Discussion Paper

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Litter decomposition in B.C. forests: controlling factors and influences of forestry activities

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Abstract

Four commonly held beliefs about litter decomposition rates were tested in a suite of field experiments in B.C. forests: (1) decomposition is slower in cold (northern and high-elevation) forests, (2) decomposition is faster in clearcuts than in forests, (3) broadleaf litter decomposes faster than needle litter, and (4) decomposition is faster in N-fertilized forests. Litter decomposition was slowest in dry biogeoclimatic zones and fastest in wet zones. Overall, it appears that moisture is more limiting than temperature for litter decomposition across British Columbia. The effect of clearcutting on litter decomposition rates varied among forest types. Province-wide, mass loss of pine needle litter was significantly slower in clearcuts than in adjacent forests, but this difference disappeared after 3 years. Aspen leaves and forest floor material decomposed at similar rates in forests and clearcuts. Decomposition of broadleaf litter was slightly faster than needle litter during the first 2 years but slowed in subsequent years. After 3 years there was no significant difference between the mass remaining for broadleaf and conifer litter. In N-fertilized plots, higher N concentrations did not affect the rate of decay in litter or in forest floors. Many of our beliefs about litter decomposition and influences of forestry practices thereon should be revised in light of new empirical evidence.

KEYWORDS: *climate, biogeoclimatic zones, mixed-species forests, nitrogen fertilization, clearcut, British Columbia, mass loss, litter decay*

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Introduction

Decomposition of organic matter is one of the ecological processes critical to the functioning of forest ecosystems. Through the related processes of decomposition and mineralization, litter is broken down, and the carbon and nutrients within the litter are released into the forest floor where the nutrients are available for plant uptake. The rate and completeness of decomposition are primarily the result of microbial activity, but are also influenced by the composition and activities of the soil fauna (Figure 1). The community of soil organisms present and their activities are in turn related to environmental (largely climatic) conditions and the chemical and physical nature of the litter. By influencing any of these factors, forestry activities have the potential to alter rates of litter decomposition in forests. There are currently several commonly held beliefs about litter decomposition rates in B.C. forests and the effects of forestry practices on these rates. These beliefs, their basis in the literature, and the results of experiments that test their validity are described below.

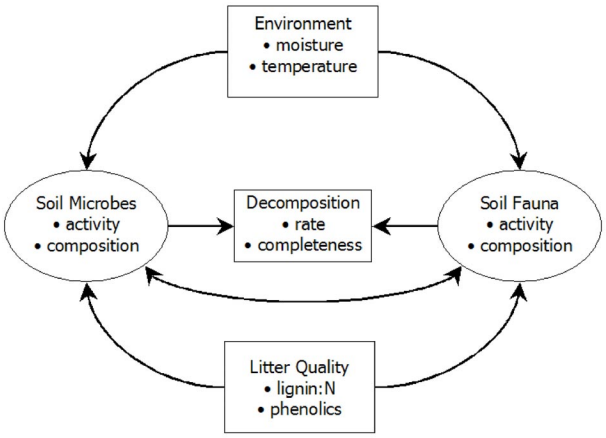

FIGURE 1. Factors that control the rate and completeness of decomposition. Source: Prescott *et al.* (2000b).

1. Decomposition is slowest in cold (northern and high-elevation) forests

It is often stated that litter decomposition is slow in cold forests (i.e., those forests at high elevation or northern latitudes), which leads to large accumulations of humus in these forests. This is true globally, i.e., comparing tropical and taiga forests (Kimmins 1997); however, it is not clear if this is true regionally, as in British Columbia. Laboratory experiments (Bunnell *et al.* 1976) have shown that adequate conditions of both temperature and moisture must be present for decomposition to proceed. Measures such as actual evapotranspiration (AET) that incorporate both temperature and moisture have been used successfully to predict rates of decomposition across a wide range of climates (Meentemeyer 1978). To date, no comparative studies of either litter decomposition rates or humus accumulations have been conducted across the range of climates in British Columbia.

2. Decomposition is faster in clearcuts than in forests

It is also generally believed that litter decomposition is faster in clearcuts than in undisturbed forests. Clearcutting forests often results in increased availability of nutrients (Bormann and Likens 1979; Vitousek *et al.* 1979; Smethurst and Nambiar 1990), which has been attributed to faster decomposition and mineralization of the residual organic matter (Covington 1981; Kimmins 1997). This, in turn, has been attributed to greater microbial activity resulting from the warmer, moister conditions in clearcuts (Edmonds and McColl 1989; Frazer *et al.* 1990). However, decomposition rates have been reported to be faster, slower, or the same in clearcuts compared with forests, depending on the regional climate (Yin *et al.* 1989). Further, the influence of clearcutting on decomposition rates may differ with depth in the forest floor (Binkley 1984; Yin *et al.* 1989).

3. Broadleaf litter decomposes more rapidly than needle litter

Another general belief is that broadleaf litter decomposes faster than needle litter and that a broadleaf component in a stand will hasten decomposition rates and nutrient cycling in forests for several reasons. First, broadleaf litter generally has higher nutrient concentrations and lower lignin and polyphenol concentrations than needle litter, and so would be expected to decompose faster (Perry *et al.* 1987; Peterson *et al.* 1997). Cornelissen (1996) found that leaves of deciduous species decomposed twice as fast as those of evergreens under controlled conditions. In the International Biological Program studies (Cole and Rapp 1981, cited by Perry *et al.* 1987), turnover of forest floor organic matter in temperate deciduous stands was more than four times faster than in temperate coniferous stands. Flanagan and Van Cleve (1983) found that birch (*Betula papyrifera* Marsh.) litter decomposed six times faster than spruce (*Picea mariana* [Mill.] B.S.P.) litter. However, other studies have not consistently reported

faster decomposition or N mineralization of broadleaf litter compared with needle litter (McClaugherty *et al.* 1985; Gower and Son 1992).

