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Decomposition of pure and mixed foliage litter in a young lodgepole pine – Sitka alder stand in the central interior of British Columbia

P.T. Sanborn and R.P. Brockley

Abstract: A 7-year litterbag experiment examined mass loss dynamics of Sitka alder (*Alnus viridis* (Chaix) DC. subsp. *sinuata* (Regel) A. Löve & D. Löve) and lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm. ex S. Watson) foliage litter in a young stand dominated by these species in the Sub-Boreal Spruce biogeoclimatic zone of central British Columbia. Although mass loss was initially faster for alder litter, the amounts of mass remaining for alder, pine, and mixed pine–alder (50:50 by mass) litter began to converge after 2 years. Mass loss by the mixed litter differed significantly from that predicted from the behaviour of its pure components, but the mechanisms responsible could not be determined from this experiment. Limit values for the projected maximum extent of mass loss ranged from 63.5% (alder) to 76.9% (pine), with the latter value considerably below estimates reported for lodgepole pine in Scandinavia. Despite these differing limit values, forest floor mass measurements prior to the experiment did not show significantly higher organic matter accumulations under long-established alder clumps on this site.

Résumé : Des sacs de litière ont été utilisés pendant sept ans pour étudier la dynamique de la perte de masse des litières de feuille d'aulne vert de Sitka (*Alnus viridis* (Chaix) ssp. *sinuata* (Regel) A. Löve & D. Löve) et de pin tordu latifolié (*Pinus contorta* Dougl. var. *latifolia* Engelm.) dans un jeune peuplement dominé par ces deux espèces et situé dans la zone biogéoclimatique de la pessière subboréale du centre de la Colombie-Britannique. Même si la perte de masse était initialement plus rapide dans la litière d'aulne, les masses résiduelles de litière d'aulne, de litière de pin et de litière de pin et d'aulne mélangée (50:50 en poids) commençaient à converger après deux ans. La perte de masse de la litière mélangée était significativement différente de la prédiction faite à partir du comportement de ses composantes pures mais le mécanisme responsable ne pouvait être déterminé dans le cadre de cette étude. Les valeurs limites de l'étendue maximum projetée de perte de masse allaient de 63,5 % (aulne) à 76,9 % (pin), cette dernière valeur étant considérablement inférieure aux estimations rapportées pour le pin tordu latifolié en Scandinavie. Malgré ces valeurs limites différentes, les mesures de masse de la couverture morte avant le début de cette étude indiquaient que l'accumulation de matière organique n'était pas significativement plus élevée sous les bouquets d'aulne établis depuis longtemps dans cette station.

[Traduit par la Rédaction]

Introduction

Sitka alder (*Alnus viridis* (Chaix) DC. subsp. *sinuata* (Regel) A. Löve & D. Löve) is a common shrub species in lodgepole pine (*Pinus contorta* Doug. ex Loud. var. *latifolia* Engelm. ex S. Watson) forests in the central and southern interior of British Columbia (BC) (Haeussler et al. 1990). As a nitrogen (N)-fixing species, Sitka alder can offset N losses as a result of fire, harvesting, and site preparation. Because of its moderate shade tolerance, a well-developed Sitka alder understory can persist under mature forest canopies (Wurtz 1995). Following clear-cut harvesting, increased light levels promote vigorous regrowth of the surviving alder clumps and competition for site resources (light, water, and nutrients) with conifer crop species (Haeussler et al. 1990). This rapid regrowth could result in alder-derived litter comprising a large proportion of total litterfall in young stands.

Although lodgepole pine litter decomposition has been studied both within the species' native range (Prescott et al. 2000*a*, 2004) and in Scandinavia (Berg and Ekbohm 1993; Berg and Laskowski 1997), these studies have not compared lodgepole pine and Sitka alder litters. Laboratory and field studies indicate that leaf litter of other alder species initially loses mass faster than other conifer and broadleaf litter types (Taylor et al. 1989; Fyles and Fyles 1993). Longer term (4 years) field studies suggest that this trend eventually re-

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verses, with cumulative mass loss for pine needles exceeding that for alder leaves (Berg et al. 1995).

