

Decomposition and nutrient dynamics of ponderosa pine needles in a Mediterranean-type climate

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A litter-bag technique was used to measure decay rates and assess changes in organic and inorganic constituents of ponderosa pine (*Pinus ponderosa* Laws.) needle litter during decomposition over a 2-year period in old- and young-growth forests in the Sierra Nevada of California. Rates of mass loss were among the lowest reported for temperate and boreal forests, with annual decomposition constants of about 0.08 and 0.18 year⁻¹ for the old- and young-growth forests, respectively. Apparently, the temporal separation of warm temperatures and moist conditions found in Mediterranean-type climates severely limits decomposition in these coniferous forests. In the old-growth forest, comparison of estimates of tree nutrient uptake with net releases of nutrients from fine litter during their 1st year of decomposition suggests that recent litter fall potentially acts as a significant source of P, Mg, and K for tree uptake in this forest; in contrast, recently fallen litter acts as a net sink for N, S, and Ca. Despite initially lower indices of litter quality for litter originating from the old-growth relative to the young-growth forest, no significant difference in decomposition rates of these two litter age-classes was found when placed at either site. This result does not support the hypothesis that decreases in decomposition rates during forest development are driven by decreases in the quality of litter fall.

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Une technique de sacs à litières a été utilisée pour mesurer les taux de décomposition et pour évaluer les changements des constituants organiques et inorganiques de litières d'aiguilles de pin ponderosa (*Pinus ponderosa* Laws.) durant la décomposition sur une période de 2 ans dans une vieille et une jeune forêt dans les montagnes de la Sierra Nevada en Californie. Les taux de perte de masse étaient dans les plus bas rapportés pour les forêts tempérées et boréales, avec des constantes annuelles de décomposition de l'ordre de 0,08 et 0,18 an⁻¹ pour la vieille et la jeune forêt respectivement. Apparemment, la séparation temporelle des températures chaudes et des conditions humides rencontrées dans les climats de type méditerranéen a sévèrement limité la décomposition dans ces forêts conifériennes. Dans la vieille forêt, la comparaison des estimés des prélevements de nutriments par les arbres avec les libérations nettes de nutriments originant de la litière fine durant leur 1^{re} année de décomposition suggère que la litière fraîche agit potentiellement comme une source significative de P, Mg et K pour le prélevement par les arbres dans cette forêt; au contraire, la litière fraîche agit comme une perte pour N, S et Ca. En dépit d'indices initiaux plus bas de la qualité de la litière originant de la vieille forêt comparée à la jeune forêt, aucune différence significative dans les taux de décomposition de ces litières de classes d'âge différentes n'a été trouvée lorsque les différentes litières ont été placées à chacune des stations. Ces résultats ne supportent pas l'hypothèse qu'une diminution des taux de décomposition avec le développement de la forêt origine des diminutions de la qualité de la litière.

[Traduit par la rédaction]

Introduction

The Mediterranean-type climate of California is characterized by warm, dry summers and cool, wet winters. The general asynchrony of favorable temperature and moisture conditions for biological activity in this climate have profound effects on many ecosystem processes. Plant growth, nutrient uptake, and nutrient cycling processes appear to be most active during the fall and spring seasons in Mediterranean-type climates, when soils are moist and warm (Jackson *et al.* 1988; Hart and Firestone 1989, 1991). This temporal separation of warm temperatures and moist conditions also might limit rates of litter decomposition, and prolonged retention of essential plant nutrients in litter may reduce ecosystem productivity. This effect would likely be most severe in ecosystems having litter that is inherently recalcitrant to decomposition, such as

coniferous forests. However, few measurements of rates of litter decomposition and nutrient release exist for coniferous forests with Mediterranean-type climates.

The quality of litter returned to the soil may decline during forest development, and this process has been suggested as a possible explanation for the generally lower rates of decomposition and nutrient cycling in older forests (Vitousek 1982; Gholz *et al.* 1985). However, most previous studies of decomposition processes in different-aged forests have either used the same substrate for all stands (Edmonds 1979; Binkley 1984; Klemmedson *et al.* 1985) or only measured decomposition rates of litter native to each stand (Gholz *et al.* 1985). The lack of reciprocal litter treatments in these studies has prevented separation of the effects of changes in the quality of litter inputs from concurrent changes in litter environment (i.e., soil temperature, moisture, and nutrient availability) as forests mature. In this study, we assessed the relative importance of litter quality and microenvironment as controlling factors of ponderosa pine (*Pinus ponderosa* Laws.) needle

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litter decomposition and nutrient release by reciprocally transplanting needle litter between an old- and a young-growth forest.

Study sites

Two forest sites were used in this study (described in more detail in Hart and Firestone 1989). An old-growth mixed-conifer site (greater than 100 years old) comprised the following: white fir (*Abies concolor* (Gord. & Glend.) Lindl.), incense-cedar (*Calocedrus decurrens* (Torr.) Florin), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), ponderosa pine, sugar pine (*Pinus lambertiana* Dougl.), and California black oak (*Quercus kelloggii* Newb.). A mixed-conifer plantation (hereafter referred to as the young-growth site) was established after clear-cutting a portion of the previous forest in 1975. The species composition of the young-growth site was similar to the old-growth site. Prior to planting, logging slash was raked into piles and burned. The forest was 9 years old at the beginning of the study and had an open canopy. The two sites were located within 500 m of each other in Blodgett Forest Research Station, at an elevation of 1300 m in the western slopes of the Sierra Nevada of California, United States ($38^{\circ}52'N$, $120^{\circ}40'W$).

In this region, annual precipitation averages about 170 cm, about 85% of which falls primarily as snow between October and March. However, snow accumulation for more than a few days is rare at this elevation owing to widely fluctuating daily temperatures during the winter months. Annual precipitation during the study was 108 and 171 cm in 1985 and 1986, respectively. Mean daily maximum air temperatures ranged from $9^{\circ}C$ in winter to $28^{\circ}C$ in summer; mean daily minimum air temperatures ranged from $2^{\circ}C$ in winter to $14^{\circ}C$ in summer.

The mineral soil is a well-drained, sandy-loam Ultic Haploxeralf, formed on granodiorite parent material. In the young-growth site bare mineral soil was exposed between trees because site preparation had removed most of the forest floor. A substantial mor-type organic layer (approximately 53 Mg organic matter $\cdot ha^{-1}$, 10-cm thick) was present in the old-growth site (Hart and Firestone 1991).

