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With 2 figures

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Contents

1. Introduction

In spite of the widespread occurrence of *Populus* spp. in coniferous and deciduous woodlands of the northern cold temperate zone, few estimates have been made of litter production. No aspen sites are included in the IBP woodlands list of 65 sites prepared by SHUGART et al. (unpublished). Information on litter production in aspen stands is available for the U.S.S.R. (RODIN and BAZILEVICH 1967) and for Alaska (VAN CLEVE and NOONAN 1971, 1975). In northern Wisconsin, U.S.A., CROW (1974) studied litter fall in predominantly aspen and aspen-paper birch stands.

In the literature, references to litter fall do not necessarily refer to the same litter components. Very often, only leaf litter fall has been measured and, in some studies, estimates of total litter fall do not include input from large branches and stems. In this particular study, attention is given to all litter components from the above ground parts of the overstory vegetation in an aspen (*Populus tremuloides* MICHX.) woodland in the Canadian Rockies. Reference is also made to above ground input from the understory vegetation.

Data were collected for the period 1968—1970 (with some readings in 1967 and 1971) and include an assessment of the concentrations of certain chemical elements in various litter components. Amounts of chemical elements of above ground litter returned annually to the soil have been calculated. The major objective of the study was to obtain background information on which to assess the roles of decomposer organisms which were being studied in the same woodland. The results extend our knowledge of organic mass and chemical input via litter fall in the world's woodlands.

2. Study area

2.1. Vegetation and soil

The aspen woodland site was on the south slope of Pigeon Mountain, close to Barrier Lake in the Kananaskis Valley some 80 km west of Calgary (50° 02′ N, 115° 03′ W; altitude approx. 1380 m N.H.). The major tree species was the trembling aspen (*Populus tremuloides* MICHX.), with some specimens of balsam poplar (*P. balsamifera* L.), spruce [*Picea engelmanni* PARRY x *P. glauca* (MOENCH) VOSS.], pine (*Pinus contorta* DOUGL.), fir [*Abies lasiocarpa* (HOOK) NUTT.], and willow (*Salix* sp.). A few DOUGLAS fir [*Pseudotsuga menziesii* (MIRB.) FRANCO] were also present. DENNIS (1970) described the ground flora. It was dominated by grasses with *Rosa* spp., *Castilleja* spp., *Epilobium angustifolium* L., *Campanula rotundifolia* L., *Heracleum lanatum* MICHX. and *Vaccinium* spp.

The soil, of calcareous origin, was described by KARKANIS (unpublished) as orthic gray luvisol. According to KARKANIS, the organic horizon (L — H) overlies a degraded chernozem. The *p*H of fresh samples from the litter to the humus layers lay within the range 6.4—6.7. KARKANIS (unpublished) recorded *p*H of 7.32 for the 0—5 cm layer in a 1 : 3 soil water suspension of stored samples passed through a 2.00 mm mesh sieve. Sampling was concentrated in Plot 2 (Environmental Sciences Centre designation). The stand of Plot 2 was not studied in detail but it was similar in constitution to Plot 3 investigated by PETERSON (unpublished). Plot 3 was situated within 50—60 m of Plot 2 at a slightly higher average elevation (1440 m). Its makeup determined in 1969 was as follows: aspen density 1900 stems/ha; mean age 69 ± 4 (SD) years; mean tree height 15 ± 0.6 m; range of d.b.h. 0.11—0.26 m; above-ground wood and bark 211,130 kg (dry wt)/ha; foliage 2,870 kg (dry wt)/ha; total fresh wt (above ground) 385,670 kg/ha; estimated net primary production 6,450 kg/ha/yr.

2.2. Climate

The site experienced long cold winters and short warm summers with warm Chinook conditions occurring suddenly and spasmodically during the winter months. The ground was frozen usually from late November to April and snow cover sometimes reached a depth of 1 m. The soils were usually subjected to drought conditions sometime during the July—September period. In 1968—1969 DASH (1970) obtained detailed records of soil temperature for one site in the aspen woodland (Appendix 1). The general weather conditions summarized for a period of twenty years (KARKANIS, unpublished) is given in Appendix 2. The KARKANIS data were obtained at a permanent weather station within 2 km of the aspen site.

3. Methods

3.1. Leaf and associated litter ("small" litter)

Throughout the period August 1967 to October 1972 leaf litter and other small components of leaf litter were caught in two types of litter trap. Type A were wooden frames 0.55 m × 0.55 m, 0.1 m deep, area 0.3025 m^2. Type B were similar to those used by SYKES and BUNCE (1970). They were galvanized metal trays 0.42 m diam., 0.07 m deep, area 0.1386 m^2. The trays (Type B) were suspended within the top rim of plastic garbage containers which raised the trays some 0.5 m above ground surface. The bottoms of both types of trap were covered with fine metal gauze approx. 0.2 mm mesh.

Eight trapping sites, each approximately 5 m × 5 m, were selected in the woodland and three traps of each type installed at each site. The trapping sites were randomly distributed within a 2 ha plot (Plot 2).

Litter samples were removed from the traps, stored in brown paper bags and the contents sorted in the laboratory. They were oven dried at 40 °C, sorted and stored prior to being weighed after drying at 85 °C for 24 hours. Litter material was classified according to the following categories: aspen leaves, other leaves (balsam poplar and shrubs), twigs (less than 0.40 m in length), pine needles, detritus (bud scales, small pieces of bark and insect frass) and reproductive parts (male and female catkins of *Populus* spp.). As NEWBOULD (1967) and others have indicated litter traps should be emptied frequently, preferably once a week. The frequency of emptying is shown in Table 1. Traps were not emptied during the winter months because of snow conditions. In only one year, 1969, was a November collection possible.