4. Decomposition is faster in N-fertilized forests

It is generally assumed that increasing N availability through fertilization will increase rates of litter decomposition. However, direct studies of the effects of N fertilization on decomposition rates have produced variable results, and indicate that external N supply has little effect on decay rate (Hunt *et al.* 1988; Prescott 1994). The effect of higher N concentrations in litter of a single species on decay rates is also unclear. Berg *et al.* (1987) found that greater N availability in pine needles stimulated decay in the early stages but inhibited decay during the later lignin decay phase, but Prescott (1994) found no influence. Prescott *et al.* (1992) suggested that decay of litter with low lignin and high labile C contents may be stimulated by fertilization, whereas decay of litter with high lignin and low labile C contents will not be affected.

The applicability of these four beliefs about litter decomposition rates and the influences of forestry practices on them to B.C. forests were tested in field experiments across the province. The results of these and related experiments have been presented in greater detail in the cited publications. Here we synthesize the key findings of interest to forest managers, scientists, and educators in British Columbia.

Materials and Methods

In all experiments, rates of litter mass loss were measured using the litterbag technique. Freshly fallen foliar litter was collected in 0.125-m^2 plastic trays with fibreglass mesh in the bottom to minimize leaching. For forest floor material, the litter layer was brushed away and the F layer, excluding any underlying humus or mineral soil, was collected. Litterbags were constructed of fibreglass screening and were usually 10 × 10 cm, with 1.5-mm rectangular pores. Bags used to contain forest floor material were made of mesh with 0.5-mm pores. Two grams of air-dried litter or forest floor were inserted into the bags and the open end was stapled shut. All bags were transported to sites in separate envelopes and spillage into the envelopes was weighed and subtracted from original weights. Bags containing foliar litter were pinned to the surface of the forest floor; bags containing forest floor material were horizontally buried in the lower F layer of the forest floor. At annual intervals for up to 5 years, seven bags of each type were collected from each plot. The contents of each bag were dried at 65°C, and the weight of litter remaining was measured. Significant differences were reported at $p < 0.05$ for all experiments.

Question 1: Is decomposition slower in colder biogeoclimatic zones?

Rates of decomposition of standard litter substrates were determined at 28 sites in nine biogeoclimatic zones across British Columbia (Table 1, Figure 2). Three litter types were selected to represent a range of substrate types: lodgepole pine (*Pinus contorta* Dougl.) needle litter, trembling aspen (*Populus tremuloides* Michx.) leaf litter, and forest floor material. The pine needle litter was collected from a lodgepole pine site in the Kananaskis Valley of Alberta described by Prescott *et al.* (1989). The aspen leaf litter was collected from a nearby aspen grove described by Taylor *et al.* (1989). The forest floor material was collected from a 125-year-old stand of Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco), western hemlock (*Tsuga heterophylla* [Raf.] Sarg.), and western redcedar (*Thuja plicata* Donn), in the University of British Columbia (UBC) Malcolm Knapp Research Forest near Vancouver, B.C. Thirty-five bags of pine needle litter and 21 bags of aspen leaf litter were installed at each site. Forest floor material was installed in 13 of the sites representing eight of the nine biogeoclimatic zones. Seven bags of pine and aspen were collected from each site annually for 4 and 3 years, respectively, and the dry weight of material remaining in each bag was measured. Forest floor material was collected annually for 4 years at most sites with the exception of the Boreal White and Black Spruce (BWBS) and Mountain Hemlock (MH) zones from which there were no collections during the third year. An Interior Douglas-fir (IDF) site was lost to fire after only 2 years of data had been collected.

Climatic measurements (annual mean temperature and total precipitation) during the incubation period were collected from the nearest B.C. Ministry of Forests Fire Weather Station. Data gaps were filled with corrected data from nearby weather stations. Mass loss rates were compared with simple and multiple linear regression analyses to determine the best relationship for predicting relative rates of decomposition in B.C. forests. Coefficients of determination (R^2), ANOVA F-values, and scatter in the residuals were used as indicators of the best regressions. Variables investigated include rainfall, average temperature, degree-days, potential evapotranspiration, actual evapotranspiration, relative humidity, and wind speed.

TABLE 1. Location and treatments of the 28 sites used in experiment 1 (in B.C. unless otherwise noted)

Location	Zone[a]	Subzone	Map #	Treatments[b]	Elevation (m)	Clearcut size (ha)
Bear Mt.	BWBS	mw1	1	F C	850	62
Inga Lake	BWBS	mw1	2	C	900	141
Fairbanks, AK	BWBS	-	3	F C	400	6
Topley	SBS	mc2	4	F C	1100	30
Beedy Creek	SBS	dw1	5	F Pr	1000	-
Aleza Lake	SBS	wk2	6	F C	700	89
Paul Ridge	MH	mm	7	F	1400	-
Strachan Mt.	MH	mm	8	F	1040	-
Otter Creek	ESSF	wc2	9	F C	1500	15
Spanish Lake	ESSF	wc3	10	F C Pc	1550	29
Sicamous Creek	ESSF	wc2	11	F C Pr	1700	10
Lucille Mt.	ESSF	mm	12	F C Pc Sw	1500	17
Skihist	PP	xh	13	F	175	-
Trout Creek	PP	xh	14	F	700	-
Boston Bar	IDF	ww	15	F C Pr Gt	700	5
Valentine Lake	IDF	dk4	16	F C	1200	43
Opax Mt.	IDF	xh	17	F C Pr Pc	1100	2
Shawnigan N	CDF	xm2	18	F C	382	25
Shawnigan S	CDF	xm1	19	F C	303	8
Date Creek	ICH	mc1	20	F C Pr	450	18
Adams Lake	ICH	mw3	21	F C	700	30
Malakwa	ICH	mw3	22	F C	750	27
Hidden	ICH	mw2	23	F C	650	20
Mount Seven	ICH	mk1	24	F C Sw	1200	1
Ice Road	ICH	mw2	25	F C Sw	910	1
Port McNeill	CWH	vm1	26	F C	100	97
Blaney Lake	CWH	vm1	27	F C Pc	240	1
MASS Trial	CWH	mm2	28	F C Pc Sw Gt	800	65

[a] BWBS = Boreal White and Black Spruce, SBS = Sub-Boreal Spruce, MH = Mountain Hemlock, ESSF = Engelmann Spruce–Subalpine Fir, PP = Ponderosa Pine, IDF = Interior Douglas-fir, CDF = Coastal Douglas-fir, ICH = Interior Cedar–Hemlock, CWH = Coastal Western Hemlock.