Materials and methods

Freshly fallen ponderosa pine needles were collected on nylon screens placed under at least 10 different ponderosa pine trees in each site in October 1984. Needle litter was retrieved 1 month later, composited within litter age-classes (i.e., ponderosa pine needle litter originating from old- and young-growth sites), and air dried in the laboratory. Microinvertebrates and other non ponderosa pine litter contaminants were removed by exposing the litter to heat lamps followed by handpicking using forceps and a dissecting microscope. Hereafter, needle litter collected from the old- and young-growth sites will be referred to as old and young litter, respectively. Ten grams of air-dried litter were placed in 10×20 cm nylon litter bags (3×4 mm mesh). This density of litter per bag was similar to the annual fine litter fall in the old-growth site (Hart and Firestone 1991). The ash-free, ovendry ($65^{\circ}C$) mass equivalent was 9.01 and 8.62 g per bag for old and young litter, respectively. All mass and nutrient quantities in litter have been expressed on an ash-free, ovendry mass basis; therefore, we will refer hereafter to ash-free, ovendry mass as simply mass.

In January 1985, a 45-m transect was randomly located in the old- and young-growth sites. Clusters of 10 litter bags (5 containing old litter and 5 containing young litter) were placed at 5-m intervals along the transect in each site, giving 10 replicate litter bags per litter age-class per site for each of five sampling dates (total of 100 litter bags per site). This experimental design produced four treatments: old litter placed in the old-growth site, old litter placed in the young-growth site, young litter placed in the old-growth site, and young litter placed in the young-growth site. Litter bags were brought to the field and removed after each sampling date in paper bags to reduce spillage inaccuracies in our decomposition estimates (Suffling and Smith 1974). Litter bags were secured to the surface of the forest floor

(old-growth site) or mineral soil (young-growth site) using steel pins. One litter bag from each treatment was randomly selected and removed from each cluster immediately after placement and after 1, 3, 12, and 24 months, and brought back to the laboratory. Litter was air dried and then removed from the bag; mineral soil adhering to the needles was removed with a brush. Microinvertebrates and non ponderosa pine litter contaminants were removed as described previously. Air-dry mass was determined on all retrieved litter bags ($n = 10$ per treatment), and five litter bags from each treatment were randomly selected for estimation of ash and water content, and for chemical analyses. The selected litter was ground in a Wiley mill to ≤ 40 mesh (425 μm). From the five selected litter bags from each treatment, subsamples were taken to determine both water ($65^{\circ}C$ for 48 h) and ash ($550^{\circ}C$ for 6 h) content. Additional subsamples from these same litter bags were used for total carbon (C) (wet digestion – diffusion titration; Synder and Trofymow 1984), total nitrogen (N) (using a salicylic acid – thiosulfate modification of the micro-Kjeldahl procedure that includes NO_2^- and NO_3^- ; Bremner and Mulvaney 1982), and phosphorus (P), sulfur (S), calcium (Ca), magnesium (Mg), and potassium (perchlorate – nitric acid digestion; Zasoski and Burau 1977) determinations. Total N and P were determined colorimetrically on a Lachat flow-injection analyzer (Stewart et al. 1976; QuikChem Systems 1987). Calcium, Mg, and S were determined on a Perkin-Elmer Plasma 40 inductively coupled plasma spectrophotometer. Potassium was measured on a Perkin-Elmer 372 atomic adsorption spectrophotometer using flame-emission methods (Perkin-Elmer Corporation 1976). A laboratory standard reference plant material (Douglas-fir needles) was digested separately, and its nutrient concentrations were analyzed with all litter analyses to help maintain analytical quality control. Recovery of nutrients in this reference material averaged within 5% of the accepted value.

For organic constituent analyses, the ground litter was composited within treatments, and three subsamples were used from each composite to determine hot water soluble (HWS) mass as well as lignin, hemicellulose, and cellulose concentrations using a sequential extraction, gravimetric analysis procedure (Harper and Lynch 1981). In addition, total organic C (using a Dohrmann DC-80 C analyzer with an infrared detector) and total N (modified micro-Kjeldahl procedure) were determined on the HWS mass extracts.

Separate full-factorial, three-way analysis of variance (ANOVA) models were used to test for significant effects on dependent variables, with site, litter age-class, and sampling date as main effects. Dependent variables were expressed relative to their initial quantities within the litter for these analyses. A logarithmic transformation was applied to the dependent variables prior to statistical analyses to meet the homogeneity of variance criterion. Because significant interactions between main effects occurred in the ANOVA using the amount of mass remaining as the dependent variable, significant differences in decomposition rates were tested by comparing decomposition rate constants (k) using a Student's t -test (Wieder and Lang 1982). Decomposition rate constants were calculated as the negative slope of the line produced by linear regression of the natural logarithm of the mass remaining at each sampling date over the entire 2-year period (Schlesinger and Hasey 1981). This analysis assumes an exponential litter-decay model. All statistical analyses were conducted using the SAS software package (SAS Institute Inc. 1985).

Results

Decomposition rates

Composites of freshly fallen ponderosa pine needle litter from old- and young-growth sites differed in several characteristics that have been previously used as indices of litter quality (Table 1). Old litter initially had a significantly lower N and HWS mass concentrations than young litter; however, the lignin concentration was similar between the two litter age-classes. Further, the C:N ratio was initially higher for the old-growth litter (Table 1).

TABLE 1. Some initial quality characteristics of ponderosa pine needle litter originating from old- and young-growth sites

Litter age-class	N (g·kg ⁻¹)	HWS mass (kg·kg ⁻¹)	Lignin (kg·kg ⁻¹)	C:N ratio	Lignin:N ratio
Old	5.71 (0.05)	0.187 (0.007)	0.261 (0.021)	89.3 (1.7)	45.7 (3.7)
	8.14 (0.08)	0.214 (0.009)	0.309 (0.025)	64.9 (0.7)	38.0 (3.1)
Significant difference ^a	0.001	0.10	ns	0.001	ns

NOTE: Results are shown as the mean with 1 SE in parentheses. Nitrogen, hot water soluble (HWS) mass, and lignin concentrations are expressed on an ash-free, ovendry mass basis; $n = 5$ for N and C:N ratio, and $n = 3$ for HWS mass, lignin, and lignin:N ratio.

^aSignificance level at which means within the same column are significantly different (by Student's *t*-test); ns, not significantly different ($p > 0.10$).