In calculating the annual litter fall for 1969 and 1970 the 1969 November collection was treated as part of the 1969—1970 overwintering fall. It is, therefore, included in the 1970 yield and excluded from the 1969 calculations. Thus, each year's catch comprises litter fall from the previous November through to the following October.

Table 1. The number and distribution of samples 1968—1970

	May	June	July	August	Sept.	Oct.	Nov.
1968	4	2	1	2	3	2	0
1969	1	1	2	2	2	4	1
1970	0	1	1	1	1	2	0

Table 2. Annual leaf and associated small litter 1968—1970 (kg/ha dry wt ± 1 SD)

Year	Aspen leaves	Other leaves	Pine needles	Reproductive Parts	Detritus	Twigs (< 0.40 m)	**Total**
1968							
Trap A	1613 ± 329	144 ± 198	73 ± 151	53 ± 53	92 ± 19	336 ± 128	**2310 ± 274**
Trap B	1536 ± 328	127 ± 158	75 ± 169	46 ± 52	81 ± 26	183 ± 76	**2048 ± 280**
1969							
Trap A	1660 ± 299	140 ± 92	96 ± 160	79 ± 185	149 ± 80	343 ± 136	**2466 ± 224**
Trap B	1414 ± 277	110 ± 97	69 ± 138	22 ± 45	123 ± 87	209 ± 113	**1947 ± 323**
1970							
Trap A	1482 ± 300	132 ± 65	114 ± 127	37 ± 31	98 ± 35	367 ± 174	**2267 ± 369**
Trap B	1370 ± 311	170 ± 132	85 ± 148	35 ± 27	89 ± 27	234 ± 149	**1980 ± 440**
Mean Catch (1968—1970)							
Trap A	1585 (*67.6*)	149 (*6.4*)	94 (*4.0*)	56 (*2.4*)	113 (*4.8*)	349 (*14.9*)	**2346** (*100*)
Trap B	1440 (*72.3*)	136 (*6.8*)	76 (*3.8*)	34 (*1.7*)	98 (*4.9*)	208 (*10.4*)	**1992** (*100*)

Note: Mean annual catch expressed as % of total small litter fall in italics.

3.2. Tree litter ("large" litter)

The fall of boles, branches and large twigs (> 0.40 m) with or without leaves, was measured on three 15 m × 15 m plots within the same block of woodland where leaves and associated small litter were sampled. The plots were cleared of previous years' litter, as distinct from new litter, in June and July 1967. The major 1967 collections were made in September, October and December. In 1968 the collection period was July to October and in 1969 only one collection, in May, was made.

3.3. Chemical analyses

The chemical analyses of litter components collected in 1968 and 1969 were made as follows: a *CHN* analyzer-Model 185 was used to determine carbon, hydrogen and nitrogen; inorganic chemical elements were determined on a Perkin-Elmer 303 Atomic Spectrophotometer. Phosphorous was determined by the Molybdenum blue procedure.

All samples were dried for 24 hours at 105 °C and then weighed on a Cahn Gram Electrobalance. Samples to be analyzed for phosphorous and inorganic chemical elements were digested with 30% perchloric acid and 70% nitric acid.

4. Results

4.1. Small litter fall (Table 2)

4.1.1. *Effects of type of trap on catch*

The total amount of litter of all types caught by Type A traps was always numerically greater than that caught by Type B traps. The difference was only significantly different in the totals summed for the whole three-year period. The statistical analysis for the summed catches is as follows: mean annual litter fall for Traps A and B, t = 3.82, d.f. 46; F ratio 14.55, d.f. 1, 46. The twig component was the only component to show significant differences between the two types of trap (t = 3.34, d.f. 46; F ratio 11.15, d.f. 1, 46). This difference indicated that Type B had a lower efficiency for catching twig material under the conditions in which it was used, compared with traps placed directly on the ground. Sykes and Bunce (1970) used Type B traps in their study of litter fall in a mixed deciduous woodland in England but their estimates of twig input were based on hand collections. The consistently higher catches of leaf litter by Type A traps in the present study compare with leaf fall estimates obtained in a site north of the ones sampled in this study (Mitchell 1974, Carter unpublished). Thus, data based on litter collected from Trap A are used below to calculate fluxes in organic mass and amounts of chemical elements in small litter fall. However, because litter caught in this type of trap on the ground was subjected to precipitation splash, only the litter collected in Type B traps was used for chemical analysis.

4.1.2. *Differences between sites*

The eight sites were selected on a random basis. The catches of the various litter components and total litter fall at the different sites are shown in Table 3. When the catches for the whole period of study were summed, significant differences at the 0.01 level were shown between sites for some of the components listed in Table 3. The results expressed as individual site versus all other sites indicated that: the largest aspen leaf fall occurred at site 8, the smallest at site 7; the largest "other leaves" fall at site 3, the smallest at site 7; pine needles showed their largest fall at site 7. Twig fall showed no significant differences.

Table 3. Comparative amounts (kg/ha/y) of small litter components collected between 1968—1970 at each of the study sites in the aspen woodland

	Sites							
	1	2	3	4	5	6	7	8
Aspen leaves	1558.0	1494.3	1787.0	1575.9	1418.1	1651.3	1135.7	2060.1
Other leaves	121.7	145.4	375.6	59.9	235.0	158.2	25.7	69.4
Twigs	439.9	487.3	369.3	168.4	337.6	319.3	241.4	424.7
Pine needles	122.2	35.3	30.0	91.2	37.0	4.6	431.4	2.0
Detritus	101.5	144.0	161.8	94.3	95.2	75.6	153.5	78.5
Reproductive parts	19.6	12.6	39.1	74.7	36.6	11.7	253.7	3.2

In the category "other leaves", catch composition varied according to site (Table 3). Catches at site 3 were of balsam poplar and willow leaves while catches at site 5 consisted mainly of balsam leaves as did those at site 2. Thus, the ratio of aspen to balsam leaves varied according to site. LOUSIER and PARKINSON (1976) sampled leaf fall in a site north of the sites sampled during this study and found a ratio of aspen to balsam of 6:1 which approximated the ratio found in the catches at site 5.