[b] F = forest, C = clearcut, Pr = partial cut, Pc = patch cut, Sw = shelterwood, Gt = green-tree retention.

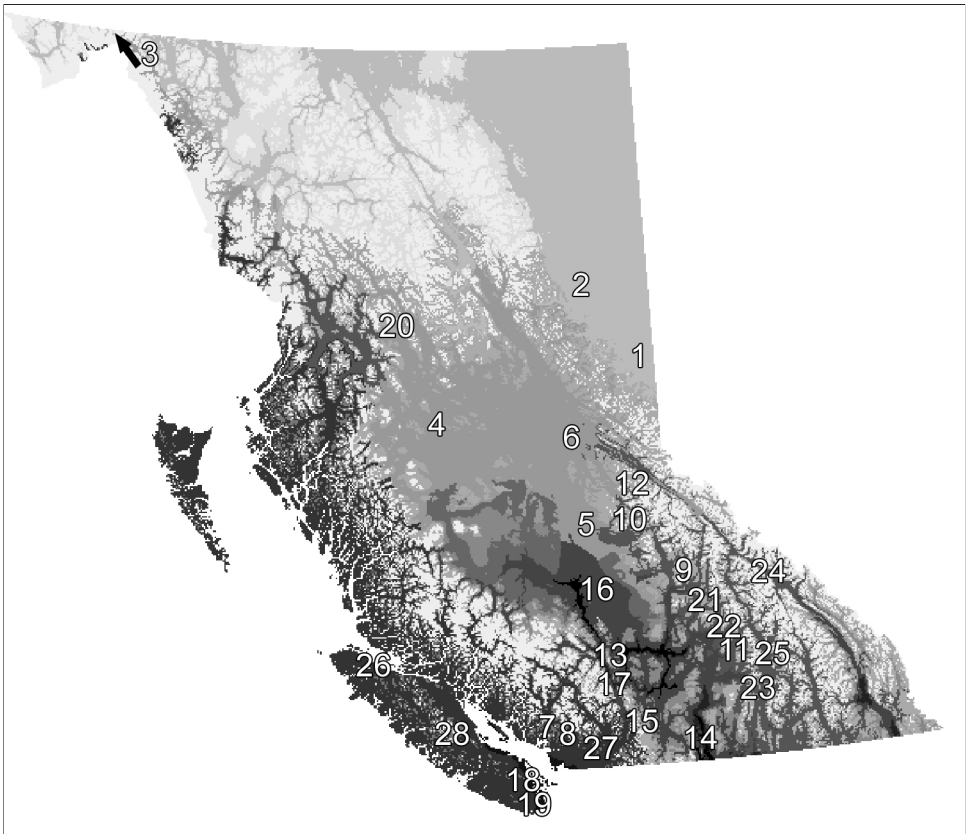

FIGURE 2. Locations of the 28 study sites overlaid on a map of biogeoclimatic zones of British Columbia. The shading was applied such that "warmer" zones (lower elevation or more southerly zones) are darker than "cooler" zones (high elevation or more northerly zones). Original BEC map from ftp://ftp.for.gov.bc.ca/hre/external/!publish/becmaps/

Question 2: Are decomposition rates faster in forests than in clearcuts?

Experiments to determine the effects of forest openings on rates of decomposition of litter and forest floors were established in seven biogeoclimatic zones in British Columbia. At 22 of the 28 mature forests used for Question 1, litterbags containing pine needles were installed in a forest and in an adjacent clearcut. The size of the clearcuts ranged from 1 to 141 ha (Table 1). Bags of aspen leaf litter and forest floor material were installed at 22 and 11 of the locations, respectively. Forest floor decomposition was measured in six biogeoclimatic zones. Seven bags of each material were collected from each location annually, and the dry mass of material remaining in the forests and clearcuts were compared using a two-way ANOVA with study location and forest opening as independent variables. Additional details about this experiment can be found in Prescott *et al.* (2000a).

Question 3: How do decomposition rates of broadleaf and needle litter differ?

Three experiments were established to determine the relative decay rates of foliar litter of the main tree species in British Columbia. Additional details about these experiments can be found in Prescott *et al.* (2000c).

Fourteen species

In the fall of 1993, foliar litter of the following 14 tree species was collected from sites across B.C.: lodgepole pine, western white pine (*Pinus monticola* Dougl.), ponderosa pine (*Pinus ponderosa* Laws.), western hemlock, western larch (*Larix occidentalis* Nutt.), Engelmann spruce (*Picea engelmannii* Parry), subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.), western redcedar, Douglas-fir, amabilis fir (*Abies amabilis* [Dougl.] Forbes), trembling aspen, black cottonwood (*Populus trichocarpa* Brayshaw), red alder (*Alnus rubra* Bong.), and vine maple (*Acer circinatum* Pursh).

Two grams of litter were put into litterbags; the size of the bags varied from 10 × 10 cm to 20 × 20 cm depending on the size of the leaves. Rates of decomposition of each litter were measured in a coastal mixed-conifer forest at the UBC Malcolm Knapp Research Forest near Vancouver, B.C., in the Coastal Western Hemlock dry maritime (CWHdm) zone. Bags were installed in December 1993 and collected annually for 5 years. Data were analyzed using a one-way ANOVA and Tukey's procedure.