TABLE 2. Measured and predicted mass loss and decomposition rate constants (*k*) for ponderosa pine needle litter during a 2-year litter-bag study

Litter age-class	Site	Time (years)	Mass loss (%)		<i>k</i> (year ⁻¹)		
			Measured	Predicted ^a	Olson ^b	Schlesinger and Hasey ^c	Predicted ^d
Old	Old	1	6.8	16.9	0.07	0.08	0.20
		2	15.5	—	0.08	0.08	—
	Young	1	14.5	16.8	0.16	0.16	0.19
		2	30.7	—	0.18	0.18	—
Young	Old	1	7.8	14.5	0.08	0.09	0.18
		2	17.5	—	0.10	0.09	—
	Young	1	13.6	14.4	0.15	0.15	0.18
		2	31.2	—	0.19	0.18	—

^aPredicted mass loss based on Meentemeyer (1978), Fig. 3; no estimates are presented for 2-year values because Meentemeyer's model was based on 1-year data.

^bCalculated from Olson (1963) using $X = X_0 e^{-kt}$, where X is the mass of needles in litter bags at time t , X_0 is the initial mass of needles in litter bags, and k is the decomposition rate constant.

^cCalculated using a negative exponential equation fit using least-squares regression to mean measured values ($n = 4$; Schlesinger and Hasey 1981); the regression equation was forced through the origin so that the equation predicted the initial mass of needles in litter bags at time zero; r^2 -values ranged from 0.84 to 0.98, and all were significant ($p < 0.01$).

^dPredicted *k*-values based on Meentemeyer (1978), Fig. 2; no estimates are presented for 2-year values because Meentemeyer's model was based on 1-year data.

Mass losses from litter placed in both sites were very low; about 7 and 15% of the mass disappeared during the 1st year in the old- and young-growth sites, respectively (Table 2). Mass loss from litter in the 2nd year was slightly greater than in the 1st year for all treatments. The two litter age-classes showed similar patterns of mass loss in both sites over the 2-year period, although a significant site \times litter age-class interaction did occur ($p = 0.093$, Table 3). Annual litter-decay rate constants (*k*), calculated using both Olson's (1963) method and the regression method of Schlesinger and Hasey (1981) to fit mass-loss data to an exponential-decay model, were also very low and were in good agreement with each other (Table 2). Values of *k* for litter incubated in the old-growth site were about one-half those for litter incubated in the young-growth site (significantly different at $p = 0.0001$). Litter age-class had no significant effect ($p > 0.10$) on *k*-values in either site. Further, annual litter-decay constants calculated using the 2-year mass-loss data were not significantly different from the 1-year values (Table 2). A linear-decay model typically fit the mass-loss data as well as the exponential decay

model (i.e., r^2 -values of both models ranged from 0.84 to 0.98, $p < 0.01$) and gave similar estimates of annual decay rates (data not shown).

Measured changes in litter mass loss and calculated *k*-values were compared with Meentemeyer's (1978) predicted values, which are based on the initial lignin concentration of the litter and an estimate of actual evapotranspiration. In the present study, actual evapotranspiration values for each site were estimated using a water balance model (Warrington and Weatherred 1983). Inputs to the model included monthly precipitation and mean monthly air temperature (measured at a single, nearby location within Blodgett Forest Research Station), and slope, aspect, vegetative cover, and soil moisture storage capacities determined for each site. Predicted mass loss and *k*-values using Meentemeyer's model were about twice as large as our measured values in the old-growth site. However, the estimates based on Meentemeyer's model were only slightly higher than our measured values for both litter age-classes placed in the young-growth site (Table 2).

TABLE 3. Probability values for main effects and interactions generated using a three-way ANOVA of amounts of mass and nutrients remaining in ponderosa pine needle litter during decomposition in the field

Effect	df	Mass	C	N	P	S	K	Ca	Mg
Site	1	0.0001	0.0001	0.7991	0.1893	0.0036	0.1166	0.5530	0.0245
Litter	1	0.2834	0.0001	0.0002	0.0419	0.0346	0.4643	0.1476	0.4219
Date	3	0.0001	0.0001	0.0001	0.0001	0.0004	0.0001	0.0001	0.0027
Site × litter	3	0.0930	0.3523	0.0528	0.3093	0.5674	0.4428	0.7905	0.9201
Site × date	3	0.0001	0.0001	0.6837	0.6186	0.0001	0.2839	0.8883	0.4526
Litter × date	3	0.0604	0.0074	0.4835	0.0801	0.7372	0.5523	0.2301	0.9475
Site × litter × date	3	0.8544	0.7807	0.5173	0.7036	0.6383	0.9348	0.4668	0.7420

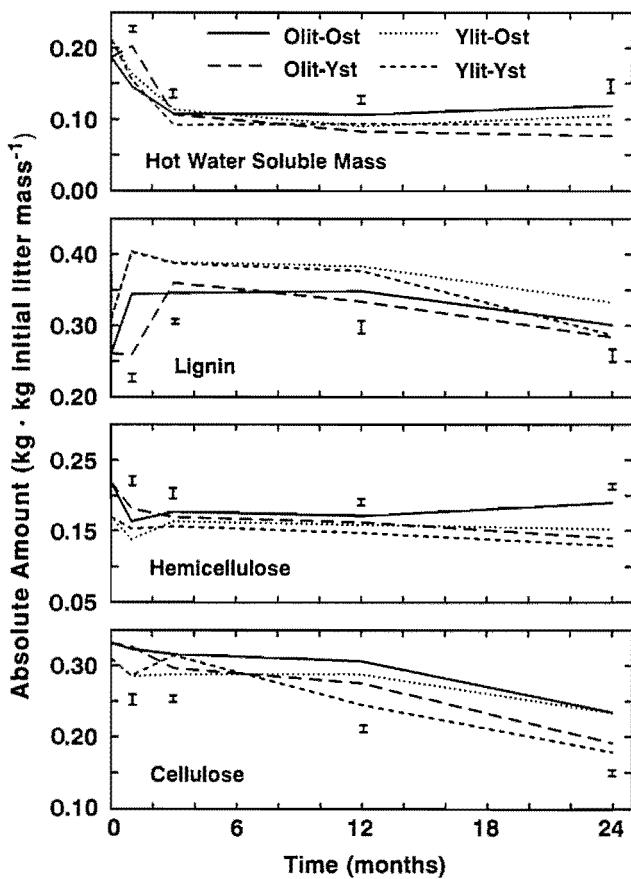


FIG. 1. Changes in the organic constituents of ponderosa pine needle litter decomposing over a 2-year period. Absolute amounts are expressed relative to the initial ash-free, ovendry mass of litter. Vertical bars denote the maximum standard error observed during that sampling date. Olit-Ost, litter originating from the old-growth site placed in the old-growth site; Olit-Yst, litter originating from the old-growth site placed in the young-growth site; Ylit-Ost, litter originating from the young-growth site placed in the old-growth site; Ylit-Yst, litter originating from the young-growth site placed in the young-growth site.