4.2. Seasonal variation of small and large litter fall

Aspen leaves dominated the small litter fall in the Kananaskis Valley woodland forming 70% of the annual fall. Twigs were the only other component to exceed 10% of the annual catch (Table 2).

Figures 1 and 2 show the seasonal variation in the fall of individual components. Ninety percent of the fall of aspen and "other leaves" occurred in October.

Of the other small litter components (Fig. 1), approximately 70% of the fall of pine needles occurred in September and October. The category of reproductive parts comprised only male and female catkins of *Populus* spp. Their fall varied over the three years. In 1968 and 1969 it was bimodal with the largest amounts occurring in the winter period (shown in the May collection) and in August. Detritus fall was mainly during the winter months. The fall of twigs depended on wind strength and occurred throughout the autum and winter months.

The measurements obtained on the fall of large litter are limited but they provide some indication of the amount of tree litter that can be expected to occur in a mature stand of aspen. The time and amount of fall was obviously related to the occurrence of strong winds and of snow accumulation. The pattern of fall with its maximum in winter accords with visual observations in cold temperate woodlands.

In 1967, the December fall accounted for 100% of annual input of large branches and boles, 50% of the large twigs and 70% of the total annual fall of large litter. In 1968—1969, assuming that the single collection made on one plot in 1969 represented the winter fall, then the winter fall accounted for 60% of the annual input of the large branches and boles component, 30% of the large twigs and 45% of the total amount of large litter.

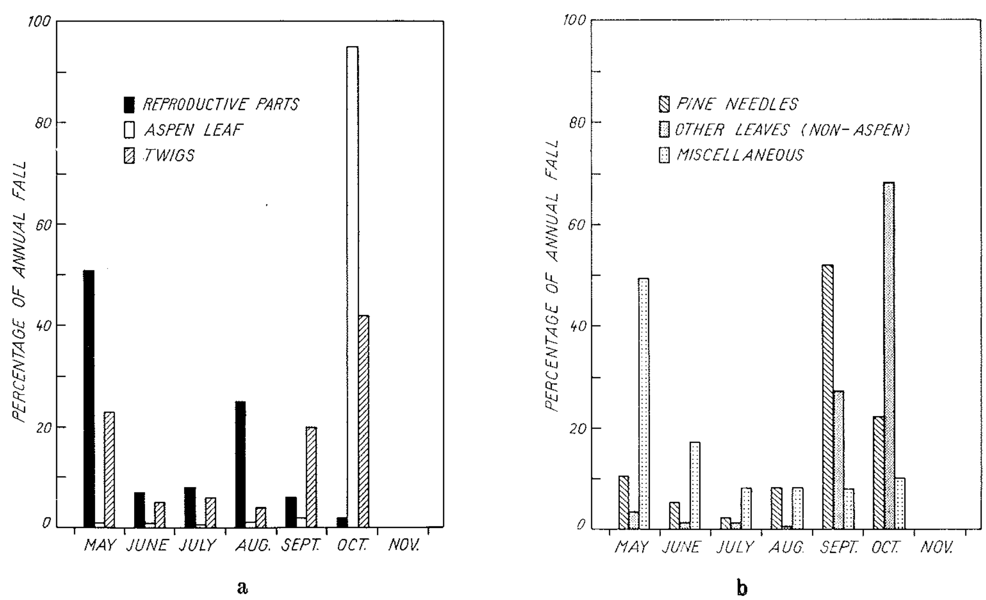

Fig. 1. Mean annual fall of small aspen litter (a) and of small non-aspen litter (b).

Appendix 1. Soil temperatures (°C) at 1—3 cm deep on the Aspen site for the period June 1968 to November 1969

	1968							1969										
Month	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.
Mean Max.	15.63	18.52	14.90	8.75	6.00	2.00	—0.75	—5.66	—3.00	—1.00	4.20	11.10	15.95	14.45	15.90	15.05	6.30	3.40
Mean Min.	9.16	13.18	10.82	6.75	4.00	2.00	—0.75	—5.66	—3.00	—1.00	3.00	7.24	10.61	11.80	12.40	9.02	5.60	3.15
Average	**12.38**	**15.85**	**11.36**	**7.75**	**5.00**	**2.00**	**—0.75**	**—5.66**	**—3.00**	**—1.00**	**3.60**	**9.18**	**13.28**	**13.11**	**14.15**	**10.04**	**5.93**	**3.27**
No. of days*)	18	19	20	8	4	3	4	3	2	3	10	21	22	21	23	18	25	10

Soil temperatures were measured at approximately 9.00 hr and 15.00 hr local time (MST).

*) "No. of days" records the number of occasions on which temperature readings were made.