Spruce–aspen

Decomposition of aspen leaf litter and spruce needle litter (both pure and mixed) was compared at four sites near Dawson Creek, B.C. (55°46'N, 120°14'W). Three of the plots (aspen, mixedwood, and clearcut) were in the Bear Mountain Community Forest, 10 km southwest of Dawson Creek. The third was a spruce stand near Taylor, B.C. All plots were in the Peace moist warm Boreal White and Black Spruce zone (BWBSmw1). Foliar litters of white spruce and trembling aspen were collected in September 1992 from mature aspen and spruce stands near Dawson Creek. Litterbags (10 × 10 cm) were constructed of a double layer of 1.5-mm mesh fibreglass screening, and filled with either 2.0 g (dry mass) of spruce needles, 2.0 g of aspen leaves, or 1.0 g of both species (mixed). Double bags were used to reduce spillage of spruce needles while allowing movement of soil fauna. Litterbags were pinned onto the surface of the forest floor at the four sites in November 1992. Seven bags of each type were collected from each plot after the first year (November 1993) and five litterbags of each type were collected from each plot annually for 4 more years. The dry mass of litter of each species was compared between species, and among mixed and pure litters (to determine the influence of litter mixing). The design of the experiment was a randomized complete block (RCB) with factorial allocation of litter species and mixing. The mass remaining of spruce, aspen, and mixed litter samples at each time period (RCB) and for the entire 5-year period (split-plot RCB) were analyzed using analysis of variance and Bonferroni's multiple range test.

Douglas-fir–alder

Decomposition of red alder leaf litter and Douglas-fir needle litter (both pure and mixed) was compared in three pure plots of Douglas-fir and of red alder at the UBC Malcolm Knapp Research Forest near Maple Ridge, B.C. (49°17'N, 122°36'W), in the CWHdm. Foliar litter of Douglas-fir and red alder was collected in October 1994 from the three pure plots of each species. Recently fallen alder leaf litter was collected from the forest floor on three occasions; Douglas-fir litter was collected in plastic trays with mesh in the bottom to allow drainage. Litterbags (15 × 15 cm) were constructed of a single layer of 0.5-mm mesh fibreglass screening, and filled with either 2.0 g (dry mass) of Douglas-fir litter, 2.0 g of alder foliar litter, or 1.0 g of each litter (mixed). The small mesh size was necessary to contain the Douglas-fir needles. Litterbags of each type were pinned to the surface of the forest floor in the three plots of each species in July 1995. Five bags of each type were collected from each of the six plots at 6-month intervals for 2 years and again after 3 years. The dry mass of litter of each species at each time was compared among litter types (species), and between mixed and pure litters. The design of the experiment was a split-plot RCB with factorial allocation of litter species and litter mixing. The remaining mass of Douglas-fir and alder litter samples at each time period (split-plot RCB) and for the entire 3-year period (split-split plot RCB) was compared using analysis of variance and Bonferroni's multiple range test.

Douglas-fir–paper birch–lodgepole pine

Decomposition of foliar litters of these species was compared in three pure plots of each species near Skimikin (50°48′N, 119°26′W), in the Thompson moist warm Interior Cedar–Hemlock zone (ICHmw3). Foliar litter was collected in October 1994 in the three plots of each species in plastic trays with mesh in the bottom. Litterbags (15 × 15 cm) were constructed of a single layer of 0.5-mm mesh fibreglass screening, and filled with 2.0 g (dry mass) of litter of one species. Litterbags were pinned to the surface of the forest floor in the three plots of each species in April 1995. Three bags of each type were collected from each of the nine plots at yearly intervals for 4 years. The mass of each litter type remaining at each time was compared using analysis of variance and Bonferroni's multiple range test.

Question 4: Are decomposition rates faster in fertilized forests?

Two experiments were established: one in a Douglas-fir forest at the Pack Forest near Seattle, Washington, and one in a trembling aspen forest in northeastern British Columbia.

Douglas-fir

Foliar litter was collected from three plots that received sewage sludge applications (SU1-3 in Prescott *et al.* 1993) and three unfertilized (control) plots (CU1-3). Average N concentrations in Douglas-fir foliar litter were 0.69% in

the control plots and 0.75% in the sludge-amended plots ($p < 0.05$). Bags containing 2.0 g of litter of each type were placed in a plot that had been fertilized six times with N, P, and S for a total of 1082 kg N/ha^{-1} (plot F42 in Prescott *et al.* 1993), and in an adjacent control plot (F41) in September 1993. Seven bags of each type were collected annually for 4 years and the mass of litter remaining in each bag was measured. To determine effects of N-fertilization on the decomposition rate of Douglas-fir foliar litter, a two-factor ANOVA was used, using the fertilized and non-fertilized plots as the block effect.

Aspen

This experiment was in a 24-year-old stand of aspen 45 km north of Chetwynd, B.C. (55°42'N, 121°38'W), in the BWBSmw1 zone (DeLong *et al.* 1990). The stand had been fertilized once with ammonium nitrate at 200 kg N/ha^{-1} (Prescott *et al.* 1999). There were three blocks, each containing one plot of each treatment. Foliar litter was collected from all six plots and bags containing litter from each plot were placed in that plot and in the plots of the other treatments in the block in September 1993. Nitrogen concentrations in foliar litter were significantly greater ($F = 14.4$, $p < 0.05$) in N-fertilized plots (1.29% N) than in control plots (0.86% N). Five bags of each type were collected from each plot annually for 4 years and the mass of litter remaining in each bag was measured. The effect of N-fertilization on the decomposition rate of aspen foliar litter was assessed using a randomized complete block split-plot ANOVA. Additional details about this experiment can be found in Prescott *et al.* (1999).

Results and Discussion

Question 1: Is decomposition slower in colder biogeoclimatic zones?

Lodgepole pine needle litter mass loss after 4 years was greatest in the CWH and ICH zones and least in the Ponderosa Pine (PP) followed by the BWBS zones (Figure 3a). The other five biogeoclimatic zones (MH, Coastal Douglas-fir [CDF], Interior Douglas-fir [IDH], Sub-Boreal Spruce [SBS], and Engelmann Spruce–Subalpine Fir [ESSF]) had intermediate rates of decomposition. For aspen leaf litter, mass loss after 3 years was greatest in the CWH followed by the MH zone (Figure 3b). The slowest decomposition rates of aspen leaf litter were in the PP, followed by the BWBS and IDF zones. Forest floor material decomposed more slowly than either pine or aspen litter (Figure 3c). Forest floor decomposition was fastest in the ICH and SBS zones and slowest in the PP and MH zones.

