

Biophysical controls on surface fuel litterfall and decomposition in the northern Rocky Mountains, USA

Robert E. Keane

Abstract: Litterfall and decomposition rates of the organic matter that comprise forest fuels are important to fire management, because they define fuel treatment longevity and provide parameters to design, test, and validate ecosystem models. This study explores the environmental factors that control litterfall and decomposition in the context of fuel management for several major forest types in the northern Rocky Mountains (Idaho and Montana), USA. Litterfall was measured for more than 10 years using semiannual collections of six fine fuel components (fallen foliage, twigs, branches, large branches, logs, and all other canopy material) collected from a network of 1 m² litterfall traps installed at 28 plots across seven sites. Decomposition of foliage, twigs, branches, and large branches were measured using litter bags installed on five of the seven sites. Measured litterfall and decomposition rates were correlated with major environmental and vegetation variables using regression analysis. Annual foliage litterfall rates ranged from 0.057 kg·m⁻²·year⁻¹ for dry *Pinus ponderosa* Dougl. ex Laws. stands to 0.144 kg·m⁻²·year⁻¹ on mesic *Thuja plicata* Donn ex D. Don stands and were correlated with the vegetation characteristics of leaf area index, basal area, and tree height ($r > 0.5$), whereas decomposition rates were correlated with the environmental gradients of temperature and relative humidity ($r > 0.4$).

Résumé : Les taux de chute de litière et de décomposition de la matière organique qui constituent les combustibles forestiers sont importants pour la gestion du feu parce qu'ils déterminent la longévité du traitement des combustibles et fournissent les paramètres pour mettre au point, tester et valider les modèles d'écosystème. Cette étude explore les facteurs environnementaux qui régissent la chute de litière et la décomposition dans le contexte de la gestion des combustibles de plusieurs types forestiers importants de la partie nord des montagnes Rocheuses en Idaho et au Montana, aux États-Unis. La chute de litière a été mesurée pendant plus de 10 ans en effectuant une collecte semi-annuelle des composantes des combustibles légers (feuilles, rameaux, branches, grosses branches, billes et tous les autres matériaux de la canopée tombés au sol) grâce à un réseau de trappes à litière de 1 m² installées dans 28 parcelles réparties dans sept stations. La décomposition des feuilles, des rameaux, des branches et des grosses branches a été mesurée à l'aide de sacs à litière installés dans cinq des sept stations. Les taux de chute de litière et de décomposition ont été corrélés aux principales variables environnementales et à celles de la végétation à l'aide de l'analyse de régression. Le taux annuel de chute de litière sous forme de feuillage variait de 0,057 kg·m⁻²·an⁻¹ dans les peuplements xériques de *Pinus ponderosa* Dougl. ex Laws. à 0,144 kg·m⁻²·an⁻¹ dans les peuplements mésiques de *Thuja plicata* Donn ex D. Don et il était corrélé ($r > 0,5$) aux caractéristiques de la végétation par l'indice de surface foliaire, la surface terrière et la hauteur des arbres tandis que le taux de décomposition était corrélé ($r > 0,4$) aux gradients environnementaux de température et d'humidité relative.

[Traduit par la Rédaction]

Introduction

The successful suppression of many wildland fires in the western United States and Canadian ecosystems over the last 70 years has resulted in increased accumulations of surface fuels that have increased the potential for severe fires (Ferry et al. 1995). Many government agencies are advocating extensive fuel treatments and ecosystem restoration activities to reduce the severity of these intense wildfires that could potentially damage ecosystems, destroy property, and take human life (Lavery and Williams 2000; GAO 2002). Knowledge of fuel litterfall deposition and decomposition rates could help managers prioritize, design, and implement

more effective fuel-treatment programs. However, these rates remain relatively unknown for many forest ecosystems. This is especially true for down dead woody fine fuels, because most studies determine only leaf litter or large log fuel decay and accretion rates (Harmon et al. 1986).

Quantification of surface fuel dynamics across managed landscapes is important to fire managers and researchers for many reasons. Rates of fuel buildup and decomposition can be used to define temporal (how long will a treatment last) and spatial (what areas are best to effectively treat) limits to fire hazard reduction treatments (Fernandes and Botelho 2003). These rates could also help determine how fast treated landscapes would reach undesirable fuel loadings to warrant another treatment. Fuel and fire modeling efforts need litterfall and decomposition rates to realistically simulate fuel dynamics across landscapes to compare alternative fuel treatment strategies (Keane et al. 1996). The rates can also be used as validation of simulated ecological processes in existing and future ecosystem process models (Pastor and

Received 20 July 2007. Accepted 9 January 2008. Published on the NRC Research Press Web site at cjfr.nrc.ca on 3 May 2008.

R.E. Keane. USDA Forest Service, Rocky Mountain Research Station, Missoula Fire Sciences Laboratory, 5775 Highway 10 West, Missoula, MT 59808, USA (e-mail: rkeane@fs.fed.us).

Post 1985; Botkin 1993). Carbon fluxes can also be approximated from measured fuel dynamics rates to determine the contribution of the fuelbed to atmospheric carbon sources and sinks (Thornton et al. 2002).