Organic constituent dynamics

Changes in the concentration of organic constituents and nutrients in litter provide information concerning the composition of the residual litter. However, changes in absolute amounts of these litter components are needed to assess which classes of organic compounds and nutrients are being released

or accumulated during decomposition. Because rates of decomposition for both litter age-classes placed in each site were fairly constant over the 2-year period (Table 2), the dynamics of absolute amounts of organic constituents and nutrients in the litter generally paralleled changes in concentration of these compounds and elements (data not shown).

HWS mass of all litter decreased rapidly during the first 3 months of decomposition and accounted for about half of the total mass loss from litter over the entire 2-year period (Fig. 1). The absolute amount of lignin, however, increased by a similar magnitude during the first 3 months of decomposition, then generally declined at a slow rate for the remainder of the 2-year period (Fig. 1). The absolute amounts of lignin in all litter after 2 years of decomposition were similar to initial amounts. The absolute amount of hemicellulose in litter decreased slightly in all treatments during the first 3 months and then remained relatively unchanged thereafter (Fig. 1). Loss of cellulose from all litter (Fig. 1) roughly paralleled the loss in mass and accounted for about half of the total mass loss in the litter during the 2-year period.

As would be expected, changes in the absolute amount of carbon in the HWS litter fraction showed a similar pattern as changes in HWS mass; however, the dynamics of HWS N were quite different (Fig. 2). Only a slight loss in HWS N was found for the old litter during the 1st month. The young litter, which initially had a substantially higher HWS N concentration, lost HWS N very rapidly over the first 3 months. By the end of the 2-year period, similar absolute amounts of HWS N remained in litter from all treatments (about $0.6 \text{ g} \cdot \text{kg initial litter mass}^{-1}$).

In general, the main effects were all significant ($p < 0.10$) in the ANOVA for the amounts of organic constituents remaining in the litter (data not shown). Exceptions occurred for the HWS mass and cellulose fractions, where site and litter age-class were not significant, respectively. Site and litter age-class effects on the amount of organic constituents remaining appeared to be due simply to greater decomposition rates in the young-growth site coupled with differences in the initial organic composition of the litter, because no significant interactions between these effects were found. An exception to this finding occurred for HWS N, where the site × litter age-class interaction was significant ($p = 0.073$).

Nutrient dynamics

Figure 3 shows the changes in the absolute amounts of nutrients contained in litter for all treatments during decomposition. As expected, changes in the absolute amount of C during decomposition (Fig. 3) were similar to changes in mass.

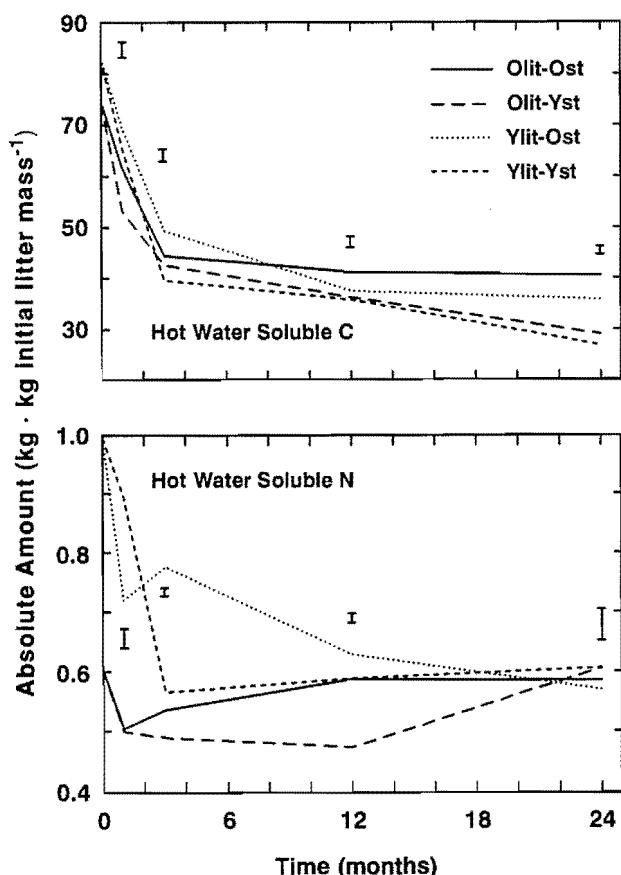


FIG. 2. Changes in the absolute amounts of hot water soluble C and N in ponderosa pine needle litter decomposing over a 2-year period. Absolute amounts are expressed relative to the initial ash-free, oven-dry mass of litter. Vertical bars denote the maximum standard error observed during that sampling date. See Fig. 1 for key to treatment abbreviations.

Nitrogen dynamics of litter from all treatments were generally similar (Fig. 3); however, the effect of the site in which a given litter age-class was placed on litter-N dynamics was different for each litter age-class (significant stand \times litter interaction, $p = 0.053$; Table 3). Nitrogen was lost rapidly from litter during the first 3 months, followed by a period of net increase in N (net immobilization) between 3 and 12 months, and after 12 months a period of net N release (Fig. 3). At the end of the 2-year period, between 82 and 94% of the original N mass remained in the litter.

Litter-P dynamics were different from N dynamics (Fig. 3). Litter age-class had a significant effect ($p = 0.042$) on litter-P dynamics (Table 3), despite both litter age-classes having similar initial P concentrations (Fig. 3) and similar decomposition rates within each site. After 2 years, between 68 and 78% of the original P mass remained in the litter.