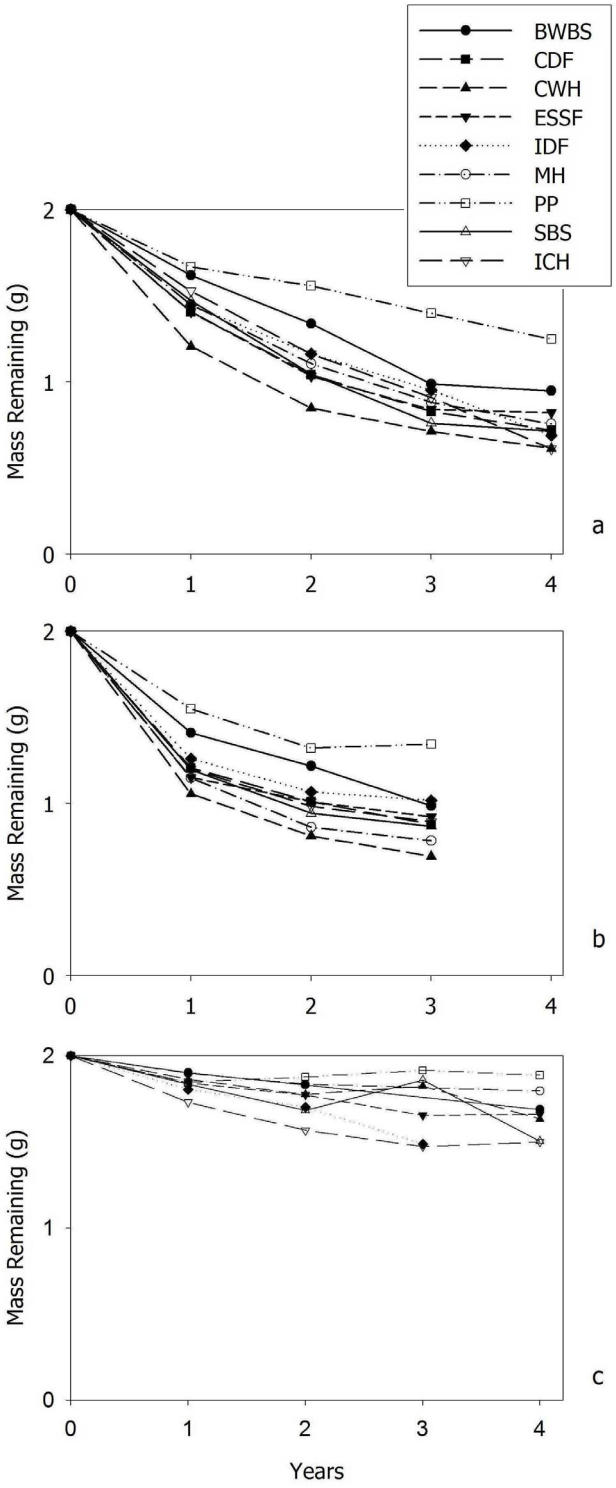

FIGURE 3. Mass loss of (a) pine needle litter, (b) aspen leaf litter, and (c) forest floor material in sites in each biogeoclimatic zone.

These results indicate that, within the range of climates in British Columbia, moisture most affects decomposition. All litter types decomposed the slowest in the PP zone, which is the driest zone (Table 2). Mass loss rates were about twice as fast in the CWH compared with the PP zone. Mean annual temperatures are similar in these zones, but average annual precipitation is about four times greater in the CWH (Table 2). Decomposition was also more rapid in zones with greater moisture but similar temperatures (e.g., ICH vs. IDF, CWH vs. CDF). The slow decomposition rates in the BWBS may be largely due to moisture, as they were slower than ESSF sites that have similar temperature but greater moisture. A temperature effect was evident when comparing the decomposition rates of pine needle litter and the forest floor between the MH and CWH zones. In the MH zone, which has greater moisture but lower temperature than the CWH zone, the decomposition rates for both were slower. However, decomposition of aspen leaves was almost as rapid in the MH as in the CWH zone.

Pine litter decomposition rate was negatively correlated with potential evapotranspiration (PET) and positively correlated with precipitation (Table 3). The slower decomposition associated with high PET values may be due to growing season droughts. This is supported by the relationship of mass loss and precipitation. Actual evapotranspiration (AET), which incorporates these two variables, was also significantly related to pine mass loss (Table 3). There was no relationship between the mass loss of aspen and climate (Table 3). Although PET and average precipitation were significantly related to mass loss, these two variables explained little of the variation in mass loss. The best equation to predict pine litter mass loss from climate was:

$$Loss = 0.75 - (0.00010205)\ ETP + (0.00012963)\ PA$$

where: Loss = pine needle mass loss (g) after 3 years, *ETP* = potential evapotranspiration (cm) calculated using the Thornthwaite-Mather equation, and *PA* = average annual precipitation (cm) during the 3-year incubation.

The greater importance of moisture for litter decomposition in B.C. forests probably reflects the extreme variation in moisture in British Columbia that results from the considerable topography and the maritime influence. Other litter decomposition experiments have used transects that differed more in temperature than in moisture. For example, Moore *et al.* (1999) found that decomposition was most strongly related to mean annual temperature in a cross-Canada transect; at 18 sites, average annual temperatures ranged from –10 to +10°C while annual precipitation ranged from 261 to 1783 mm. In a north–south transect in Sweden, Johansson *et al.* (1995) found a strong relationship between decomposition rate of Scots pine needles and average annual temperature.

TABLE 2. Average temperature and precipitation ranges in each of the nine biogeoclimatic zones in the decomposition study. Data are from Meidinger and Pojar (compilers and editors, 1991). Values are the range of average values for sites in each zone.