This study quantified the rates of forest litterfall and decomposition for a number of forest types across the northern Rocky Mountains (Idaho and Montana, USA) to estimate fuels parameters for use in complex landscape models of fire and vegetation dynamics (Keane et al. 1996; White et al. 1998). Because it is impossible to measure fuel deposition and decomposition for all stand types in all northern Rocky Mountain ecosystems, the estimated rates were then correlated to a number of biophysical and vegetation variables that were either directly estimated at the field plots or simulated with ecosystem process models so that these rates of fuel dynamics could be extrapolated across all areas of northern Rocky Mountains landscapes.

Six surface fuel components are recognized in this study. Freshly fallen leaves and needles from trees, shrubs, and herbs are considered foliage, whereas all other nonwoody material, such as fallen cones, bark scales, lichen, and bud scales, are lumped into a category called other canopy fuels. The woody material is sorted into four diameter classes using the size ranges required by the fire behavior and effects models (Fosberg 1970; Rothermel 1972; Reinhardt and Keane 1998). The smallest size class, called twigs, defines 1 h timelag (time it takes to dry or wet the fuel particle to 67% of its equilibrium moisture content) fuels with diameters <6 mm. Branches with diameters between 6 and 25 mm are 10 h timelag fuels, and large branches with diameters ranging from 25 to 75 mm are 100 h timelag fuels. The logs, downed woody fuels >75 mm in diameter, define the 1000 h timelag fuel component (Hagan and Grove 1999), which does not include snags or stumps. In this paper, the fuels described above are considered "litter" for simplicity; devices used to collect fuels are referred to as litter traps. Fuel accumulation is considered litterfall minus decomposition. Duff decomposition rates, along with tree, shrub, and herbaceous growth rates, were not measured in this study, because there are abundant other efforts in these areas. This study is primarily concerned with the dynamics of the foliage, fine woody, and log surface fuel components.

Most litterfall studies have only measured the rate of foliage or log deposition (Harmon et al. 1986; Vogt et al. 1986) (Table 1). Small woody debris additions to the forest floor, such as twigs and branches, are rarely reported, even though they may be the most important to fuels management and fire behavior prediction because they contribute to fire spread (Rothermel 1972). Deposition rates for logs (Table 1) are usually measured from historical tree mortality and snag fall rates over time, which assumes tree fall is the only input to log accumulation. However, large branches and tree tops also contribute to log inputs to the forest floor in some ecosystems (Harmon et al. 1986).

Studies of decomposition rates are usually for only the foliage and large log material, especially in the western United States (Table 1), much like litterfall studies. The exceptions are Edmonds (1987) and Taylor et al. (1991), who measured decay of twigs, branches, and cones, and Carlton and Pickford (1982) and Christiansen and Pickford (1991), who estimated small wood losses by sampling different aged timber

slash. These studies usually use the parameter k in an exponential decay curve to describe rates of decay (Olson 1963; Robertson and Paul 2000).

Several studies have attempted to relate litterfall and decomposition rates to environmental variables. Mackensen et al. (2003) successfully correlated values of the decomposition rate k to rainfall, temperature, and altitude using decomposition studies conducted around the world, whereas Johannsson (1994) estimated decomposition along a latitudinal gradient. Log loadings have been correlated with topographic gradients of slope, aspect, and landform (Jenkins et al. 2004; Sanchez-Flores and Yool 2004; Webster and Jenkins 2005) and fire regime (White et al. 2004; Brais et al. 2005). Huebschmann et al. (1999) correlated needle fall to stand, site, and weather characteristics and found that spring temperatures were the best predictors. Meentemeyer (1978) developed a global model of litter production using climate factors, such as evapotranspiration.

It is difficult for fire managers to determine litterfall and decomposition rates at the stand level and almost intractable at the landscape level, because it requires extensive networks of collection devices that must be frequently monitored over long time periods (5–10 years) to accurately estimate annual fluxes. The density and spacing of the collection devices are highly dependent on the type of fuel collected. Coarse woody fuels usually require installing larger traps across larger areas and are monitored for longer time periods, whereas fine fuels would require smaller traps but frequent visitation to minimize decomposition losses. An alternative would be to predict fuel dynamics from those environmental variables that control deposition and decomposition. The objectives of this study were to (i) measure rates of litterfall and decomposition for important fuel components, (ii) determine important relationships of biophysical variables to the measured rates, and (iii) create empirical predictive equations that could be used to extrapolate stand-level fuel dynamics estimates across entire landscapes to support spatial fuels modeling efforts and landscape planning.

Materials and methods

Study sites

This study began as an extension of two previous studies that explored the use of ecosystem modeling and gradient analysis to create digital maps of current and future landscape characteristics. In 1993, a set of litter traps were installed on two sites in western Montana to parameterize and validate two ecosystem models: BIOME-BGC (White et al. 2000) and Fire-BGC (Keane et al. 1996) (Table 2, sites CO and SB). Then, in 1995, an extensive field sampling project was initiated to explore the use of measured and simulated environmental gradients to map ecosystem characteristics, such as fuels, across landscapes (Keane et al. 2002; Rollins et al. 2004). To validate the models used in the two studies, the number of sites was expanded from two to six by establishing four new sites along elevational and aspect gradients within the larger northern Rockies study area (Fig. 1). In 1997, one more site was included to represent the ubiquitous lodgepole pine (*Pinus contorta* Dougl. ex Loud.) ecosystem that occurs east of the Continental Divide (Table 2, site TF; Fig. 1). Other forest types represented by these sites include

Table 1. Litterfall and decomposition rates for foliage and woody material measured in various western US ecosystems.