There was a rapid absolute accumulation of S in litter during the first 3 months (Fig. 3). The magnitude of this increase was about twice as large for litter placed in the old-growth site (significant site effect at $p = 0.004$; Table 3). Litter age-class also affected the magnitude of net S accumulation during this period (significant litter age-class effect at $p = 0.035$; Table 3). In each stand the young litter accumulated more S than the old litter despite similar initial S

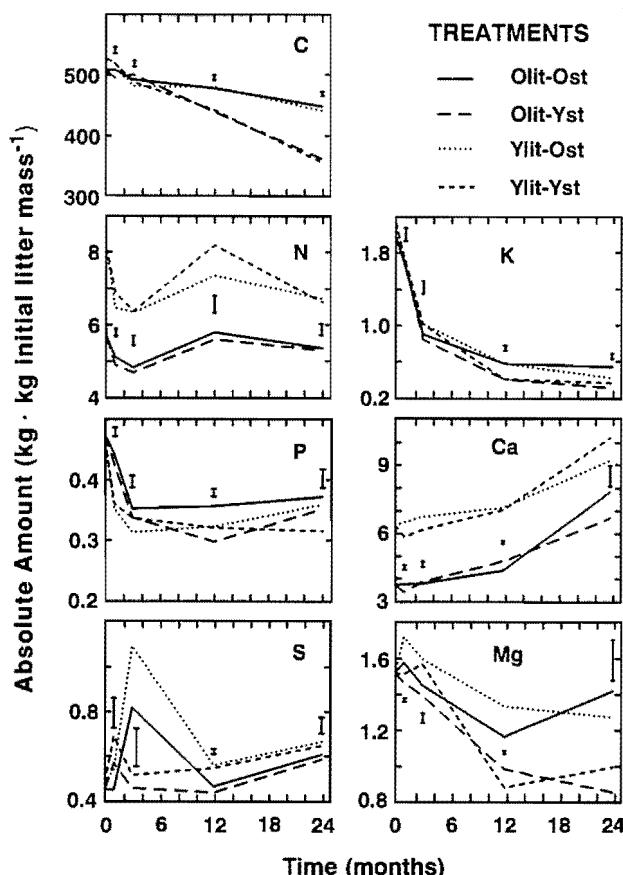


FIG. 3. Changes in the absolute amounts of C, N, P, S, K, Ca, and Mg in ponderosa pine needle litter decomposing over a 2-year period. Absolute amounts are expressed relative to the initial ash-free, oven-dry mass of litter. Vertical bars denote the maximum standard error observed during that sampling date. See Fig. 1 for key to treatment abbreviations.

concentrations. After this period of rapid net accumulation, S was released until the absolute mass of S in litter was similar to the initial amount. Subsequently, S again appeared to increase over the last 12 months of the 2-year study period. Between 130 and 142% of the original amount of S remained in the litter after 2 years.

Litter-K dynamics were very similar in all treatments, with K decreasing in absolute amount in an exponential fashion (Fig. 3). No significant effect of site, litter age-class, or interaction between these factors was found (Table 3). After 2 years, only 20–30% of the original amount remained.

The absolute amount of Ca in litter generally increased throughout the study in all litter treatments, and between 145 and 210% of the original amount remained after 2 years (Fig. 3). Old litter initially contained substantially less Ca than young litter (significantly different by t -test, $p < 0.001$); however, the absolute increases in Ca were similar for both litter age-classes within each site (Table 3, Fig. 3).

The absolute amount of Mg in litter decreased substantially in all treatments during the 1st year of decomposition (Fig. 3). Magnesium accumulated during the 2nd year in old litter placed in the old-growth site and in young litter placed in the young-growth site. Litter from the other two reciprocally transplanted treatments continued to release Mg during the

2nd year. The site where litter was placed had a significant effect ($p = 0.025$) on the amount of Mg remaining during decomposition (Table 3). The amount of Mg remaining in the litter after 2 years ranged from 56 to 93% of the original amount.

Carbon:nitrogen ratios of total litter and the HWS litter fraction are presented in Fig. 4. Despite a fairly large difference in initial C:N ratios of the total litter, the C:N ratio of old and young litter showed similar dynamics during decomposition (Fig. 4a). During the first 3 months of decomposition the C:N ratio increased, and then generally decreased for the rest of the 2-year period. The C:N ratio of the HWS fraction (Fig. 4b), presumably representing the most labile fraction of the total litter, showed a different pattern during decomposition than the C:N ratio of the total litter.

Discussion

Decomposition rates

Decomposition rates of ponderosa pine needles at these two sites experiencing a Mediterranean-type climate were among the lowest reported for coniferous leaf litter in temperate or boreal environments. The lowest decomposition rate of coniferous litter in temperate and boreal environments that we could find was reported by Bruhn (1980) for Jeffrey pine (*Pinus jeffreyi* Grev. & Balf.), having a decomposition constant of only 0.05 year^{-1} . This estimate was also for a Mediterranean-type climate in the mountains of southern California, which is cooler than our Sierra Nevada site and receives about one-fourth the mean annual precipitation. Apparently, the temporal separation of warm temperatures from moist conditions found in Mediterranean-type climates severely limits the rate of decomposition in these coniferous forests. Slow rates of decomposition coupled with large annual inputs of fine needle litter (about $4000 \text{ kg} \cdot \text{ha}^{-1}$ for the old-growth site; Hart and Firestone 1991) generally result in large accumulations of organic matter on the forest floor in mature stands of these forest ecosystems (Jenny *et al.* 1949; Stohlgren 1988; Hart and Firestone 1991).

Several previous studies have shown that decomposition of needle litter or cellulose substrates occurs faster in younger forests and clearcuts than in older forests (Edmonds 1979; Vogt *et al.* 1983; Binkley 1984; Klemmedson *et al.* 1985), although exceptions do exist (MacLean and Wein 1978; Edmonds 1979; Edmonds and Bigger 1984). Differences in observed decomposition rates among different-aged forests have been attributed to between-site differences in microclimate and nutrient availability. The effect of changes in within-species litter quality as a forest matures on decomposition rates has received surprisingly little attention and has not been previously tested. The importance of litter quality factors in controlling decomposition rates of litter from different species has been well documented by numerous investigators, and several indices of litter quality have been proposed (Fogel and Cromack 1977; Berg and Staaf 1980, 1981; Aber and Melillo 1980; Melillo *et al.* 1982; McClaugherty and Berg 1987). All of the indices of litter quality that we tested except lignin concentration (e.g., N and HWS mass concentrations and C:N and lignin:N ratios) suggested that at a given site, decomposition would be slower for litter originating from the old-growth site than from the young-growth site (Table 1). We found, however, no significant difference in decomposition rates of these two litter age-classes in either