Data obtained from litterbag experiments can be extrapolated to estimate the ultimate extent of mass loss. Such "limit values" (Berg et al. 1996; Berg 1998, 2000) can vary between species, as well as within species for litters obtained from stands with differing nutrient regimes. Explanations proposed to account for such patterns include the artificial exclusion of soil animals by litterbag mesh, increasing recalcitrance of organic compounds synthesized during decomposition, and incomplete assemblages of decomposer microorganisms in some settings (Berg et al. 1996). Species-related differences in limit values could have implications for relative long-term accumulation of forest floor organic matter under stands of differing species composition. Yet, it is not clear why extrapolations of litterbag experiments that seldom last more than 5 years should necessarily explain the size of organic matter pools in stands that could exist for many decades between major disturbances.

In field settings, litter mixtures are common. Several recent experiments have compared mass loss rates for pure and mixed substrates, including litter of broadleaf and coniferous trees, forest humus, and charcoal (Prescott et al. 2000*b*; Wardle et al. 2003, 2008; Gartner and Cardon 2004). Decomposing mixtures can display mass loss rates that are simple additive combinations of those of pure substrates, as well as rates that are nonadditive or interactive. Explanations for observed patterns have included species-related differences in the nutrient content and availability, and water retention properties of decomposing organic materials. Litter decomposition experiments involving mixtures of lodgepole pine and Sitka alder foliage litter have not been conducted, although such mixtures should be common in forest floors of interior BC forests.

This study used the litterbag method to address four aspects of litter decomposition in lodgepole pine and Sitka alder foliage litter in a young central interior BC forest:

(1) Do short- and longer-term mass loss patterns differ between foliage litters of these species?
(2) Do limit values differ for these litter types?
(3) Does the mass loss pattern for mixed litter display nonadditive effects?
(4) Can the results of this 7-year experiment be reconciled with measurements of forest floor mass under these species?

Methods

Location and site description

The study site is located approximately 55 km southwest of Prince George, B.C., (53°40′N, 135°39′W) within the Stuart Dry Warm variant (SBSdw3) of the Sub-Boreal Spruce (SBS) biogeoclimatic zone (DeLong et al. 1993). No climatic data are available for this site, but DeLong et al. (1993) cite mean annual precipitation of 494 mm and mean annual temperature of 2.6 °C for the SBSdw3 variant. Vegetation matches the submesic (04) site series for this variant. The site has a west aspect, with slopes ranging from 5% to 20% and a mean elevation of approximately 1030 m.

After logging of an approximately 150-year-old lodgepole pine stand in 1987 (Sanborn et al. 2002), the site naturally regenerated to a mixture of lodgepole pine and Sitka alder, with most of the latter originating from well-established clumps growing from substantial rootstocks. In 1995, the density of lodgepole pine was approximately 10 500 trees/ha (mean height 1.5 m), while the alder density averaged 4100 clumps/ha (mean height 1.8 m), with a mean alder cover of 51% (Sanborn et al. 2001). A thinning experiment was established in 1995, with four alder retention levels (0, 500, 1000, 2000 clumps/ha) superimposed on a uniform pine density of 1000 trees/ha. Alder cover in the highest-density treatment was initially reduced to 38.2% but increased to 45.1% in 1998 and 55.6% in 2001 (Brockley and Sanborn 2003).

Brunisolic Gray Luvisols are the dominant soil type at this site (Sanborn et al. 2001). The humus form most closely resembles a Hemimor (Green et al. 1993), with an abrupt lower boundary to the mineral soil. Qualitatively, the L and F horizons of the forest floor directly under the alder clumps consist almost entirely of decomposing alder leaves, seed cones, and twigs.

Field methods

Litterbags were constructed as in the Canadian Intersite Decomposition Experiment (Trofymow and CIDET Working Group 1998). In September 1996, senescent alder leaves and pine needles were collected at the study site on a clean tarpaulin by lightly shaking and brushing branches and stems. These materials were air-dried and the moisture content was determined (70 °C, 24 h). Litterbags were assembled by heat-sealing (National Instrument Co., model M-450-1) and stapling shade cloth (Synthetic Industries, product no. 525F/565) into 20 cm × 20 cm pouches after adding 10 g (air-dry weight) of pure alder leaf litter, pure pine litter, or a 50:50 mixture. The shade cloth has 0.25 mm × 0.50 mm openings and was cleaned by rinsing in dilute hydrochloric acid and demineralized water.