Zone	Annual temperature range (°C)		Annual precipitation range (mm)	
	Min.	*Max.*	*Min.*	*Max.*
CWH	5.2	10.5	1000	4400
CDF	9.2	10.5	647	1263
MH	0	5.0	1700	5000
PP	4.8	10.0	280	500
IDF	1.6	9.5	300	750
ICH	2.0	8.7	500	1200
SBS	1.7	5.0	440	900
ESSF	–2.0	2.0	400	2200
BWBS	–2.9	2.0	330	570

TABLE 3. Significance level (*p*-values) and correlation coefficients (*r*) of 3-year pine and aspen mass loss and average temperature, average precipitation, potential evapotranspiration, and actual evapotranspiration

	Pine litter	
	***p*-value**	***r***
Average temperature	0.3186	0.199
Average precipitation	**0.0709**	0.319
Potential evapotranspiration	**0.0001**	0.732
Actual evapotranspiration	**0.0028**	0.553
	Aspen litter	
	***p*-value**	***r***
Average temperature	0.6667	0.089
Average precipitation	**0.0289**	–0.429
Potential evapotranspiration	**0.0696**	0.361
Actual evapotranspiration	0.3529	0.190

At the 22 sites in the Swedish study, average annual temperatures ranged from –0.5 to +8°C, and average annual precipitation ranged from 425 to 1070 mm. In the B.C. experiment annual temperatures ranged from about 0 to –10°C, while precipitation averages ranged from about 400 to 3000 mm. This extreme variation in moisture in British Columbia is probably the reason that moisture, rather than temperature, is more closely related to decomposition rates in B.C. forests.

Question 2: Are decomposition rates faster in forests than in clearcuts?

Pine needle litter lost mass more rapidly in forests than clearcuts during the first 3 years, and faster in the clearcut during the fourth year, by which time the differences were no longer significant (Figure 4a). Clearcutting did not significantly affect rates of mass loss of aspen leaves (Figure 4b). Forest floor material lost mass slowly at all sites and was not significantly affected by clearcutting (Figure 4c).

Overall, litter decomposition in clearcuts was either slower or the same as that in forests. This may be related to surface drying during the snow-free season when decomposers are most active. The increased temperature and wind movement across a clearcut may exacerbate drying of litter, thus slowing decomposition to rates similar or lower than those in adjacent forests. This finding is in keeping with the conclusion of Yin *et al.* (1989) that the effect of forest opening on litter decomposition rate depends on the regional climate.

Question 3: How do decomposition rates of broadleaf and needle litter differ?

Fourteen species

Some differences in mass loss rates between broadleaf and needle litter are apparent in Figure 5. Vine maple litter decomposed much faster ($p < 0.0001$) than all other litters, losing 75% of its original mass during the first year. Thereafter, mass loss from vine maple was negligible. However, because of the large amount of mass lost during the first year, the total mass loss for vine maple was significantly different from all other litters through year 3. The other broadleaf litters lost mass more rapidly than some of the needle litters during the first 2 years although the rates were not significantly different from many of the conifers. Thereafter broadleaves decomposed more slowly so that there was no significant difference in mass remaining between hardwood and conifer litter after 3 years.

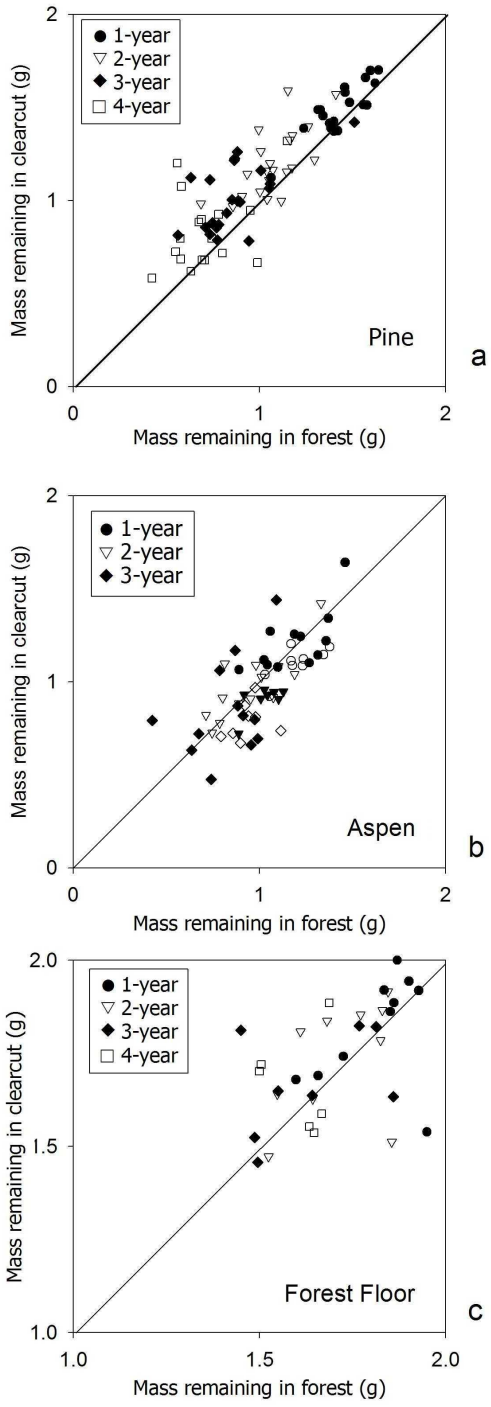

FIGURE 4. Mass of (a) lodgepole pine needle litter, (b) aspen leaf litter, and (c) forest floor remaining after decomposing for 4, 3, and 4 years, respectively, in adjacent forests and clearcuts at 16 sites for pine and aspen litter and six sites for forest floor. Each point is the average mass remaining in the forest (*x* axis) and that in the clearcut (*y* axis) at one site after 1 (•), 2 (▽), 3 (♦), and 4 years (ᵏ). The line indicates equal mass remaining in forest and clearcut. Source: Prescott *et al.* (2000a).