Appendix 2. Weather records for 20 yr period (1951—1971) for the Kananaskis Forest Experimental Station (115°03′ W, 51°02′ N) Elevation 1390 m. From Karkanis (unpublished)

A. Average daily temperature (°C) records

Temperature	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Year
Mean daily	—9.8	—6.8	—3.9	2.1	7.2	11.0	14.1	13.2	9.1	4.8	—1.9	—6.8	2.7
Mean maximum	—2.9	0.1	2.6	8.1	13.9	17.7	22.0	20.8	16.1	10.9	3.7	—1.1	9.3
Mean minimum	—16.1	—12.6	—10.4	—3.8	0.4	4.2	6.2	5.8	2.0	—1.2	—7.6	—12.6	—3.8
Maximum	17.2	15.6	17.8	23.9	27.8	31.1	33.9	33.3	30.0	27.2	18.9	16.1	33.9
Minimum	—45.6	—41.1	—40.6	—31.1	—21.7	—5.0	—5.0	—2.2	—9.4	—22.2	—44.4	—38.9	—45.6

B. Precipitation records [on daily basis (mm)]

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Year
Mean rainfall	0	0	0	12.7	55.8	104.1	61.0	61.0	38.1	12.7	30.5	0	375.9
Mean snowfall	317.5	360.7	383.5	535.9	193.0	53.3	0	0	144.8	276.9	261.6	297.2	2824.5
Mean total precip.	33.0	35.6	38.1	66.0	76.2	109.2	61.0	61.0	53.3	40.6	55.9	30.5	660.4
Rain days	0	0	0	1	7	13	11	11	7	2	1	0	53
Snow days	7	8	8	8	3	1	0	0	2	5	5	7	54
Precipitation days	7	8	8	9	10	14	11	11	9	7	6	7	106
Max. precipitation in 24 hrs.	20.3	31.7	45.7	47.2	54.1	73.6	45.0	65.3	54.6	30.5	24.1	33.0	73.7

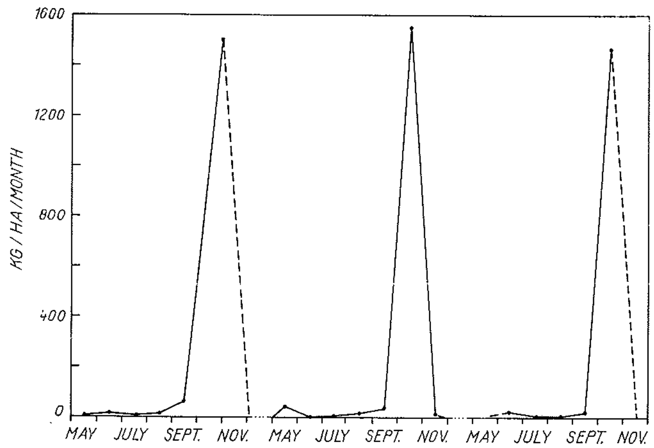

Fig. 2. Aspen leaf litter fall (kg/ha/month).

Table 4. Fall of large litter (kg/ha dry wt) prior to and during winter period

a. 1967

Plot	Large branches and boles		Large twigs (> 0.40 m) with or without leaves		Total large litter	
	Dec. Fall	Total for year	Dec. Fall	Total for year	Dec. Fall	Total for year
A	875	**875**	783	**1056**	1658	**1931**
B	0	0	106	**566**	106	**566**
C	839	**839**	76	**315**	915	**1154**
Mean ± 1SD	571 ± 350	**571** ± 350	322 ± 283	**646** ± 267	893 ± 549	**1217** ± 489

b. 1968—1969

Plot	Large branches and boles		Large twigs (> 0.40 m) with or without leaves		Total large litter		
	Winter period 1968—1969	Total for Jan.—Oct. 1968	Winter period 1968—1969	Total for Jan.—Oct. 1968	Winter period 1968—1969	Total for Jan.—Oct. 1968	Total Jan. 1968 to May 1969
A	—	186	—	264	—	450	—
B	—	128	—	415	—	543	—
C	35	25	137	300	172	325	497
Mean ± 1SD		**113** ± 58		**326** ± 56		**439** ± 77	

Table 5. Chemical composition (± 1 SD) of aspen leaves and twigs collected in litter fall at various times in 1969

	% dry wt			mg/g dry wt		
	C	*H*	*N*	*P*	*Ca*	*Mg*
Leaves						
2.—5. June	*43.6 ± 2.7*	*6.1 ± 0.3*	*2.6 ± 0.4*	3.06 ± 0.30	8.90 ± 0.82	2.31 ± 0.67
22. Aug.	*46.5 ± 2.2*	*6.2 ± 0.3*	*1.8 ± 0.5*	2.39 ± 1.65	10.76 ± 3.10	1.92 ± 0.62
30. Sept.	*47.4 ± 1.3*	*6.2 ± 0.4*	*0.8 ± 0.2*	1.71 ± 0.88	20.16 ± 8.43	3.23 ± 0.66
Twigs						
16.—22. Apr.	*46.2 ± 1.7*	*6.5 ± 0.2*	*2.2 ± 0.5*	3.54 ± 0.71	2.79 ± 0.44	1.86 ± 0.53
5. May	*44.2 ± 1.6*	*6.5 ± 0.3*	*4.2 ± 0.6*	6.19 ± 0.95	1.97 ± 0.38	1.94 ± 0.42
2. June	*45.4 ± 1.5*	*5.9 ± 0.4*	*2.1 ± 0.3*	4.08 ± 0.57	7.10 ± 1.60	2.70 ± 1.20
22. Aug.	*48.2 ± 1.7*	*6.2 ± 0.3*	*0.9 ± 0.1*	1.64 ± 0.28	12.52 ± 2.46	1.52 ± 0.37
30. Sept.	*48.0*	*6.7*	*1.1*	1.54	11.42	1.25

4.3. Total litter fall

An approximate assessment of total litter fall from the overstory for 1968 (the only year for which estimates of both small and large litter are available) is 2310 + 439 = 2749 kg/ha Table 4). The large litter thus represented 16% of the total fall from the overstory. If an average small litter fall (average for Trap A over three years) of 2346 kg/ha is assumed for 1967, then the total litter fall that year would have been 3563 kg/ha, with the large litter representing 34% of the fall.