In October 1996, the litterbags were secured to the forest floor with aluminum nails in sets of three (one of each litter type) at 20 random locations in each of the three 0.08 ha plots of the 2000 alder clumps/ha treatment. Two sets of litterbags per plot were recovered at approximately 6-month intervals for 3 years, followed by annual recoveries for 4 years. On recovery, the bag contents were oven-dried (70 °C, 24 h) after removal of root detritus and weighed.

Forest floor mass was measured in 1995 prior to installation of the thinning experiment (Sanborn et al. 2001). Forest floors were sampled using a 20 cm × 20 cm frame at 15 random points in each of the 12 plots of the thinning experiment. The position of each sampling point was classified as either lying under the canopy of an alder clump or between clumps. Samples were air-dried, and woody components were removed and weighed separately. Only the nonwoody forest floor mass data are reported here and are presented on an oven-dry (105 °C, 24 h) basis.

Data analysis

Mass loss data were analyzed for each litterbag recovery as a randomized complete block design (with plots as

Table 1. Randomized block split-plot analysis of variance comparing observed vs. expected mass remaining for mixed litter.

Source	df	Mean square	F ratio	p value
Plot	2	1.904	—	—
Mixture	1	9.663	44.94	0.0215
Plot × mixture	2	0.215	—	—
Time	9	3047.218	183.03	7.89×10^{-16}
Plot × time	18	16.649	—	—
Mixture × time	9	22.89	1.82	0.1333
Plot × mixture × time	18	12.565	—	—
Subsampling error	59	23.094		

Note: The main-plot factor is mixture (mixed litterbag or average of two pure litterbags) and the split-plot factor is time.

blocks), with multiple comparisons adjusted using the Bonferroni method (Miller 1981).

The effects of litter mixing on mass remaining in litterbags were detected by comparing the observed mass remaining in the mixed litterbag with the average of the masses remaining in the two litterbags with pure alder or pine litter in each set. These observed and expected values were analyzed as a randomized block split-plot, with time as the split-plot factors and plots as blocks. The effect time was not handled as a repeated effect, since different litterbags were destructively sampled every 6 months.

Pretreatment forest floor mass in relation to position under or between alder clumps was analyzed as a randomized complete block design with plots as blocks.

Limit values (m) for mass loss were estimated by fitting the following equation to each litter type (i.e., species):

$$\mathrm{ML} = m[1 - \exp(-k_0 t/m)]$$

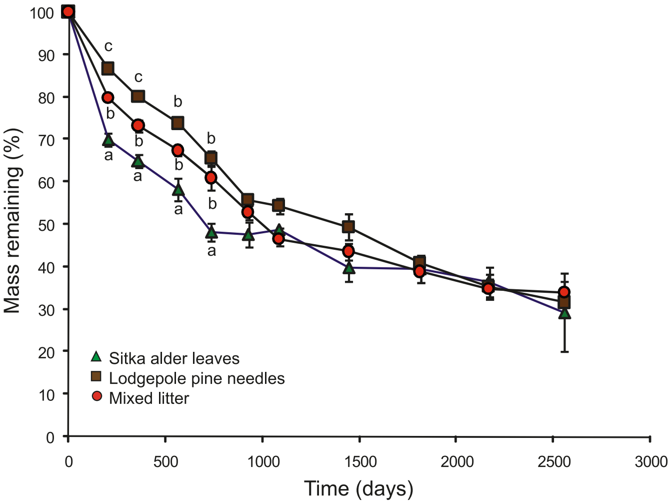
where ML is mass loss (%), k_0 is the initial mass loss rate, and t is time (days) (Berg and Ekbohm 1991). Differences in m parameters were tested using the extra sum-of-squares principle (Draper and Smith 1981); the fit of a model that allowed both m and k_0 to differ among the three litter types was compared with a model that allowed only k_0 to differ. All statistical analyses were performed with SYSTAT v. 10.2 software (Systat Software Inc. 2002).