Ecosystem and fuel component	Litterfall rate (kg·m ⁻² ·year ⁻¹)	Decay constant <i>k</i> (year ⁻¹)	Province or state	Reference(s)
<i>Pinus ponderosa</i>				
Logs	0.03	0.05	Arizona	Avery et al. 1976; Klemmedson 1992
Foliage	0.29	0.05, 0.14, 0.08–0.18	California, Arizona	Bray and Gorham 1964; Yavitt and Fahey 1982; Stohlgren 1988; Klemmedson et al. 1990; Hart et al. 1992
<i>Pseudotsuga menziesii</i>				
Logs	0.70, 0.45, 0.04, 0.15–0.45, 0.28	0.006–0.050	Oregon, Washington	Wright and Lauterback 1958; Grier and Logan 1977; Gottfried 1978; Sollins 1982; Harmon et al. 1986; Spies et al. 1988; Edmonds and Eglitis 1989; Harmon and Hua 1991
Twigs and branches	—	0.007–0.129, 0.06–0.14, 0.06, 0.005–0.05	Washington	Fogel and Cromack 1977; Edmonds et al. 1986; Edmonds 1987; Edmonds and Eglitis 1989; Christiansen and Pickford 1991; Maguire 1994
Foliage	0.50, 0.17–0.33, 0.114–0.177	0.005–0.010, 0.44, 0.27, 0.41–0.56, 0.178–0.284	Oregon, British Columbia, Washington	Dimock 1958; Turner and Long 1975; Fogel and Cromack 1977; Edmonds 1979; Graham 1982; Means et al. 1985; Sollins et al. 1987; Edmonds 1991; Harmon and Hua 1991; Trofymow et al. 1991; Prescott et al. 2000
<i>Pinus contorta</i>				
Logs	0.02	0.027, 0.082, 0.0016–0.0027, 0.115, 0.015	Colorado, Alabama	Alexander 1954; Pearson et al. 1987; Taylor et al. 1991; Busse 1994; Laiho and Prescott 1999; Kueppers et al. 2004
Twigs	—	0.055	Alabama	Taylor et al. 1991 ; Prescott et al. 1993
Foliage	0.362	0.115, 0.14, 0.09–0.11	Alabama, Wyoming	Yavitt and Fahey 1982; Taylor et al. 1991; Berg and Ekbohm 1993; Stump and Binkley 1993; Laiho and Prescott 1999
<i>Tsuga heterophylla</i>				
Logs	—	0.016–0.018	Oregon	Graham 1982
Twigs and branches	—	0.08–0.24	Washington	Edmonds 1987
Foliage	—	0.3–0.5	British Columbia	Keenan et al. 1996
<i>Abies lasiocarpa</i> – <i>Picea</i> spp.				
Logs	—	0.001–0.0015	Colorado	Kueppers et al. 2004
Foliage	0.2–0.23	0.09–0.17	Alabama	Taylor et al. 1991; Laiho and Prescott 1999; Prescott et al. 2003

Note: Twigs and branches are assumed to be less than 8 cm (3 in.) in diameter.

Table 2. General description of the study sites and plots included in this study.

Study site and plot	Cover type ^a	Habitat type ^a	Elevation (m)	Aspect ^b	Collection years	Basal area (m ² ·ha ⁻¹) ^c	Tree density (stems·ha ⁻¹) ^c	Fuel loading (kg·m ⁻²) ^d	LAI (m ² ·m ⁻²) ^e
Coram (CO)									
1	DF/WL	GF/CU	1185	SW	1993–2005	29.87	296.4	27.26	1.75
2	WC/WH	WH/CU	1184	NW	1993–2005	50.44	741.0	1.84	2.24
3	SF	SF/MF	1937	NE	1993–2005	10.58	222.3	8.43	0.63
4	WP	SF/XT	1915	SW	1993–2005	34.34	938.6	18.45	3.10
Snowbowl (SB)									
1	PP	DF/VS	1680	NW	1995–2005	31.28	864.5	1.02	2.85
2	DF	DF/PM	1596	S	1995–2005	36.57	666.9	1.37	2.77
3	LP	SF/XT	1972	SW	1995–2005	30.11	988.0	2.61	1.74
4	SF/WP	SF/MF	2073	E	1995–2005	32.76	568.1	2.19	3.17
Red Mountain (RM)									
1	PP	DF/CR	943	E	1995–2005	34.96	197.6	3.10	4.01
2	WC/WH	WH/CU	942	E	1995–2005	55.68	395.2	28.12	3.38
3	WP	SF/XT	1988	SE	1995–2005	19.00	395.2	2.22	1.81
4	SF	SF/MF	1529	NW	1995–2005	31.31	395.2	8.42	2.47
Spar Lake (SL)									
1	WC	WH/CU	1090	SE	1995–2005	64.85	1284.4	9.67	7.90
2	DF	GF/XT	1124	S	1995–2005	48.48	419.9	9.33	6.58
3	WC	WH/CU	1260	S	1995–2005	52.71	988.0	6.02	6.10
4	WL	WH/CU	1600	SE	1995–2005	68.22	617.5	19.87	7.02
Red River (RR)									
1	PP	DF/LB	1425	N	1995–2005	37.41	345.8	19.94	4.40
2	GF/DF	GF/LB	1407	SW	1995–2005	35.42	172.9	4.82	2.69
3	LP	SF/XT	1988	W	1995–2005	28.65	543.4	6.27	2.21
4	LP	SF/XT	1979	E	1995–2005	32.32	889.2	6.98	2.69
Keating Ridge (KR)									
1	GF	GF/LB	1041	E	1995–2005	46.53	518.7	20.09	8.39
2	PP	PP/SA	1340	W	1995–2005	47.35	345.8	10.12	3.01
3	LP	SF/XT	2004	W	1995–2005	51.31	1630.2	2.35	4.41
4	SF	SF/XT	2078	E	1995–2005	70.72	1654.9	5.20	6.59
Tenderfoot (TF)									
1	LP	SF/VS	2302	F	1997–2005	53.75	1309.1	2.76	4.24
2	LP/SF	SF/VS	2299	F	1997–2005	44.26	839.8	0.47	3.31
3	LP	SF/VS	2143	F	1997–2005	25.95	716.3	0.71	2.23
4	LP	SF/VS	2158	F	1997–2005	38.23	1284.4	0.77	3.38

