi and Canham, 1998). The combination of the wide distribution of these species on contrasting soil types and their divergent litter quality make sugar maple and red oak ideal for examining effects of leaf litter quality and soil characteristics on mass and nitrogen dynamics in mixes of decaying leaf litter.

2. Materials and methods

2.1. Study sites

Four secondary forest sites where both sugar maple and red oak were abundant were selected at elevations of 200–300 m in northwestern Connecticut (~42°N, 73°15′W). Climate is temperate, and is similar at all sites. Soils are well-drained sandy loams; two of the sites (Point of Rocks and Lower Canaan Mountain) have calcareous soils and are derived from marble parent material, while the other two sites (Cobble Hill and Upper Canaan Mountain) have acidic soils derived from schist (Gonick and Shearin, 1970). Topographic heterogeneity increases at the four sites in the order of Lower Canaan Mountain < Upper Canaan Mountain < Cobble Hill < Point of Rocks. Litterbags were placed in areas that sloped 0–5°.

2.2. Litter collection and litterbag construction

At each site, freshly senesced leaves of sugar maple and red oak were collected from the top surface of the litter layer. Leaves were gathered by hand during peak litterfall in October 2001, shortly after leaf drop and before any rainfall, to minimize mass and nutrient loss before collection. Latex gloves were worn during all leaf handling to avoid contamination of the leaves with excess nitrogen. Gathered leaves were oven-dried at 65 °C for a minimum of 24 h, or until constant weight, since homogeneity among leaf samples improves by oven-drying rather than air-drying (Ruvinsky, 1995; Byard et al., 1996).

Litterbags 15 cm on a side were constructed of fiberglass windowscreen (1 mm mesh) and 2-lb fishing line. During decomposition, leaf litter can become matted and firmly stuck together, particularly in later stages of decay, making separation of component litter types in mixes unreliable. Litter from different tree species, therefore, was separated using a fiberglass mesh partition within each litter bag. Litterbags were carefully filled with 3 g of oven-dried leaves; though leaves were not rehydrated before placement inside the litterbags, damage of leaf material due to brittleness was minimal. Litterbags contained 1.5 g of (1) sugar maple leaves in top and bottom layers, (2) red oak leaves in both layers, or (3) sugar maple leaves in the bottom layer and red oak leaves in the top. This layering in mixed-species litter bags mimics natural layering of leaves in these forests resulting from differences in the timing of litterfall (Gartner, personal observation).

A total of 1152 bags were deployed in early December 2001, and were immediately covered by the first snowfall. In all, 48 bags (3 litter combinations, each containing litter from one of the four sites, for harvest at four time points: $3 \times 4 \times 4 = 48$) were placed in random order beneath six red oak trees at each of the four sites. Placing bags only under oak canopies simplifies analysis of site influences on decomposition by avoiding potentially dramatic effects of canopy tree species (e.g. sugar maple vs. oak vs. hemlock) on decomposition within bags. Litterbags were arranged in two rows in an arc approximately 3 m from the north side of the trunk, a distance that ensured litterbags were away from the main trunk yet still beneath the oak canopy. Litterbags were fastened flat to the litter layer surface by steel landscape staples so that upper layers of leaves in bags remained on top throughout the experiment. A single litter trap (42.5 cm diameter plastic container, 45 cm deep, lined with concave fiberglass windowscreen) also was deployed beneath each of the six oak trees at each site. To assess litterfall amounts, litter was collected from the traps every 2 weeks during October and November 2002.

Every three months, six replicates of each type of litterbag were destructively harvested, one from under each oak tree at each site. Each harvested litterbag was brushed clear of external soil and litter, placed in a paper bag, and oven dried at 65 °C. After reaching constant mass, litterbags were cut open and leaves from each layer were weighed. Mass loss in