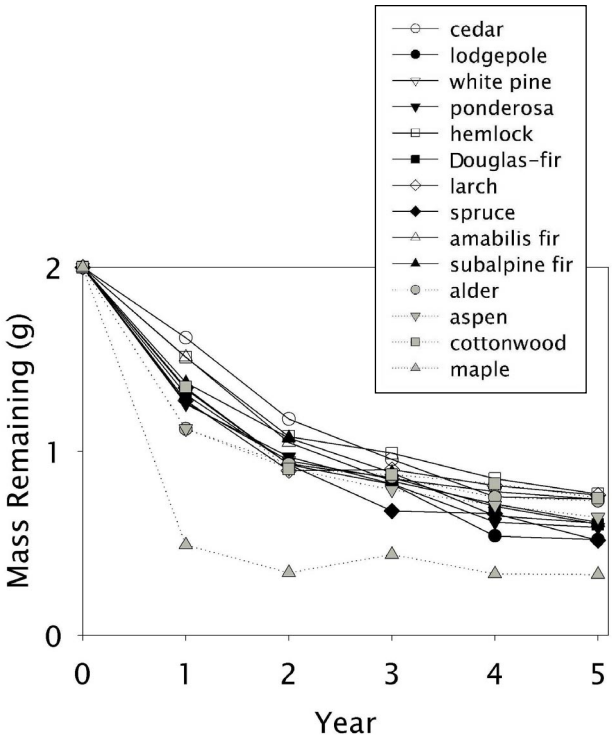

FIGURE 5. Mass remaining of foliar litter from 14 tree species in a coastal forest near Maple Ridge, B.C., during 5-year incubations.

Spruce–aspen

Aspen leaf litter lost significantly more mass than spruce needle litter during the 5-year incubation. The remaining mass for the two species was significantly different at all sampling times (Figure 6a). This was primarily due to significantly greater mass loss from aspen during the first year (65.5%) compared with spruce (29.2%). After the first year, aspen lost mass more slowly than spruce, resulting in more similar masses of aspen (19.3%) and spruce (27.5%) remaining after 5 years. There was no effect of mixing litters on decomposition rate of either spruce or aspen leaf litter at any sampling time or over the entire 5-year period.

Douglas-fir–alder

Alder litter decomposed faster than Douglas-fir litter during the first 6 months, but thereafter there were no significant differences in mass remaining between the two species (Figure 6b). There was no significant effect of mixing litter on the litter mass of either species remaining at any sampling time.

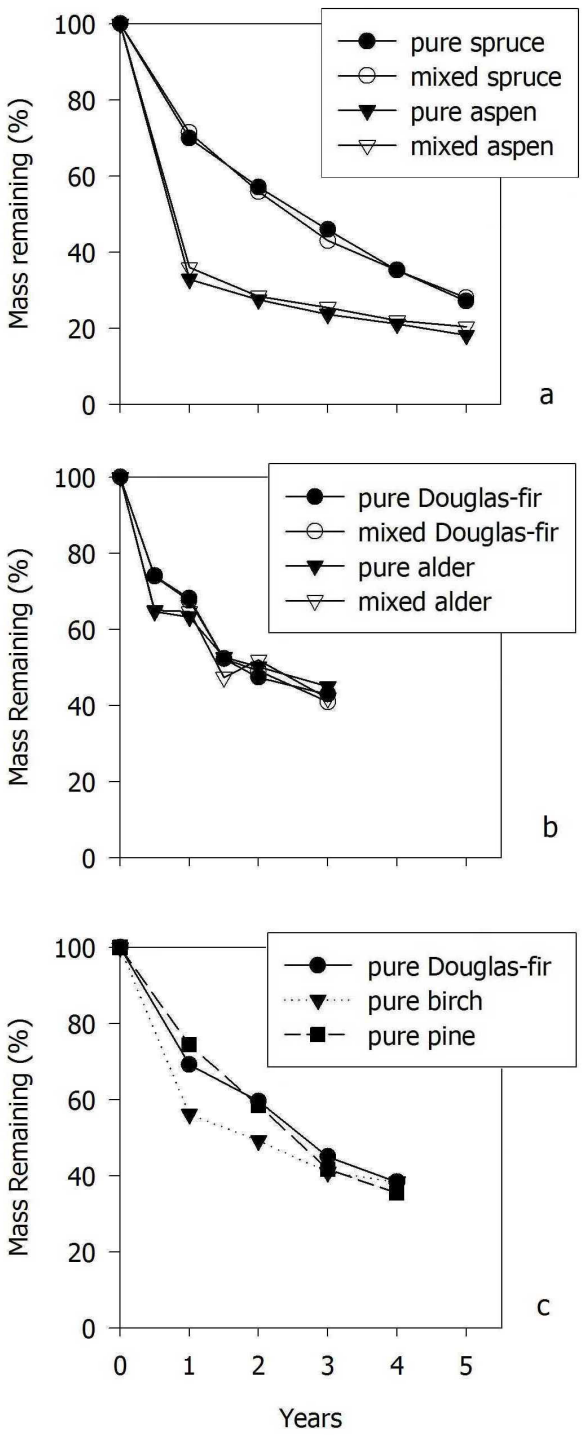

FIGURE 6. Mass remaining of (a) pure and mixed foliar litter of interior spruce and trembling aspen during 5-year decomposition near Dawson Creek, B.C.; (b) pure and mixed foliar litter of Douglas-fir and red alder during 3-year decomposition near Maple Ridge, B.C.; and (c) foliar litter of Douglas-fir, paper birch, and lodgepole pine during 4-year decomposition near Skimikin, B.C. Source: Prescott *et al.* (2000b).

Douglas-fir–paper birch–lodgepole pine

Birch leaf litter decomposed faster than either of the needle litters during the first year, but by year 3 there was no significant difference between the three species in the percentage of original mass remaining (Figure 6c).

In our experiments broadleaf litter lost mass more quickly and then more slowly than needle litter. This result may be attributable to the broadleaf litter having greater concentrations of labile (leachable) material. The rapid initial decay of broadleaves was not sustained and so may not indicate more complete decay or more rapid turnover of organic matter in broadleaf or mixed forests. There was no evidence that mixing broadleaf litter with needle litter hastened the decomposition of the needle litter. The effects of mixing litters on decomposition have been inconsistent; Fyles and Fyles (1993) suggested that the effects may be species specific and perhaps mixture specific. Our results clearly indicate that the mixing of needle litter with broadleaf litter is unlikely to hasten decomposition in mixedwood forests of British Columbia.

Question 4: Are decomposition rates faster in fertilized forests?