^aCover type and habitat type species are as follows: trees are PP, ponderosa pine (*Pinus ponderosa* var. *ponderosa*); DF, Douglas-fir (*Pseudotsuga menziesii*); WL, western larch (*Larix occidentalis* Nutt.); WC, western red cedar (*Thuja plicata*), WH, western hemlock (*Tsuga heterophylla*); LP, lodgepole pine (*Pinus contorta* var. *contorta*); WP, whitebark pine (*Pinus albicaulis*); SF, subalpine fir (*Abies lasiocarpa*); GF, grand fir (*Abies grandis* (Dougl.) Lindl.); and undergrowth species are CR, *Calamagrostis rubescens* Buckley; CU, *Clintonia uniflora* (Menzies ex Schult. f.) Kunth; LB, *Linnaea borealis* L.; MF, *Menziesia ferruginea* Sm.; PH, *Physocarpus malvaceus* (Greene) Kuntze; VS, *Vaccinium scoparium* Leiberg ex Coville; XT, *Xerophyllum tenax* (Pursh) Nutt. Cover types are based on plurality of basal area and habitat types are from Pfister et al. (1977).

^bAspect codes are as follows: N, north; S, south; E, east; W, west; F, flat.

^cOnly overstory trees (>10 cm DBH) were used to compute basal area and density.

^dFuel loading only includes downed dead woody fuels summed across all four size classes.

^eLAI, projected leaf area index.

pure or mixed stands of ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), western red cedar (*Thuja plicata* Donn ex D. Don), subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), and whitebark pine (*Pinus albicaulis* Engelm.) (Table 2).

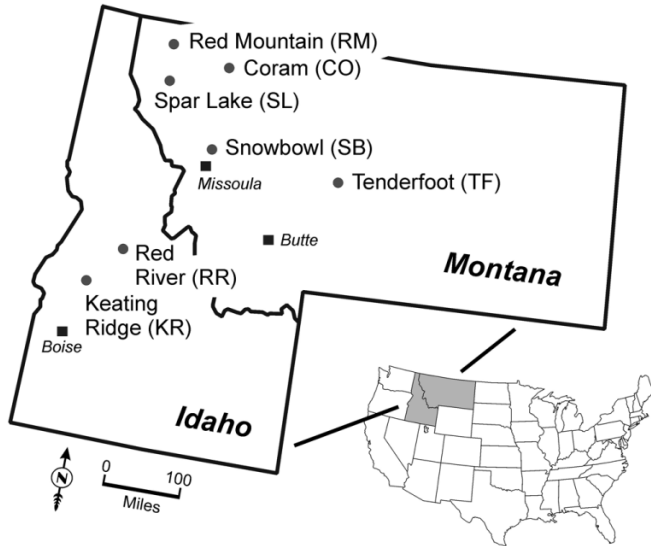
Each study site consisted of four 0.04 ha circular plots established along the major topographic gradients of elevation and aspect. Plots were established in readily accessible areas at low and high elevations and on north and south aspects to adequately describe the diversity of important direct environmental gradients, such as productivity, moisture, and temperature (Keane et al. 2002). At each plot, a wide variety of topographic, vegetation, and ecosystem variables were measured or estimated on plots using sampling protocols in the ECODATA sampling package (Hann et al. 1988). The entire list of sampled attributes is provided in Keane et al.

(2002), but the most important among them are an inventory of all trees in the plot to compute basal area, leaf area, and stand density and a network of 30 m fuel transects (Brown 1970) to estimate fuel loadings for the six fuel components used in this study. Details of all methods used in this study, especially litterfall collection and decomposition measurement discussed next, can be referenced in Keane (2008).