In studies of the understory in the Kananaskis Valley aspen ecosystem, DENNIS (1970) obtained mean organic mass estimates of 2310 and 1440 kg/ha in areas of open and closed canopies, respectively. He estimated that reproductive structures of the understory accounted for approximately 5% of the total litter fall. KRAUTER (1976) estimated that the dominant herbaceous plant, *Epilobium angustifolium*, contributed 375 kg/ha to litter input in 1974 and 1975.

Based on late August samples in 1972 and 1973 (CARTER, unpublished) an estimate of 980 kg/ha for litter input of herbs and dead parts of *Rosa* spp. was obtained in an area of closed canopy, close to the sites sampled in the present study. This figure is an underestimate for it includes litter contributions from only the dominant shrub, *Rosa* sp. Litter input from reproductive parts of the understory was estimated to have been 52 kg/ha.

4.4. Amounts of chemical elements of above ground litter

Elemental concentration in aspen leaves and twigs, unlike concentrations in other litter components, fluctuated according to time of year. Chemical data on the two former litter components are presented in Table 5. Nitrogen and potassium levels in leaves decreased with increasing age, as did sodium levels in twigs. The latter is of interest because high sodium levels in the twigs coincided with the period of high twig input. In leaves, calcium levels increased to a maximum at the time of major leaf fall, in October. These fluctuations in potassium and calcium levels during the growing season accord with patterns observed in other studies, both in warm and cool temperate regions (CURLIN 1970, TEW 1970, VAN CLEVE and NOONAN 1975). Overall concentrations of *Ca*, *Mg*, *K* and *P* in aspen leaves collected in the present study are similar to those summarized by RODIN and BAZILEVICH (1967) and those reported by YOUNG and GUINN (1966) and TEW (1970). Nitrogen content, of 2.5%, in aspen leaf tissue from the Russian stands was considerably higher than the mean content in leaves collected in the Kananaskis Valley stand near to major leaf fall (Table 5).

The amounts of chemical elements in above ground litter and in soil are reported in Table 6. As noted above, small litter fall from the overstory vegetation occurred predominantly in October while large litter fall occurred predominantly in the winter months. For the former type of litter, maximum input of chemical elements coincided with the heavy October leaf fall (Table 7). Of the inorganic elements, input was greatest for calcium (Tables 6 and 7), a result of high levels in leaf and twig litter and the high biomass of leaf fall. Sodium input in October was only slightly greater than that in the winter months and in April and May. This largely resulted from high sodium levels in twigs in April and May.

	mg/g dry wt				
K	*Na*	*Cu*	*Fe*	*Mn*	*Zn*
15.95 ± 2.07	0.106 ± 0.053	0.029 ± 0.020	0.038 ± 0.033	0.027 ± 0.008	0.164 ± 0.029
10.65 ± 4.87	0.155 ± 0.173	0.014 ± 0.008	0.079 ± 0.123	0.033 ± 0.012	0.172 ± 0.049
5.64 ± 2.08	0.044 ± 0.042	0.012 ± 0.008	0.076 ± 0.028	0.044 ± 0.019	0.234 ± 0.068
7.14 ± 2.75	5.892 ± 5.323	0.079 ± 0.021	0.309 ± 0.285	0.056 ± 0.021	0.176 ± 0.084
13.83 ± 2.99	1.114 ± 0.566	0.042 ± 0.016	0.323 ± 0.186	0.041 ± 0.018	0.297 ± 0.362
17.72 ± 3.37	1.626 ± 1.222	0.042 ± 0.011	0.399 ± 0.247	0.055 ± 0.019	0.196 ± 0.099
4.81 ± 0.78	0.309 ± 0.179	0.020 ± 0.006	0.148 ± 0.122	0.027 ± 0.009	0.125 ± 0.023
3.93	0.648	0.014	0.135	0.022	0.115

Table 6. Amounts of chemical elements (kg/ha) in above ground litter and in soil of an aspen woodland ecosystem

	C	*H*	*N*	*P*	*Ca*	*Mg*	*K*	*Na*	*Cu*	*Fe*	*Zn*
a) Annual standing crops											
Small litter											
Aspen leaves	755.311	99.551	13.504	2.809	31.458	5.087	9.578	0.0907	0.0202	0.1173	0.3688
Other leaves	68.603	8.345	1.036	0.313	4.332	0.645	0.909	0.0019	0.0015	0.0250	0.0339
Twigs	179.217	25.185	8.032	1.225	3.176	0.637	3.322	0.3501	0.0099	0.0799	0.0678
Pine needles	—	—	—	—	0.424	0.123	0.245	0.0053	0.0041	0.0104	0.0290
Detritus	—	—	—	—	3.116	0.157	1.132	0.0190	0.0126	0.0765	0.0301
Reproductive parts	—	—	—	—	0.170	0.042	0.121	0.0048	0.0025	0.0060	0.0060
Large litter	—	—	2.158	0.332	3.320	0.330	0.996	—	0.0080	0.0370	0.0500
Understory vegetation litter											
Stems and leaves	434.140	58.80	13.720	2.138	8.701	2.155	14.003	0.144	0.0196	0.1343	0.0363
Reproductive parts	23.244	3.172	1.560	0.223	0.367	0.112	1.053	0.018	0.0010	0.0412	0.0023
b) Accumulated standing crops											
Soil horizons											
Litter	4,829.77	573.44	178.80	12.32	314.41	20.67	21.38	0.55	0.11	12.44	3.20
Fermentation	9,975.86	1,058.11	475.84	27.62	668.26	42.99	35.48	1.04	0.27	29.92	8.96
Humus	23,514.44	2,664.26	1,332.13	78.44	1,593.14	65.71	215.22	73.39	0.85	263.64	3.72