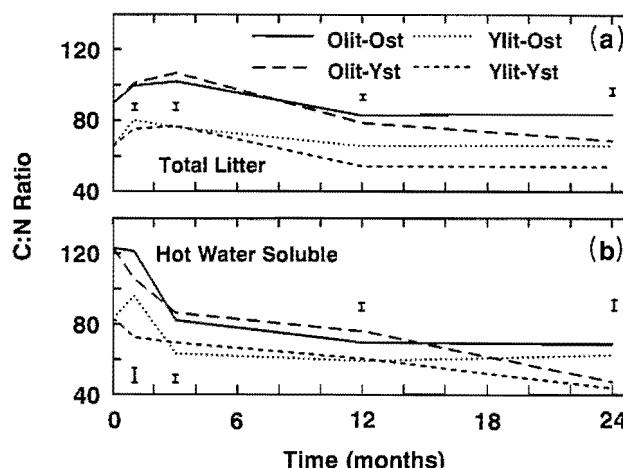


FIG. 4. Changes in the mean C:N ratio of (a) the total litter and (b) the hot water soluble fraction during decomposition of ponderosa pine needle litter. Vertical bars denote the maximum standard error observed during that sampling date. See Fig. 1 for key to treatment abbreviations.

site (Table 2). This result suggests that the changes in litter quality within a tree species that occur during forest development may not be responsible for the decline in decomposition rates observed in mature relative to young forests. However, because our study consisted of only two forest age-classes that were unreplicated, this interpretation should be viewed with caution.

Unmeasured differences in microenvironmental factors between sites might account for the twofold lower rates of decomposition in the old-growth site relative to the young-growth site (Vogt *et al.* 1983). Whitford *et al.* (1981) suggested that clear-cut forests might represent an exception to Meentemeyer's (1978) actual evapotranspiration – lignin model of decomposition, because the extreme fluctuations in environmental conditions experienced at the mineral-soil surface (where the litter bags are placed) would not be reflected in a macroclimate actual evapotranspiration estimate. Their data showed that for both dogwood (*Cornus florida* L.) and chestnut oak (*Quercus prinus* L.) leaf litter, Meentemeyer's model substantially overestimated the annual mass loss in a clearcut, especially for the more recalcitrant (lignin-rich) oak litter. Predicted and actual decomposition rates were more similar for litter placed in the mature hardwood forest. In our study, we found just the opposite pattern; predicted decomposition rates from Meentemeyer's model were relatively similar in the recently clear-cut, young-growth forest, while predicted rates were substantially higher than actual rates in the old-growth forest (Table 2). Nevertheless, our results also suggest that litter lignin concentration and macroclimatic indices (i.e., actual evapotranspiration) alone cannot explain the observed differences in decomposition rates between our two sites.

Mineral soil N availability was substantially greater in the young-growth site (Hart and Firestone 1989). Greater exogenous N availability may in part account for the observed higher rates of needle litter decomposition in the young-growth site (Vogt *et al.* 1983), because the rate of litter decomposition is apparently N limited (suggested by the net accumulation of N in the litter; Fig. 3). However, ^{15}N tracer studies in these same two sites have shown a greater N flux (presumably

via fungal translocation) from the mineral soil to overlying litter (on a per gram of litter basis) in the old-growth site (Hart 1990; Hart and Firestone 1991). Thus, it appears that between-site differences in soil N availability alone also cannot account for the large observed differences in litter decomposition rates in these sites.

Organic constituent dynamics

Our results suggest that within-species differences in initial organic-chemical composition had little effect on litter decomposition rates. The rapid initial loss in ponderosa pine litter mass originated from the labile fraction (i.e., HWS mass) and is typical of other residues during the early stages of decomposition (Swift *et al.* 1979). The concomitant increase in the absolute amount of lignin has also frequently been observed and may be due to the alteration in the efficiency of extraction procedures, or to chemical or microbial synthesis of compounds that are extracted in the lignin fraction (Swift *et al.* 1979; Berg and Staaf 1980; Berg and Wessén 1984).

The substantially faster decay of cellulose relative to hemicellulose may in part be an artifact of our extraction procedure, because the products of cellulose decomposition include short-chain oligosaccharides that are alkali soluble and sugars that are water soluble. If these substances accumulate to any extent they will be estimated as components of the hemicellulose and HWS mass fractions, respectively, thus underestimating the apparent decomposition rate of the hemicellulose fraction (Swift *et al.* 1979).

Nutrient dynamics

Coniferous forests typically occupy sites of relatively low fertility, and the inherent recalcitrance of coniferous forest needle litter has been hypothesized as a mechanism for maintaining soil nutrient stocks (Gosz 1981; Vitousek 1982; Johnson *et al.* 1982; Waring and Schlesinger 1985). In coniferous forests with Mediterranean-type climates, environmental constraints on decomposition processes in concert with litter-quality factors may accentuate the retention of essential plant nutrients within litter. We evaluated the nutrient source-sink properties of recently fallen needle litter in the old-growth site by comparing net changes in pool sizes of nutrients in litter after 1 year of decomposition with estimates of aboveground annual uptake of these same nutrients (Table 4). No data on nutrient uptake by trees were available in this forest, so we estimated annual nutrient uptake values by adding the mean annual accumulation of nutrients in bole and branch wood, reported for the 13 International Biological Program temperate coniferous forests, to the annual loss of nutrients through litter fall in this old-growth forest (Cole and Rapp 1981; Hart and Firestone 1991). Sulfur concentrations were not reported for the International Biological Programme sites, so we used the net accretion of S in wood found by D. Binkley (Department of Forest Sciences, Colorado State University, unpublished data) for a 60-year-old mixed-conifer forest in Oregon. Initial nutrient content and dynamics during decomposition of all fine litter fall were assumed to be similar to those of ponderosa pine needle litter in this analysis (ponderosa pine needle litter constitutes about 75% of the total fine litter fall by mass in this forest; S. Hart, unpublished data). These comparisons illustrate that fine litter fall may be a significant source of P, Mg, and K for tree uptake in this forest, potentially supplying 16, 7, and 40% of the annual aboveground uptake of these nutrients, respectively

TABLE 4. Estimated rates of annual net nutrient release from fine litter fall relative to aboveground nutrient uptake by trees in an old-growth mixed-conifer forest

	Net release (kg·ha ⁻¹ ·year ⁻¹) ^a	Tree uptake (kg·ha ⁻¹ ·year ⁻¹) ^b	% of the uptake potentially supplied by fine litter ^c
N	-0.4	33	0
P	+0.5	3.1	16
S	-0.1	3.2	0
Ca	-2.6	22	0
Mg	+0.5	7.6	7
K	+5.6	14	40

^a Annual net rates of nutrient release were estimated using the net change in nutrient content of ponderosa pine needle litter and an estimate of total annual fine litter fall at this site; positive values denote net release from litter, and negative values denote net accumulations in litter.