Measuring litterfall

Within each plot, seven to nine litter traps were placed on the forest floor in the pattern shown in Fig. 2 to collect fallen biomass. Nine litter traps were established at the two sites installed in 1993 (Table 1, sites CO and SB), but a subsequent analysis of variance of fallen foliage and woody material in 1995 showed that only seven traps were needed to adequately sample litterfall. Litter traps were constructed by

Fig. 1. Geographic locations of the seven sites included in this study. Four litter collection plots were established at each of the seven sample sites at high and low elevations and on north and south aspects.



creating a 1 m × 1 m frame with 2 cm × 14 cm boards and then tacking a coarse grid hardware cloth on the bottom of the frame to allow water to rapidly drain from the trap and minimize losses from accumulated material due to decomposition and wind. A plastic screen (mesh size 0.7 mm) was secured on top of the hardware cloth at the bottom of the trap to block fine material from falling through the coarse hardware grid.

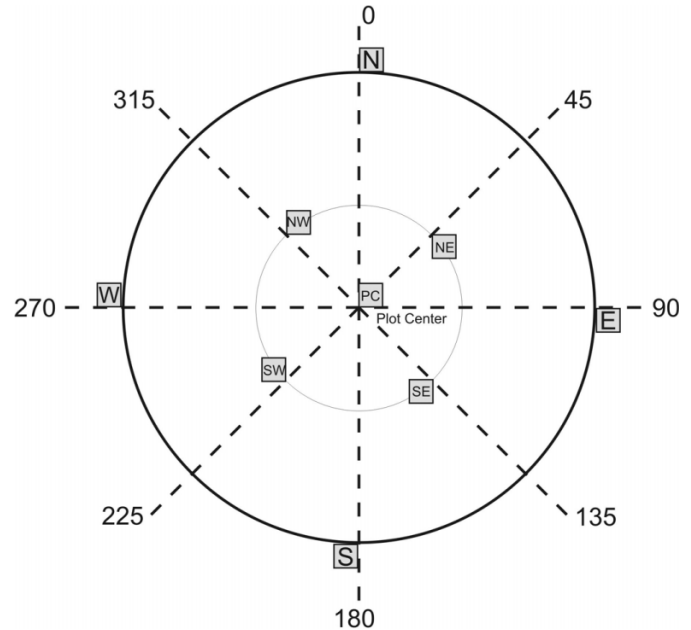
Each plot was visited once a month during the snow-free periods of the year, and all materials in each trap were placed into heavy paper bags. Woody fuel particles that lay partially out of the trap were sawed directly at the trap border as defined by the inside dimension of the trap boards. An estimate of projected leaf area index, (LAI, m²·m⁻²) was taken with a LI-COR LAI-2000 (LI-COR Inc., Lincoln, Neb.) during each plot visit to document any major changes in the forest canopy using the Nackaerts et al. (2000) methods. The monthly visits were designed to minimize mass losses due to decomposition as the fallen material sat in the traps; however, because little decomposition was observed during the hot, dry months of summer, it was determined that the most critical times for sampling were directly after snowmelt and just before the first autumnal snows. Therefore, starting in 2002, all the plots were visited at these two times each year.

The collected materials were transported to the laboratory, and the labeled bags were placed in an oven set at 80 °C for 2 or 3 days. The dried litter was then placed in cake tins and sorted by hand into the six fuel components (foliage, twigs, branches, large branches, logs, and other canopy material) and then weighted to the nearest 0.01 g. A small sample of the dried material was set aside for the decomposition measurements.

Estimating decomposition

Litterbags were used to estimate the rate of decay for four fuel components: freshly fallen foliage, twigs, branches, and

Fig. 2. Position of the litter traps within a plot was in a cross-like pattern with the Coram and Snowbowl sites (Table 2, sites CO and SB) having nine litter traps and the remaining sites having seven traps per plot (NW and SE were missing). Circles are at 11.6 m and 5 m in radius from plot center and numbers represent azimuths. Acronyms reference compass directions: N, north; NW, north-west; NE, northeast; E, east; S, south; SE, southeast; SW, south-west; W, west; PC, plot center.



large branches (Prescott et al. 2000). The bags were made by sewing together with UV resistant thread a fiberglass screen with a pore size of about 2 mm for the top with a rumen bag or pool cover material with a pore size of 0.055 mm for the bottom (Keane 2008). Bags for foliage were roughly 170 mm × 170 mm, and bags for the woody fuels were roughly 170 mm × 130 mm (0.0221 m²). Approximately 100–150 g of freshly fallen material taken from the litter traps (see previous section) was placed into each bag, and then the bag was sewn closed. The bags with wood were dried at 50 °C for 3 days, and the foliage bags were air-dried (the low oven temperature was used to minimize chemical changes) and then weighed to the nearest 0.01 g. Log, duff, and other canopy material decomposition rates were not estimated because of limited time, lack of appropriate equipment, and logistical considerations.

Three sets of three bags each (nine bags total) for the three fine woody fuel components (twigs, branches, and large branches) and three sets of six bags each (18 bags) for the foliage material were installed at each plot. A set from each of the four fuel components (foliage, twigs, branches, and large branches) was placed near plot center, another set of four was placed at about 7 m northwest of the plot center, and the third about 7 m southeast of the plot center. The litter bags were laid on top of the litter layer in late autumn and secured using a wire that was sewn through each bag and attached to a large 20 cm spike driven into ground to a depth of 19 cm to prevent downslope movement and minimize ungulate damage. Decomposition was estimated over 3 years with one foliage bag taken from each wire set every

Table 3. Sampled, summarized, and simulated variables used to correlate with the litterfall and decomposition rates to develop predictive models.