Results

Although mass loss differed significantly by litter type during the first 2 years (Fig. 1), the patterns converged and showed no significant differences for the remaining 5 years of the litterbag experiment. Alder leaves consistently showed the greatest mass loss, and pine needles the least, during the first 2 years. During that time, the mixed litter showed an intermediate mass loss that differed significantly from alder leaves but did not differ significantly from pine after 1 year.

The observed versus expected mass remaining for mixed litter was significantly different (p = 0.0215), but the interaction between mixture and time was not significant (Table 1).

Fig. 1. Mass loss of litterbags by litter type (mean values for each recovery; n = 3). Means indicated with different letters are significantly different for a given recovery ($p < 0.05$).



Estimation of limit values (m) found that the model incorporating species-specific m provided the best fit ($F_{[2,172]}$ = 7.5, p = 0.0008). The limit values were 68.7% for mixed litter, 63.5% for alder leaves, and 76.9% for pine needles. Tests of the estimated parameters indicated that limit values differed significantly between alder and mixed litter and between alder and pine litter but not between the mixture and pine needles.

Forest floor mass in 1995 did not differ significantly ($F_{[1,11]}$ = 0.796, p = 0.393) between sampling locations under alder clumps versus between clumps: 5927 ± 397 g/m (n = 95) and 5555 ± 424 g/m (n = 85) , respectively (mean ± standard error).

Discussion

Do short- and longer-term mass loss patterns differ between foliage litters of these species?

In this study, as in other studies (e.g., Prescott et al. 2004), mass loss patterns for decomposing broadleaf and needle litter appear to converge well before the completion of this 7-year experiment, despite statistically significant differences during the first 2 years. This converging pattern occurred despite marked differences in the initial nutrient content and the morphology and particle size of the substrates.

Do limit values differ for these litter types?

Limit values calculated using Berg's methods suggest that

Table 2. Initial elemental concentrations (oven-dry basis) in litter materials used in litterbag experiment (data are the means of triplicate analyses) (Sanborn et al. 2001).

Element	Alder leaves (g/kg)	Pine needles (g/kg)
Nitrogen	14.7	5.6
Sulphur	0.77	0.41
Phosphorus	3.5	0.6
Calcium	13.1	7.1
Magnesium	2.6	0.8
Potassium	11.0	1.1
Manganese	0.9	0.9

alder and pine foliage litter differ in their ultimate extent of mass loss. The lower limit value for Sitka alder than for lodgepole pine is consistent with Berg's observation of inverse relationships between limit values and initial litter N content (Berg et al. 1996, 2001). The biological basis for this relationship may be an inhibitory effect of high N levels on the production of lignolytic enzymes (Berg et al. 1996). However, unlike Scandinavian data for lodgepole pine needle litter decomposition, which project almost complete mass loss with limit values approaching 100% (Berg and Ekbohm 1991), our estimate was much lower (76.9%).

In attempting to explain differences in limit values, considerable reliance has been placed on correlations with initial litter properties or environmental variables, despite the inherent limitations of this approach (Prescott 2005). For example, Berg et al. (1996, 2007) reported direct correlations between manganese (Mn) concentrations in litter and limit values and suggested that this relationship reflected the role of Mn in enzymatic lignin degradation. However, their data showed that this relationship was much weaker for litter types with Mn concentrations below 2 g/kg, which was more than twice the concentration in our lodgepole pine and alder litters (Table 2).

Several Canadian litter decomposition studies have included lodgepole pine needle litter but have not reported limit values, so comparative data from elsewhere in the native range of this species are lacking, making it difficult to assess the biological significance of this result. The limit value concept was based on and is still applied primarily in European research, so it would be useful to assess its significance in other settings, particularly as part of existing long-term studies with good documentation of environmental conditions and substrate characteristics (e.g., Canadian Intersite Decomposition Experiment (CIDET); Trofymow and CIDET Working Group 1998).

Does the mass loss pattern for mixed litter display nonadditive effects?