^b Aboveground nutrient uptake was estimated using the initial nutrient content of ponderosa pine needle litter and an estimate of total fine litter fall at this site; these values were then added to the mean annual accumulation of nutrients in bole and branch wood reported for the 13 International Biological Program temperate coniferous forest sites (see text).

^c A value of zero is shown for those nutrients that accumulated, on a net basis, in litter during the 1st year of decomposition.

(Table 4). In contrast, fine litter fall acts as a net sink for N, S, and Ca during its 1st year of decomposition in this site. The sink nature of fine litter fall for N and S in the old-growth forest is even more apparent seasonally, where about 1.5 kg S·ha⁻¹ accumulated between February and April, and almost 4 kg N·ha⁻¹ between April and the following January (Fig. 3). These large net accumulations of N and S in litter during the early stages of decomposition would likely alter rates and seasonal patterns of N and S uptake by trees and, in turn, may limit tree production.

The relative mobility of nutrient elements in ponderosa pine needle litter in both the old- and young-growth sites (based on the amount of the element remaining after 2 years of decomposition relative to its initial amount) was as follows: K > Mg = C = P > N > S > Ca. This mobility series is very similar to that found for ponderosa pine needle litter in Arizona for a 34-month study (Klemmedson *et al.* 1985) and for red pine (*Pinus resinosa* Ait.) needle litter in Wisconsin over a 12-month period (Bockheim and Leide 1986). Hence it appears that although decomposition rates are substantially slower in these coniferous forests of California, the relative patterns of nutrient release from ponderosa pine needle litter are similar to those of other pine forests.

Litter age-class influenced the pattern of N, P, and S release from litter, but had no significant effect ($p > 0.10$) on Ca, Mg, and K dynamics (Table 3, Fig. 3). Nitrogen, P, and S release from litter are primarily controlled by microbial mineralization-immobilization processes during decomposition (Swift *et al.* 1979), and hence we would expect differences in litter quality to have the greatest effect on the release of these nutrients.

Berg and Ekbohm (1983) reported that net N release initiated (following a period of net immobilization) at a higher C:N ratio for Scots pine (*Pinus sylvestris* L.) needle litter in a mature forest than in a clearcut (so-called "critical C:N ratios" of 109 and 63, respectively; see Berg and Staaf (1981) for a discussion of critical C:N ratios). In contrast, we found that critical C:N ratios of ponderosa pine needle litter were similar in old- and young-growth forests for both litter

age-classes (about 80 and 60 for old and young litter, respectively; Figs. 3 and 4a). However, our results do support their general conclusion that no fixed C:N ratios exist for net immobilization and release of N in litter.

Few studies have assessed the dynamics of N in different litter components during decomposition in forests. Berg (1988) found that the N associated with labile (acid-soluble) and recalcitrant (acid-insoluble) fractions behaved similarly during decomposition of Scots pine needle litter. We found quite different dynamics for N in labile (HWS) litter components and in total litter during decomposition of ponderosa pine needle litter (Figs. 2 and 3). The contrasting results between these two studies may in part be due to the different extraction procedures used to fractionate litter components. Nevertheless, in both studies the C:N ratios of the different litter fractions converged as decomposition proceeded. This suggests that the overall quality of litter becomes more uniform during decomposition, presumably owing to the redistribution of N within litter (Berg 1988). Such redistribution of N within litter during decomposition may be an important process in stabilizing N within forest litter horizons.

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- Aber, J.D., and Melillo, J.M. 1980. Litter decomposition: measuring the relative contributions of organic matter and nitrogen to forest soils. *Can. J. Bot.* **58**: 416–421.
- Berg, B. 1988. Dynamics of nitrogen (^{15}N) in decomposing Scots pine (*Pinus sylvestris*) needle litter. Long-term decomposition in a Scots pine forest. VI. *Can. J. Bot.* **66**: 1539–1546.
- Berg, B., and Ekbohm, G. 1983. Nitrogen immobilization in decomposing needle litter at variable carbon:nitrogen ratios. *Ecology*, **64**: 63–67.
- Berg, B., and Staaf, H. 1980. Decomposition rate and chemical changes of Scots pine needle litter. II. Influence of chemical composition. In *Structure and function of northern coniferous forests, an ecosystem study*. Edited by T. Persson. *Ecol. Bull. (Stockholm)*, **32**: 375–390.
- Berg, B., and Staaf, H. 1981. Leaching, accumulation and release of nitrogen in decomposing forest litter. In *Terrestrial nitrogen cycles*. Edited by F. E. Clark and T. Rosswall. *Ecol. Bull. (Stockholm)*, **33**: 163–178.
- Berg, B., and Wessén, B. 1984. Changes in organic-chemical components and ingrowth of fungal mycelium in decomposing birch leaf litter as compared to pine needles. *Pedobiologia*, **26**: 285–298.
- Binkley, D. 1984. Does forest removal increase rates of decomposition and nitrogen release? *For. Ecol. Manage.* **8**: 229–233.
- Bockheim, J.G., and Leide, J. L. 1986. Litter and forest floor dynamics in a *Pinus resinosa* plantation in Wisconsin. *Plant Soil*, **96**: 393–406.
- Bremner, J.M., and Mulvaney, C.S. 1982. Nitrogen—total. In *Methods of soil analysis. Part 2. 2nd ed.* Edited by A.L. Page, R.H. Miller, and D.R. Keeney. American Society of Agronomy, Madison, WI. pp. 595–642.