Variable name	Description	Source	Units
Topographic features			
ASPECT	Direction of exposure	Field data	degrees
ELEV	Elevation	Field data	m
SLOPE	Slope of plot	Field data	%
Vegetation characteristics			
AGE	Mean tree age	Field data tree list	years
AVEDBH	Mean diameter at base height	Field data tree list	cm
AVEHT	Mean tree height	Field data tree list	m
BAREA	Overstory basal area	Field data tree list	m ² ·ha ⁻¹
CLAY	Percent clay in soil	Direct measurement	%
DOMDBH	Dominant diameter at base height	Field data tree list	cm
DOMHT	Dominant tree height	Field data tree list	m
FUELLOAD	Fuel loading	Field data tree list	kg·m ⁻²
LAI	Leaf area index	Field data tree list	m ² ·m ⁻²
MAXAGE	Maximum tree age	Field data tree list	years
SAND	Percent sand in soil	Direct measurement	%
SAPAREA	Sapling basal area	Field data tree list	m ² ·ha ⁻¹
SAPPH	Saplings per hectare	Field data tree list	trees·ha ⁻¹
SILT	Percent silt in soil	Direct measurement	%
SNAGDBH	Snag diameter at base height	Field data tree list	cm
SNAGBA	Snag basal area	Field data tree list	m ² ·ha ⁻¹
SOILDEPTH	Soil depth for 90% rooting zone	Direct measurement	m
SPH	Snags per hectare	Field data tree list	ha
TPH	Trees per hectare	Field data tree list	m ² ·ha ⁻¹
Environmental gradients			
NPP	Net primary production	BIOME-BGC model	kg C·m ⁻²
OUTFL	Soil water outflow	BIOME-BGC model	kg H ₂ O·m ⁻²
PPT	Mean annual precipitation	DAYMET weather	cm
SRAD	Mean annual daily solar radiation	DAYMET weather	kJ·m ⁻² ·day ⁻¹
TDAY	Mean annual day temperature	DAYMET weather	°C
TMAX	Mean annual maximum temperature	DAYMET weather	°C
TMIN	Mean annual minimum temperature	DAYMET weather	°C
VPD	Mean annual vapor pressure deficit	DAYMET weather	mbar

Note: The term “tree list” signifies that the variable was summarized from individual tree data collected using methods described in Keane (2008). The DAYMET and BIOME-BGC models are described in the text.

6 months, and one bag from each of the three woody components was taken every 12 months. The retrieved bags were cut from the wire and any material that had fallen onto the bag or that was attached to the bottom of the bag was scraped off using a knife. The litterbags were placed in paper bags and brought back to the laboratory to be dried at 50 °C for 3 days and weighed.

Quantifying environmental variables

Biophysical and environmental variables were quantified for each plot using a number of techniques detailed in Keane et al. (2002) and Rollins et al. (2004). Site and vegetation descriptions were taken from the sampled data or from summaries of the data (Keane 2008). These variables included general stand measurements (e.g., tree cover, bare soil cover, and shrub cover) and site observations (e.g., elevation, aspect, and slope) at the plot level. Computed values summarized from sampled data included basal area and tree density from individual tree measurements of height, diameter, and species (see Table 3 for the most important variables).

Some of the sampled plot data and corresponding summa-

ries were used as inputs to complex climate and ecosystem models (Rollins et al. 2004). Climate variables were computed from daily weather extrapolated to the plot from a network of base weather stations using the DAYMET model (Thornton et al. 1997). Annual means of the simulated climate variables were computed over the entire 18 year length of record of the base weather stations. Additional plot data coupled with the simulated daily DAYMET weather data were used as inputs to the BIOME-BGC model to simulate a number of ecosystem process variables, such as annual net primary productivity, evapotranspiration, and respiration (Running and Hunt 1993; Thornton et al. 2002). These process variables were estimated by executing the BIOME-BGC model until equilibrium (usually about 1500 years) and then averaging the annual estimates of the process variables over the same weather record time period used for the climate variables (18 years). In all, there were over 50 simulated variables available to use in the environmental analysis, but past studies found that many of these variables are highly correlated with each other and some gradients have little value in predicting ecosystem characteristics and processes

(Keane et al. 2002; Rollins et al. 2004). The final list of computed and simulated variables used in this study is shown in Table 3.

Analyzing collected and simulated data

Annual litterfall rates ($\text{kg}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$) were computed by dividing the total amount of accumulated material across the entire sampling record by the number of days in that record to get a daily rate, and that daily rate was multiplied by 365 to estimate an annual rate (Keane 2008). Two estimates of decomposition were calculated: (i) k was estimated by parameterizing the exponential decay function below using regression analysis, and (ii) a mass loss rate ($\%$ biomass loss $\cdot\text{year}^{-1}$) was estimated from differences in bag masses over the 3 year period. The analysis to determine the decomposition parameter k in the Olson (1963) equation was performed in SPLUS (Venables and Ripley 1999) using a linear mixed effects model whose form is as follows:

$$[1] \quad \ln\left(\frac{x_{ij}}{x_{i0}}\right) = (-k + b_i)t_j + \varepsilon_{ij}$$

where x_{ij} is the mass of the i th trap at time j (t_j) and x_{i0} is the initial mass of the i th trap; b_i is the random effect of trap i representing the deviation of the slope from the fixed effect for trap i ; and ε_{ij} is the random error, which is assumed to be independently distributed with a normal distribution.

