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CONSUMPTION AND DECOMPOSITION OF LICHEN LITTER IN A TEMPERATE CONIFEROUS RAINFOREST

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Abstract: Nylon mesh litter-bags markedly reduced the rate of weight loss of lichen litter, as compared to unconfined (free) lichens, suggesting that herbivores and detritivores larger than the mesh size make a significant contribution to the disappearance of lichen litter. The half-life of free lichen litter was 1-5 months for *Alectoria sarmentosa,* 2-5 months for *Hypogymnia inactiva,* 3-5 months for *Platismatia glauca,* and 7 months for *Lobaria oregana.* The half-lives were 2–9 times longer for the same species in litter-bags. Because *A. sarmentosa* showed the greatest difference between free litter and litter-bags, we conclude that, of the four species studied, it had the highest rate of consumption by larger herbivores and detritivores.

Introduction

As part of developing a method for using epiphytic litterfall to estimate the abundance of epiphytes in tall conifer forests, we studied the rate of weight loss from the standing crop of epiphyte litter. Specifically, we needed to know the residence time for epiphyte litter on the forest floor. Very little is known about the decomposition rates of lichens (Esseen 1985; Guzman et al. 1990; Moore 1984; Wetmore 1982; Renhorn & Esseen 1992; Renhorn & Esseen, unpublished).

Traditional studies of decomposition rates enclose samples in litter-bags that exclude all but the smallest animals. If a significant amount of lichen litter is eaten by herbivores and detritivores larger than the mesh size, then litter-bags will underestimate the natural rate at which lichens are lost from the litter. Preliminary field observations suggested that this is true. Lichen litter downed in storms apparently lasts less than 1 year. However, lichens in litter-bags in the same ecosystem typically last more than 1 year (F. Rhoades and G. Carroll, pers. comm.). These observations suggest that processes besides microbial decomposition are important in the disappearance of lichen litter. To test this hypothesis we compared weight loss between lichen samples free on the forest floor and samples enclosed in litter-bags.

Materials and Methods

Litter-bags were sewn from 20 x 20 cm squares of I-mm mesh nylon netting. The mesh size was chosen to conform with the most commonly used material for litter-bag decomposition studies. Lichen samples were collected from nearby trees and shrubs. 'Free' lichens were not placed in litter-bags, but were tagged by tying a red nylon polyester thread onto the sample. Lichen samples weighed 3–12 g for *Lobaria oregana,* 2–9 g for *Alectoria sarmentosa,* and 1–3 g for *Platismatia glauca* and *Hypogymnia inactiva.*

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TABLE 1. *Repeated-measures analysis of variance of the percentage of lichen biomass remaining*

Source of variation	Sum of squares	DF*	Mean square	F-Ratio	*p*
Blocks					
Subject‡	6659	14	476	2.8	0.001
Main effects					
Litter-bags or not	149 548	1	149 548	871.1	0.000
Time	56 846	1	56 846	331.1	0.000
Species	25 170	3	8390	48.9	0.000
Interactions					
Time x litter-hags	7	1	7	*0.0*	0.843
Time x species	4755	3	1585	9.2	0.000
Litter-bags x species	22 954	3	7651	44.6	0.000
Time x litter-bags x species	6060	3	2020	11.8	0.000
Residua1	35 536	207	172		

*DF, degrees of freedom.
‡'Subject' partitions out the variation due to consistent differences between individual lichen samples.

Litter samples were placed along a transect of 15 points through an old-growth forest near Lookout Creek in the H. J. Andrews Experimental Forest, east of Eugene, Oregon, in the Cascade Range. The purpose of the transect was to make relocating the samples easier. Samples were not pinned down in any way, but windspeeds on the floor of these dense, valley-bottom forests are not high enough to disperse the samples.