A comparison of the observed and expected values for mass remaining in the mixed pine–alder litter indicated a statistically significant difference, but the biological interpretation of this apparent nonadditivity is not obvious. The lack of significant difference in mass loss by littertype after 2 years, as shown in Fig. 1, and the lack of significant interaction of mixed litter with time, as shown in Table 1, suggest that there was no consistent direction or temporal pattern for any nonadditive effect of litter mixing. This result is considerably weaker than results reported in other studies, such as that by Wardle et al. (2008), who reported a much stronger and consistent direction of nonadditivity and proposed biologically plausible mechanisms to account for these observations.

Litter mixture decomposition studies that yield results of unclear biological significance may indicate the need for more sophisticated experimental designs, as in Wardle et al. (2003). Gartner and Cardon (2004) identified additional considerations, such as limitations of the statistical methods used to analyze the data, as well as litter mixing ratios and litterbag placement. The present experiment was not designed to examine microsite influences on decomposition, such as proximity of alder clumps, which would have been difficult given the substantial expansion in alder cover during the experiment (Brockley and Sanborn 2003).

Can the results of this 7-year experiment be reconciled with measurements of forest floor mass under these species?

Although the estimated limit values suggested that a unit of alder leaf litter should make a greater contribution to forest floor organic matter than a unit of pine needle litter, this was not confirmed by the 1995 forest floor mass data. Since the alder clumps were well established at the time of the 1987 harvest and since the site had not been broadcast-burned, much of the forest floor measured in 1995 under (and between) the alder clumps would have been a legacy of long-term accumulation of organic matter under a closed-canopy, mature pine forest with a persistent Sitka alder understory. If a lower limit value for Sitka alder than for lodgepole pine foliage litter has any direct relationship to long-term forest floor accumulation, it should have been apparent from measurements of forest floor mass in relation to alder clump proximity.

Part of this discrepancy may result from trying to relate relatively short-term decomposition rates, measured well before canopy closure, to forest floor mass data, which represent the much longer-term balance between litterfall and decomposition in a closed-canopy stand.

Another explanation may lie in the role of soil fauna in litter decomposition. Prescott (2005) noted that decomposition limits have been obtained only from experiments that excluded large soil fauna. Asymptotes for mass loss in litterbag studies may indicate the completion of microbially controlled decomposition, with further decomposition requiring other agents, such as soil fauna (Berg and Ekbohm 1991). Evidence for the importance of faunal involvement in litter decomposition in the SBS biogeoclimatic zone in central BC is limited. A short-term microcosm study found that the presence of mesofauna did not increase mass loss of leaf litter incubated with forest floors obtained from an SBS conifer stand in central BC (Cárcamo et al. 2001). A 24-month study of aspen (*Populus tremuloides* Michx.) leaf decomposition recovered soil mesofauna and fecal material from litterbags installed at three SBS sites, suggesting that these organisms were involved in decomposition (Kranabetter and Chapman 1999). Population estimates for mesofauna in forest floors from mature conifer stands at these three sites (Battigelli et al. 2004) were comparable to those elsewhere in the temperate zone, so the role of soil fauna in litter decomposition in central interior BC forests should not be discounted and requires further study.

Conclusions

Despite clear differences in the chemical composition and morphology of the initial lodgepole pine and Sitka alder foliage litter, mass loss trends began to converge after 2 years. Although an equal mixture of these litters exhibited a statistically significant nonadditivity in mass loss compared with the pure litters, the biological interpretation of this result was uncertain. Additional experiments are needed that would examine controls of decomposition processes in more detail, such as the composition of microbial communities in mixed versus pure litters and the role of microsite conditions.

Limit values for the maximum extent of decomposition were lower for alder than pine litter; however, the lodgepole pine limit value (76.9% mass loss) was well below the near-complete mass loss predicted by Scandinavian studies of this species. Estimates of limit values for lodgepole pine litter decomposition are needed elsewhere in its native range. Despite the contrasts in limit values between the alder and pine litters, longer-term implications for forest floor accumulation are unclear, as forest floor mass at this site was not significantly different under long-established alder clumps. Although the duration of this 7-year litterbag study was greater than many in the literature, this result raises doubts about the relevance of such experiments to longer-term (i.e., successional or rotation-length time scales) processes of organic matter accumulation in forest floors.

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