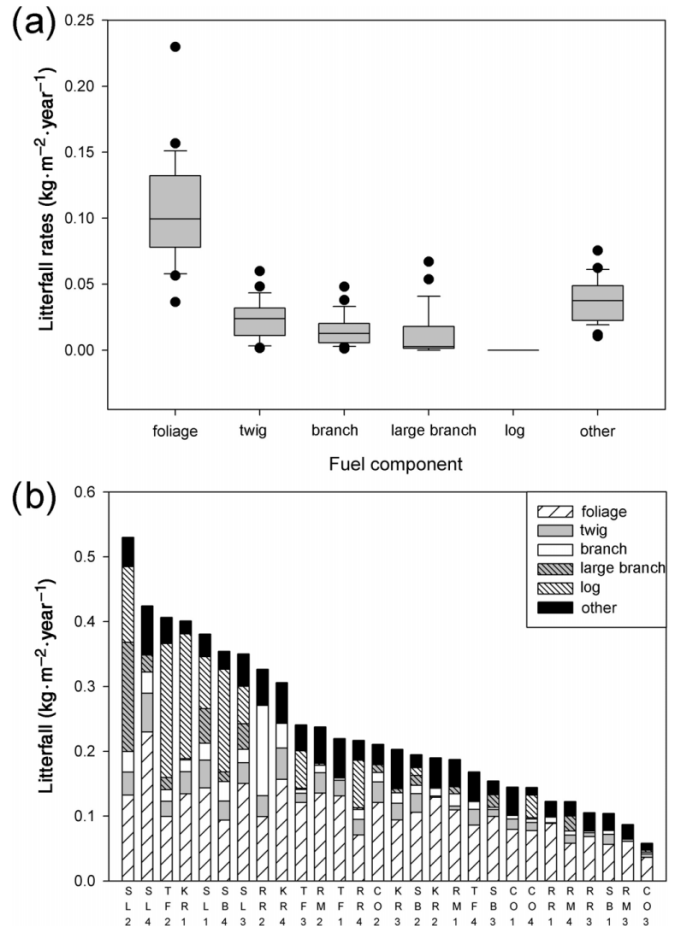
The computed annual litterfall and decomposition rates were correlated with the measured and simulated vegetation, topographic, climate, and ecosystem variables in Table 3 to determine possible empirical predictive relationships. We used a Pearson’s correlation coefficient (r) threshold of 0.40 to identify critical relationships. Multivariate least-squares regression analyses were used to create predictive models of fuel dynamics from the biophysical gradients for land management applications. A stepwise procedure was used based on the Akaike’s information criterion (AIC) to determine the “best” regression equation that contained at most, two predictive variables (only two variables were used because of low degrees of freedom and variables were deleted when $p < 0.05$). The data were transformed, if needed, to meet the assumptions of linear regression. All linear regressions were performed in SPLUS, and residual plots were examined to check the validity of the regression model (Venables and Ripley 1999).

Results

Litterfall and decomposition rates

Foliage had the highest litterfall rates of all five six fuel components ($0.068\text{--}0.23 \text{ kg}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$) across all sites, but interestingly, the deposition rates for the fine woody fuel and other canopy material components were similar across most of the sites ($0.01\text{--}0.05 \text{ kg}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$; Fig. 3a; see also Keane 2008). The highest litterfall rates occurred on plots with northern exposure, high basal area, high LAI, and cover types composed of shade-tolerant species (Fig. 3b). Log fall was recorded in only 47% (15 of 28) of the plots across all traps for the entire ≥ 10 year recording period; however, 90% of the plots experienced large branch fall, and all plots recorded foliage, twig, branchwood, and other