- Bruhn, J.N. 1980. Effects of oxidant air pollution on ponderosa and jeffrey pine foliage decomposition. Doctoral dissertation, University of California, Berkeley.
- Cole, D.W., and Rapp, M. 1981. Elemental cycling in forest ecosystems. In *Dynamic properties of forest ecosystems*. Edited by D.E. Reichle. *Int. Biol. Programme* **23**: 341–409.
- Edmonds, R.L. 1979. Decomposition and nutrient release in Douglas-fir needle litter in relation to stand development. *Can. J. For. Res.* **9**: 132–140.
- Edmonds, R.L., and Bigger, C.M. 1984. Decomposition and nitrogen mineralization rates in Douglas-fir needles in relation to whole-tree harvesting practices. In *New Forests for a Changing World: Proceedings of the 1983 Convention of the Society of American Foresters, 16–20 Oct. 1983, Portland, OR*. Society of American Foresters, Bethesda, MD. pp. 187–192.
- Fogel, R., and Cromack, K., Jr. 1977. Effect of habitat and substrate quality on Douglas-fir litter decomposition in western Oregon. *Can. J. Bot.* **55**: 1632–1640.
- Gholz, H.L., Perry, C.S., Cropper, W.P., Jr., and Hendry, L.C. 1985. Litterfall, decomposition, and nitrogen and phosphorus dynamics in a chronosequence of slash pine (*Pinus elliottii*) plantations. *For. Sci.* **31**: 463–478.
- Gosz, J.R. 1981. Nitrogen cycling in coniferous forest ecosystems. In *Terrestrial nitrogen cycles*. Edited by F.E. Clark and T. Rosswall. *Ecol. Bull. (Stockholm)*, **33**: 405–426.
- Harper, S.H., and Lynch, J.M. 1981. The chemical components and decomposition of wheat straw leaves, internodes and nodes. *J. Sci. Food Agric.* **32**: 1057–1062.
- Hart, S.C. 1990. Control of decomposition processes and nutrient flow in a California forest and grassland. Doctoral dissertation, University of California, Berkeley.
- Hart, S.C., and Firestone, M.K. 1989. Evaluation of three *in situ* soil nitrogen availability assays. *Can. J. For. Res.* **19**: 185–191.
- Hart, S.C., and Firestone, M.K. 1991. Forest floor – mineral soil interactions in the internal nitrogen cycle of an old-growth forest. *Biogeochemistry*, **12**: 103–127.
- Jackson, L.E., Strauss, R.B., Firestone, M.K., and Bartolome, J.W. 1988. Plant and soil nitrogen dynamics in California annual grassland. *Plant Soil*, **110**: 9–17.
- Jenny, H., Gessel, S.P., and Bingham, F.T. 1949. Comparative study of decomposition rates of organic matter in temperate and tropical regions. *Soil Sci.* **68**: 419–432.
- Johnson, D.W., Cole, D.W., Bledsoe, C.S., et al. 1982. Nutrient cycling in the Pacific Northwest. In *Analysis of coniferous forest ecosystems in the western United States*. Edited by R.L. Edmonds. Hutchinson Ross Publishing Co., Stroudsburg, PA. pp. 186–232.
- Klemmedson, J.O., Meier, C.E., and Campbell, R.E. 1985. Needle decomposition and nutrient release in ponderosa pine ecosystems. *For. Sci.* **31**: 647–660.
- MacLean, D.A., and Wein, R.W. 1978. Weight loss and nutrient changes in decomposing litter and forest floor material in New Brunswick forest stands. *Can. J. Bot.* **56**: 2730–2749.
- McClaugherthy, C., and Berg, B. 1987. Cellulose, lignin and nitrogen concentrations as rate regulating factors in late stages of forest litter decomposition. *Pedobiologia*, **30**: 101–112.
- Meentemeyer, V. 1978. Macroclimate and lignin control of litter decomposition rates. *Ecology*, **59**: 465–472.
- Melillo, J.M., Aber, J.D., and Muratore, J.F. 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. *Ecology*, **63**: 621–626.
- Olson, J.S. 1963. Energy storage and balance of producers and decomposers in ecological systems. *Ecology*, **44**: 322–331.
- Perkin–Elmer Corporation. 1976. Analytical methods for atomic absorption spectroscopy. Perkin–Elmer Corporation, Norwalk, CT.
- QuikChem Systems. 1987. QuikChem method No. 12-115-01-1-A. QuikChem Systems, division of Lachat Chemicals, Inc., Mequon, WI.
- SAS Institute Inc. 1985. SAS user's guide: statistics, version 5 edition. SAS Institute Inc., Cary, NC.

- Schlesinger, W.H., and Hasey, M.M. 1981. Decomposition of chaparral shrub foliage: losses of organic and inorganic constituents from deciduous and evergreen leaves. *Ecology*, **62**: 762–774.
- Stewart, J.W.B., Ruzicka, J., Filho, H.B., and Zagatto, E.A. 1976. Flow injection analysis. Part 3. Comparison of continuous flow spectrophotometry and potentiometry for the rapid determination of the total nitrogen content in plant tissues. *Anal. Chim. Acta*, **81**: 371–386.
- Stohlgren, T.J. 1988. Litter dynamics in two Sierran mixed conifer forests. I. Litterfall and decomposition rates. *Can. J. For. Res.* **18**: 1127–1135.
- Suffling, R., and Smith, D.W. 1974. Litter decomposition studies using mesh bags: spillage inaccuracies and the effects of repeated artificial drying. *Can. J. Bot.* **52**: 2157–2163.
- Swift, M.J., Heal, O.W., and Anderson, J.M. 1979. Decomposition in terrestrial ecosystems. University of California Press, Berkeley.
- Synder, J.D., and Trofymow, J.A. 1984. A rapid accurate wet oxidation diffusion procedure for determining organic and inorganic carbon in plant and soil samples. *Commun. Soil Sci. Plant Anal.* **15**: 587–597.
- Vitousek, P. 1982. Nutrient cycling and nutrient use efficiency. *Am. Nat.* **119**: 553–572.
- Vogt, K.A., Grier, C.C., Meir, C.E., and Keyes, M.R. 1983. Organic matter and nutrient dynamics in forest floors of young and mature *Abies amabilis* stands in western Washington, as affected by fine-root input. *Ecol. Monogr.* **53**: 139–157.
- Waring, R.H., and Schlesinger, W.H. 1985. Decomposition and forest soil development. In *Forest ecosystems: concepts and management*. Academic Press Inc., New York. pp. 181–210.
- Warrington, G., and Weatherred, J. 1983. Regim4. Watershed Systems Development Group, Fort Collins, CO.
- Whitford, W.G., Meentemeyer, V., Seastedt, T.R., et al. 1981. Exceptions to the AET model: deserts and clear-cut forests. *Ecology*, **62**: 275–277.
- Wieder, R., and Lang, G.E. 1982. A critique of the analytical methods used in examining decomposition data obtained from litter bags. *Ecology*, **63**: 1636–1642.
- Zasoski, R.J., and Burau, R.G. 1977. A rapid nitric–perchloric acid digestion method for multi-element tissue analysis. *Commun. Soil Sci. Plant Anal.* **8**: 425–436.