Douglas-fir foliar litter collected from fertilized (sludge-amended) plots decomposed at the same rate as litter collected from control plots ($F = 0.31$–36 for the four harvests; $p > 0.1$) (Figure 7a). During the first 2 years, litter decomposed marginally more slowly in the fertilized plot than in the control plot ($F = 75.56$ and 49.00; $p < 0.1$), but by year 3 there was no difference in the mass of litter remaining in the control and fertilized plots.

Aspen leaf litter collected from plots of each of the three treatments did not differ in rate of decomposition ($F = 1.03$–2.24 during years 1–4, $p > 0.1$) (Figure 7b). There were also no differences between rates of decomposition in control and N-fertilized plots.

This experiment provided no evidence that fertilization of forests will result in an increased rate of litter decomposition. There was no effect of increased concentrations in the litter, and the only effect of adding fertilizer to the forest floor was a slight suppression of decomposition in the fertilized Douglas-fir plots. This finding is consistent with results of earlier experiments (Prescott *et al.* 1993; Prescott 1994) that also reported no effect of N fertilization on litter decomposition rates, and a slowing of litter decomposition rates in plots treated with sewage sludge (Prescott 1994).

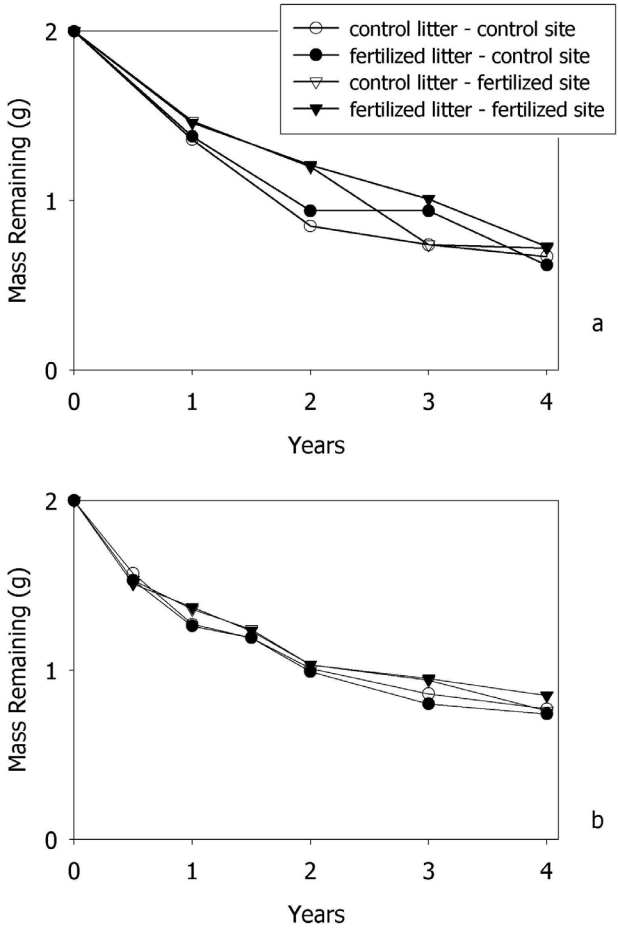

FIGURE 7. Mass remaining of foliar litter collected from (a) control and fertilized plots and incubated in control and fertilized plots in a coastal Douglas-fir forest in Washington, and (b) a trembling aspen forest near Chetwynd, B.C. For aspen, values are the means of the three sites. Source: Prescott *et al.* (1999).

General discussion

Estimation of litter mass loss rates through the use of mesh litterbags has several widely recognized sources of error. First, moisture levels may be different within the bags than in the surrounding litter layer. Second, the normal movement of litter through the forest floor is impeded when it is enclosed in bags, so it may not decompose in the same environment as unenclosed litter at the same stage of decay. Third, and most worrisome, the mesh may exclude some of the larger soil fauna and thus not incorporate their activities into estimates of decay rates. These problems can be offset to some extent

by using the smallest bags and the largest mesh possible (while still retaining the litter). However, especially in ecosystems known to have soil fauna active in processing litter, it is unlikely that litterbag data accurately represent the long-term fate of litter. Nevertheless, for comparative studies such as those described here, mass loss estimates from litterbag incubations should indicate relative rates of early decay and the factors that influence it.

The unexpected findings of these experiments have implications for management of forests in British Columbia. Although we do not actively manage litter decomposition, several assumptions about decomposition are implicit in our expectations about sites and the effects of management activities thereon. For example, we expect nutrient availability to be low and potentially growth limiting in high-elevation forests, in part because the cold climate will cause litter decay to be slow. We expect that adding or increasing the broadleaf component will improve the site by increasing nutrient cycling and availability, partly through its higher quality litter and faster decay. We expect that harvesting forests will lead to a large and potentially problematic decline in organic matter because of faster decay of litter and humus under the warmer, moister conditions in openings. Finally, we might expect fertilizing forests to cause a large or prolonged increase in nutrient availability if it increases the rate of litter decay and associated nutrient release. Our results clearly challenge many of these assumptions that we have about sites and management effects based on long-held beliefs about decomposition. Replacing these ideas about "what should happen" with evidence of "what really happens" with respect to decomposition should improve our ability to predict the outcome of management decisions.

How did we come to believe that we understood the effects of forestry activities on litter decomposition rates? Our understanding of the effects of forest management practices on the functioning of forest ecosystems is an assemblage of individual observations. The observations from individual studies with diverse treatments and forest types are assembled occasionally in an attempt to review the field and generate generalizations. Often only the interpretations and conclusions of the investigations are used, rather than the observations themselves, which can further mislead us. Previous generalizations about decomposition rates are particularly unreliable because many are based on indirect observations and presumptions, rather than direct evidence. For example, the notion that decomposition is faster in clearcuts developed from observations of higher nitrate concentrations in drainage waters, rather than measurements of decomposition rate (Prescott *et al.* 2000a). Likewise, the expectation of faster decomposition in N-fertilized forests was derived from correlations between N concentrations and decay rates of different litter types, rather than comparisons of decomposition rates in fertilized and unfertilized forests or of the same litter with differing N concentrations (Prescott 1994). Thus, many of the "well-known facts" about decomposition rates were actually only guesses derived in the absence of direct evidence, and as such need to be continuously revised in light of new evidence presented here and elsewhere.

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