Table 7. Amounts of chemical elements (kg/ha) in small litter components of the overstory during selected months

	C	*H*	*N*	*P*	*Ca*	*Mg*	*K*	*Na*	*Cu*	*Fe*	*Zn*
May											
Aspen leaves	13.277	1.841	0.785	0.092	0.269	0.070	0.481	0.0032	0.0009	0.0011	0.0049
Other leaves	0.642	0.090	0.038	0.005	0.013	0.003	0.024	0.0002	0.0000	0.0000	0.0002
Twigs	46.658	6.882	4.445	0.655	0.208	0.205	1.464	0.1207	0.0044	0.0282	0.0314
Pine needles	—	—	—	—	0.045	0.013	0.026	0.0006	0.0004	0.0011	0.0022
Detritus	—	—	—	—	1.652	0.088	0.601	0.0100	0.0037	0.0406	0.0159
Reproductive parts	—	—	—	—	0.114	0.029	0.082	0.0032	0.0017	0.0041	0.0041
August											
Aspen leaves	4.892	0.652	0.189	0.025	0.113	0.020	0.112	0.0016	0.0001	0.0008	0.0018
Other leaves	0.277	0.035	0.003	0.001	0.009	0.002	0.003	0.0000	0.0000	0.0000	0.0001
Twigs	6.040	0.780	0.113	0.021	0.157	0.019	0.061	0.0039	0.0003	0.0016	0.0016
Pine needles	—	—	—	—	0.029	0.009	0.017	0.0004	0.0003	0.0007	0.0014
Detritus	—	—	—	—	0.183	0.001	0.066	0.0011	0.0004	0.0045	0.0018
Reproductive parts	—	—	—	—	0.004	0.000	0.003	0.0001	0.0001	0.0001	0.0001
October											
Aspen leaves	708.273	93.194	11.630	2.556	30.061	4.815	8.404	0.0656	0.0180	0.1130	0.3490
Other leaves	50.646	6.131	0.700	0.228	3.276	0.483	0.637	0.0011	0.0011	0.0190	0.0252
Twigs	71.977	10.047	1.649	0.231	1.713	0.188	0.590	0.0970	0.0020	0.0200	0.0170
Pine needles	—	—	—	—	0.123	0.036	0.071	0.0015	0.0012	0.0030	0.0060
Detritus	—	—	—	—	0.278	0.015	0.101	0.0017	0.0063	0.0068	0.0027
Reproductive parts	—	—	—	—	0.004	0.001	0.003	0.0001	0.0000	0.0001	0.0001

Table 8. Biomass and amounts of chemical elements (kg/ha/y) recycled in leaf litter in particular aspen woodland stands

Reference	Country	Age of stand (years)	Biomass	*N*	*P*	*Ca*	*Mg*	*K*	*Fe*	*Mn*	*Zn*
This study	Canada	69	1734	14.5	3.1	35.8	5.7	10.6	0.1	0.07	0.40
Rodin and Bazilevich (1967)	U.S.S.R.	10	3750	93	9	63	10	53	1	1	—
		25	3620	90	9	61	9	51	1	1	—
		50	4470	111	11	76	12	63	1	1	—
Van Cleve and Noonan (1975)	U.S.A.	10	1099.9	9.0	2.0	23.9	3.7	5.2	0.6	0.2	0.10
		50	1778.0	19.7	4.4	42.6	6.3	8.8	0.7	0.7	0.18
		120	1623.1	13.5	2.7	28.1	5.3	4.7	0.6	0.4	0.19

Amounts of chemical elements in the organic mass of leaf litter in aspen woodland ecosystems in Alaska, U.S.A. and in Voronezh Province, U.S.S.R. are reported in Table 8 where they may be compared with the corresponding amounts in the organic mass of leaf litter in the Kananaskis Valley woodland. The amounts of chemical elements in leaf litter fall in the Alaskan and Kananaskis Valley woodlands are similar. The higher figures for amounts of chemical elements (excluding *N* and metals) in the Russian stands largely reflect the greater litter mass in these stands. The high *N* figure was a consequence of high level in leaf litter (as noted above) and of high leaf litter mass.

5. Discussion

Table 9 gives estimates of above ground litter fall obtained in this study and values reported in the literature for Populus stands of known ages. Compared with other North American stands, estimates of leaf litter fall for the Kananaskis Valley stand are similar. The estimate for total above ground litter fall from the overstory obtained in this study is greater than the average of 3.2×10^3 kg/ha/y calculated by Bray and Gorham (1964) for deciduous woodlands in the northern hemisphere. However, the miscellaneous measurements summarized by Bray and Gorham, in some cases did not include accurate estimates of large litter fall.

The leaf litter figures of Remezov and co-workers summarized by Rodin and Bazilevich (1967) include input from reproductive parts, seeds and small twigs as well as from leaves. These litter components are classified as small litter in Table 9. It should also be noted that the figures for total litter fall reported in Rodin and Bazilevich include inputs from leaf litter, large branches and stems, understory vegetation and dead roots. Estimates of total litter fall for 50 year old aspen woodlands in the U.S.S.R. are very high, ranging up to 13.3 metric tons/ha/y (or 13.3×10^3 kg/ha/y). Root residues accounted for approximately 11% of this figure.