The dominant tree species were *Pseudotsuga menziesii* (Mirbel) Franco, *Tsuga heterophylla* (Raf.) Sarg., and to a lesser extent, *Thuja plicata* Donn. The species list of epiphytes in Pike *et al.* (1975) is representative of the species occurring in this stand. At this site, the average annual temperature is 9,5°C, with January and July means of 2°C and 22°C, respectively (Waring *et al.* 1978). The average annual precipitation is 240 cm with 70% of that from November through March.

At each transect point we placed one sample of each treatment of each species. Thus, 15 replicates were used for each combination of treatments, for a total of 15 *x* 2 treatments x 4 species *x* 2 times = 240 data points. Over the course of the experiment, three data points were lost because of uncertainties in the field.

The samples were placed on the forest floor on May 28 of 1991, reweighed in October of the same year, then reweighed in May of the following year, keeping track of each sample's identity. In almost all cases the test samples were relocated without ambiguity; where ambiguity existed these samples were excluded from further analysis. Weights were recorded to the nearest 0.01 g after air-drying indoors for 24 h, rather than as oven-dry weights, to avoid killing the thalli by the drying procedure. Foreign material such as bryophytes and conifer needles were removed before weighing, but no attempt was made to remove small animals. Very little lichen thallus was lost in the process of cleaning and weighing. Samples were then returned to the field. Results were expressed as percentage of the original weight remaining at sampling times 1 and 2 (October of year 1 and May of year 2). These data were analysed with repeated-measures (' within-subjects ') analysis of variance (ANOVA), based on the repeated weighing of individual samples (' subjects ').

Results and Discussion

The biomass of lichen litter decreased with time, but at a faster rate in free samples than in the litter-bags (Table 1, Fig. 1). Species differed considerably in their rates of weight loss. The results are explained in more detail by working

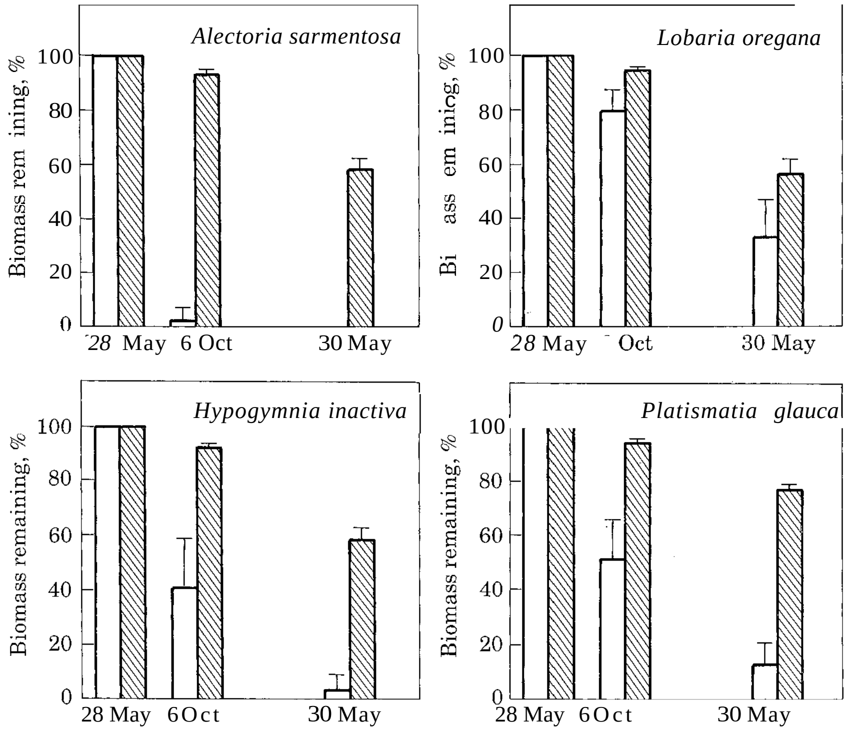

FIG. 1. Percentage of lichen biomass enclosed in litter-bags (hatched bars) and free lichen samples (open bars) remaining after 4 and 12 months on the forest floor. Error bars represent 95% confidence intervals for the means.

through the ANOVA (Table 1). Figure 1 supplements the interpretation by indicating the size of the effects in the ANOVA.