Changes in structure and chemical levels of above ground parts of plants occur during aging before the parts drop to the ground and become litter. Potassium concentrations in aspen leaves decreased during the season while calcium levels increased. The former changes were probably the result of foliar leaching because potassium is a mobile chemical element (Gosz et al. 1972, Curlin 1970, van den Driessche 1974) while changes in calcium levels may have been due to the effects of translocation. In concert with such processes, herbivores may increase foliar leaching of the more mobile elements (Kimmins 1972). Diseases will also affect chemical turnover on plants and may also render particular plants susceptible to stem and branch breakage during storms. In the Kananaskis Valley woodland, large litter fall occurred mainly in the winter during the main period of storms.

Peterson et al. (1970) obtained values of 4.72 and 4.63 kcal/g dry wt for leaves and woody parts of aspen respectively. On the basis of these figures, energy input via leaf, twig and branch fall (together accounting for 92% of the total above ground litter fall from the overstory) was approximately 13,640 kcal/ha/y. Peterson et al. (1970) estimated that 2.2% of the energy contained in the standing crop of an aspen woodland stand in the Kananaskis Valley occurred in the form of foliage.

Table 9. Annual amounts (tonnes/ha) of above ground tree litter fall in various stands of *Populus* species

Country	Taxon	Age of stand	Small litter					Large litter	Reference
			Leaves	Detritus	Twigs	Other	Total		
Canada	*Populus* sp.	—	1.00—2.04						Coldwell and DeLong (1950)
Canada	*P. tremuloides*	69	1.734	0.169	0.349	0.094	**2.346**	0.830	This study
U.S.A.	*P. tremuloides*	10	1.10	0.007	0.21		**1.32**		Van Cleve and Noonan (1975)
		50	1.78	0.089	0.32		**2.19**		
		120	1.62	0.160	0.44		**2.22**		
U.S.S.R.	*P. tremula*	10	3.75		0.10		**3.85**		Rodin and Bazilevich (1967)
		25	3.62		0.49		**4.11**		
		50	4.47		0.41		**4.88**		
U.S.A.	Mixed stand *P. tremuloides* (dominant + 72% of tree stems in stand)	17	2.28		0.275		**2.555**		Crow (1974)

Once on the ground, litter components decompose at very different rates. In other studies in the aspen ecosystem, litter of *Epilobium angustifolium* decomposed faster than aspen and balsam poplar leaves (Krauter 1976, Lousier and Parkinson 1976). Woody components of litter decomposed more slowly. Chemical changes occur during decomposition and this is demonstrated by the different elemental concentrations found in the soil horizons (Carter and Cragg 1976).

Unpublished data summarized in Table 10 show chemical changes which occurred in aspen leaves placed in litter bags of 10 mm mesh in the aspen stand, near to the main study sites. These results must be interpreted with caution because decomposition and chemical changes in litter confined in bags artificially maintained near the soil surface may be different from those in natural unconfined litter (Witkamp and Olsen 1963, Anderson 1973, Lousier and Parkinson 1976). Generally, manganese, iron and sodium levels in confined litter increased with increasing age of litter while potassium levels decreased until after 36 months (Table 10). Calcium levels fluctuated but were highest in older confined litter. The increases in levels of the first three named chemical elements correlate positively with their increased levels in the aspen soil horizons according to increased soil depth (Carter and Cragg 1976 and see Van Cleve and Noonan 1971). Calcium levels increased with increasing soil depth as far as the fermentation horizon (Carter and Cragg 1976) and was thus accumulated during the main stage of decomposition.

Similarities exist between processes such as decomposition and chemical cycling in terrestrial and fresh water ecosystems. Air borne litter can be an important source of energy and chemical input into particular aquatic ecosystems; especially in lotic systems in deciduous woodlands (see Gasith and Hasler, 1976, for references in the literature). Hodkinson (1975a) studied litter input into an abandoned beaver pond in the Kananaskis Valley. He found that allochthonous litter input was much greater than input from bank vegetation

Table 10. Chemical composition (± 1 SD) of aspen leaf litter in litter bags in the field

Time	% *dry wt*			mg/g dry wt		
(years)	*C*	*H*	*N*	*P*	*Ca*	*Mg*
0	*47.44 ± 1.26*	*6.15 ± 0.38*	*0.78 ± 0.22*	1.71 ± 0.88	20.16 ± 8.43	3.23 ± 0.66
2	*48.66 ± 1.09*	*5.78 ± 0.29*	*1.21 ± 0.13*	1.20 ± 0.22	17.02 ± 1.22	1.52 ± 0.15
3	*46.63 ± 0.70*	*5.15 ± 0 32*	*1.68 ± 0.10*	1.01 ± 0.15	43.18 ± 4.00	2.26 ± 0.26
4	*47.58 ± 1.81*	*5.28 ± 0.16*	*1.77 ± 0.07*	0.93 ± 0.12	37.09 ± 1.94	2.48 ± 0.30
5	*47.91 ± 1.87*	*5.33 ± 0.19*	*1.79 ± 0.13*	0.80 ± 0.17	34.51 ± 2.40	2.35 ± 0.14

	mg/g dry wt					
	K	*Na*	*Cu*	*Fe*	*Mn*	*Zn*
0	5.64 ± 2.08	0.044 ± 0.042	0.012 ± 0.008	0.076 ± 0.028	0.044 ± 0.019	0.23 ± 0.07
2	2.11 ± 0.28	0.133 ± 0.024	0.008 ± 0.000	0.666 ± 0.087	0.131 ± 0.012	0.41 ± 0.08
3	1.56 ± 0.22	0.104 ± 0.017	0.008 ± 0.001	0.599 ± 0.140	0.193 ± 0.041	0.54 ± 0.11
4	2.07 ± 0.20	0.102 ± 0.037	0.015 ± 0.006	0.777 ± 0.088	0.170 ± 0.031	0.45 ± 0.03
5	2.02 ± 0.48	0.140 ± 0.067	0.020 ± 0.010	0.984 ± 0.188	0.164 ± 0.030	0.17 ± 0.14

Table 11. Biomass and amounts of particular chemical elements recycled via leaf litter (aspen and other leaves) and by adult carabids and oribatid mites in the aspen woodland ecosystem

	Biomass	*Ca*	*K*	*Na*
Aspen[1])	1585	31.5	9.6	0.09
Other leaves[1])	149	4.3	0.9	0.002
Adult carabids[2])	0.37	0.001	0.025	—
Adult oribatids[2])	3.36	1.12	0.15	0.01

1) Expressed as kg/ha/y.

2) Expressed as kg/ha/month.

pushed into the pond by snow. HODKINSON pointed out that such ponds, with their well developed sediments, are conceptually intermediate between terrestrial and running water systems. In another study, on the same ecosystem, HODKINSON (1975b) described chemical changes in litter confined in bags. Potassium was initially rapidly leached from all litter substrates but elemental concentrations levelled off within a year of the start of the experiment. Phosphorous levels in the litter decreased more gradually. Similar changes in the above named chemical elements occurred in the terrestrial litter bag experiments summarized in Table 10.

Information on litter fall and chemical standing crops in litter should be considered when describing the roles of particular consumers in decomposition, chemical cycling and energy flow. Some studies have been made on the roles of particular consumers in the aspen ecosystem in the Kananaskis Valley. Estimates of ingestion and egestion of chemical elements by populations of a carabid species, *Agonum retractum* LECONTE, and a fungivorous oribatid mite, *Eupterotegaeus rostratus* HIGGINS et WOOLLEY, are available (CARTER and PRITCHARD 1976, and CARTER and CRAGG 1977, respectively). General estimates of comparative amounts of biomass and chemical elements recycled by total adult carabids and oribatids in the ecosystem are included in Table 11 where they may be compared with the corresponding amounts recycled in leaf litter.

In relation to energy input via leaf litter fall, the amounts metabolized by particular groups of soil animals were small. Dash and CRAGG (1972) estimated that enchytraeids in the aspen soil metabolized 510 kcal/ha/y and MITCHELL (1974) obtained a figure of 65 kcal/ha/y for oribatids, whereas energy input via leaf fall was approximately 8,200 kcal/ha/y. However, such comparisons must be made with caution because the total chemical and energy content of leaf litter is not available to consumers.

6. Summary · Zusammenfassung

Litter fall of the above ground parts of a predominantly aspen woodland in the Kananaskis Valley of Alberta, Canada was studied from 1967 to 1970. Elemental concentrations and the amounts of elements in various litter components were determined.

Small litter (leaves, twigs, pine needles, aspen and poplar reproductive parts and detritus) formed 74% of the total annual litter fall. Approximately 90% of the leaf fall occurred in October. Aspen leaves (*Populus tremuloides* MICHX.) constituted 70% of the annual small litter fall. Twig input (15% of annual small litter) occurred mainly during the autumn and winter months and large litter fell mainly in the winter months. Mean small and large litter fall was 2346 and 830 kg dry wt/ha/y, respectively, while input from understory vegetation was approximately 1030 kg/ha/y.

Potassium levels in leaves decreased with increasing age. In leaves, calcium levels increased to a maximum at the time of major leaf fall. Maximum chemical input via small litter fall coincided with the heavy October leaf fall. However, sodium input in October was only slightly greater than that in the winter months and in April and May. This largely resulted from high sodium levels in twigs which had fallen in April and May.

Bestandesabfall und Stoffkreislauf in einem Aspen-*(Populus tremuloides)* Wald-Ökosystem im Kanadischen Felsengebirge

Der oberirdische Bestandesabfall eines vorwiegend mit Aspen (*Populus tremuloides* MICHX.) bestandenen Waldgebietes im Kananaskis-Tal von Alberta, Kanada, wurde von 1967—1970 untersucht. Die Elementkonzentration und der Elementgehalt der verschiedenen Komponenten des Bestandesabfalls wurden bestimmt. Die Feinstreu (Blätter, Zweige, Kiefernnadeln, Blüten- und Fruchtstände und Detritus) machte 74% des totalen jährlichen Bestandesabfalls aus. Annähernd 90% der Blattstreu fällt im Oktober. Aspenblätter (Blätter von *P. tremuloides*) machten 70% der jährlichen Feinstreu aus. Der Input an Zweigen (15% der jährlichen Feinstreu) fiel hauptsächlich im Herbst und in den Wintermonaten an; die Grobstreu fiel hauptsächlich in den Wintermonaten. Die durchschnittliche Menge an Fein- bzw. Grobstreu betrug 2346 bzw. 830 kg Trockensubstanz pro Hektar und Jahr während der Input aus der Streuschicht und der Bodenvegetation annähernd 1030 kg/ha/a betrug.

Der Kaligehalt der Blätter nahm mit zunehmendem Alter ab; gleichzeitig stieg der Kalziumgehalt der Blätter bis zum stärksten Laubfall an. Mit dem stärksten Blattfall im Oktober erhält der Stoffkreislauf auch die größte Zufuhr an [umsetzbaren] Elementen. Der Natrium-Input im Oktober war jedoch nur geringfügig größer als in den folgenden Winter- und Frühjahrsmonaten. Dies ergibt sich im wesentlichen aus dem hohen Natriumgehalt der noch im April und Mai abfallenden Zweige.

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