There were consistent differences in biomass loss rates between individual lichen samples, as shown by the blocks (' subjects ') in the ANOVA. These differences probably relate to the particular microsites in which the samples were placed. Because the 'subjects' term was significant, it is clear that the repeated-measures design made a substantial contribution toward reducing the error sum of squares (' residual 'in Table 1).

Placing the lichen samples in the litter-bags strongly decreased the rate of weight loss (main effect: litter-bags). It was predictable that the weight loss changed with time (main effect: time). Different species lost weight at different rates (main effect: species), with A. sarmentosa diminishing the fastest, followed by H. inactiva and P. glauca; L. oregana had the least weight loss. These results can also be expressed as half-lives, i.e. the time elapsed until half of the initial biomass remained (Table 2) based on a linear or exponential decay function (depending on which gave a better fit in each case). These rates of weight loss from the temperate rainforest of Oregon were fairly similar to those of lichen litter in the boreal forest in Sweden (Renhorn & Esseen, unpublished), except

TABLE 2. *Approximate half-lives (months) of lichen litter in western Oregon, USA*

Species	Free	Litter-bags
Alectoria sarmentosa	1.5	14
Hypogymnia inactiva	2.5	14
Platismatia glauca	3.5	24
Lobaria oregana	7.0	13

that our *Alectoria* in litter-bags decomposed more slowly than theirs (half lives of *c.* 14 months vs. 4 months). Similarly, both studies also showed relatively slow decomposition rates for *P. glauca.* Pike (1971) using three different lichen species in an oak forest, found half-lives of 3–7 months for samples in litter-bags, with *Lobaria pulmonaria* decomposing half as fast as *Usnea* and *Ramalina. Pseudocyphellaria* and *Sticta* species lost half their weight from 1-mm mesh bags in ***3*** to over 12 months in a southern Chilean forest (Guzman *et al.* 1990).

The proportionate effect of the litter-bags did not change with time (interaction: time x litter-bags, not significant; Table 1). The litter-bag effect, therefore, neither accentuated or diminished with time. The differences among species, however, were not consistent over time (time x species).

The effect of litter-bags was not consistent among species (litter-bags x species). In particular, litter-bags had the greatest effect on loss of *Alectoria,* suggesting that *Alectoria* was most heavily predated by organisms larger than the 1-mm mesh size. *Lobaria* had the opposite pattern, showing the least difference between free samples and samples in litter-bags, suggesting little or no consumption by larger organisms. It seems likely that both lichen substances and nutritional content of the lichens would affect their rate of consumption; however, no data are available to demonstrate this. The rapid disappearance of *Alectoria* from the free samples may result from its tendency to fragment readily; however, the relatively rapid weight loss of *Alectoria* from the litter-bags suggests that it is prone to rapid decomposition. Certainly, it has a high ratio of surface area to volume, favouring rapid decomposition.

The three-way interaction among time, litter-bags, and species suggests that at least some of the two-way interactions are not consistent across levels of the third factor. Taken together these results show a clear dependence of weight loss on three highly interactive factors.

This simple experiment implies that herbivores and larger detritivores are at least as important as microbes and small arthropods in the removal of lichen litter. Further work should be initiated to identify the organisms responsible. The leading candidates include: deer *(Odocoileus hemionus),* whose taste for *Alectoria* has been documented (Stevenson & Rochelle 1984); elk *(Cervus canadensis);* rodents, including flying squirrels *(Glaucomys sabrinus)* and voles *(Clethrionomys;* Maser 1988; Renhorn & Esseen, unpublished); earthworms (D. H. Brown, pers. comm.); slugs and snails, well known consumers of lichens; and arthropods.

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