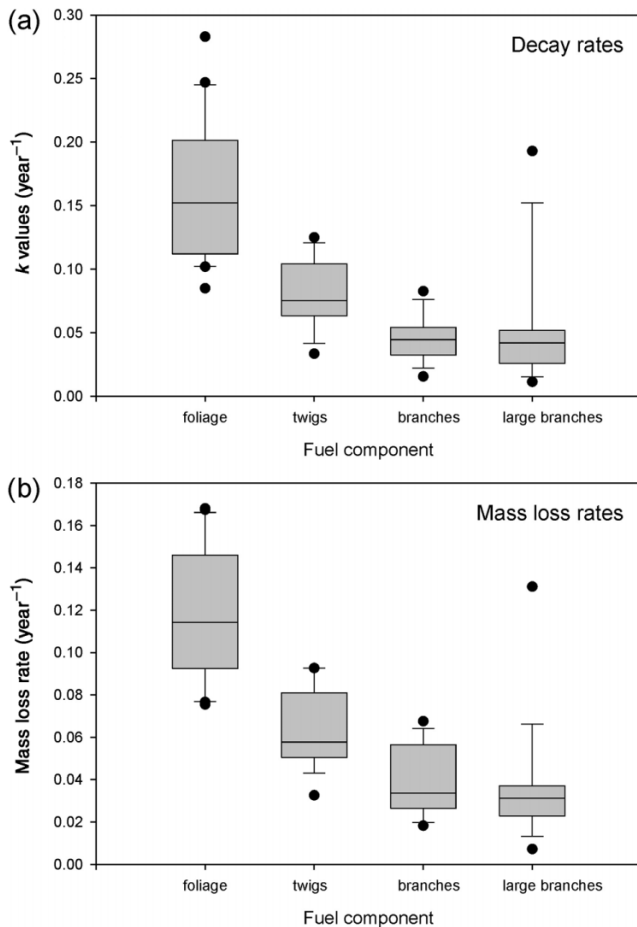
Fig. 3. Distribution of litterfall rates by surface fuel component for all fuel collected in all litter traps (a) across all plots and (b) for each plot (site abbreviations and plot numbers are given in Table 1). In the boxplots, the lower boundary of each box is the first quartile (25th percentile), the upper boundary is the third quartile (75th percentile), and the line within the box represents the median of the distribution. The upper and lower error bars are the 10th and 90th percentile, and the solid circles below and above the error bars represent outlying values.



canopy material depositions. Foliage, twigs, and other canopy material were recorded in all traps for nearly all of the visits (99.8%). Annual variation of litterfall rates was low (approximately 10% of annual mean) for fine fuel components but tended to increase with increasing fuel size, probably because large fuels were rarely found in the traps.

The slowest decomposition rates were measured in the low-elevation, southern aspect forests, especially those with high LAI (Keane 2008). Decay rates were the highest in the most productive sites, namely those sites on low-elevation north aspects or high-elevation south aspects (Pfister et al. 1977). Decay rates were higher and more variable for foliage ($k = 0.085\text{--}0.283 \text{ year}^{-1}$) than for woody fuel ($k = 0.045\text{--}0.125 \text{ year}^{-1}$) (Figs. 4a and 4b). As expected, large woody fuels had lower decay and mass loss rates than the smaller size classes, but many sites had the same decay rates across all woody size classes. The most productive sites (SB-2, KR-2, and TF-2) had woody decay rates that were equivalent to foliage decay rates. The low variability of

Fig. 4. Distribution of (a) decay rates (k values) and (b) mass loss rates (proportion loss) across all 28 plots in this study by the four fuel components. Decomposition was measured over a 3 year period, but it was not measured for logs and other canopy material. Boxplot parameters are as defined in Fig. 3.



woody fuel decay would suggest low correlation with site environment.

Biophysical relationships

As expected, the vegetation variables were better predictors of litterfall rates than the environmental variables (Table 4), even though most correlation coefficients were low ($r < 0.85$). Vegetation characteristics associated with the amount of canopy material (LAI, basal area, sapwood basal area, and tree height) had the highest correlations with litterfall rates, especially the foliage fuel component (Fig. 5). Tree density, mean diameter, and age variables were poor predictors of litterfall, but tree height seemed to be useful for predicting fine fuel deposition (Fig. 5; Table 4). Interestingly, the initial fuel loadings (FUELLOAD, Table 4) measured on the plot when the traps were installed (Table 2) had little predictive value for either litterfall or decomposition. LAI appeared to be the best variable to predict litterfall for all fuel components ($r > 0.42$, $p < 0.05$; Fig. 5), but snag basal area also appears important ($r > 0.46$ for all fuel components). Only percent clay soil (CLAY), minimum temperature (TMIN), and solar radiation (SRAD) had significant correlation coefficients with fine fuel litterfall rates for the

environmental variables (Fig. 5; Table 4). Surprisingly, net primary production (NPP), an important ecosystem process variable often associated with litterfall, had little relation to litterfall rates, possibly because of inaccurate simulation parameters and the coarse scale (1 km²) of the integrated weather variables. High variability of large branch and log rates resulted in low correlation coefficients ($r < 0.20$).

Decomposition rates (k values) were more correlated to environmental conditions than vegetation conditions (Fig. 5; Table 5). Foliage and fine woody fuel decay rates were significantly correlated with maximum and mean temperatures ($r > 0.49$) and vapor pressure deficit ($r > 0.47$) (Fig. 5), but correlations for the coarse woody fuels are not statistically significant for any variable (Table 5). Decay rates appeared to be negatively correlated with tree diameter measurements (Table 3, DOMDBH, AVEDBH, and SNAGDBH) and LAI, but the correlation was only significant for twig woody fuel decomposition ($p < 0.05$).

In the regression analysis, vegetation-based variables were found to be the best predictors of both litterfall rates and decomposition rates (Table 6). Fine fuel litterfall, especially foliage, had the strongest relationship to vegetation variables ($R^2 = 0.50$ – 0.78), but these same variables had poor predictive ability for decomposition ($R^2 = 0.16$ for foliage and branches). I expected environmental variables to have more predictive ability for decomposition (Table 6), but vegetation variables proved to have the highest value for decay prediction. As in the correlation analysis, it appears that fine fuel (foliage and twigs) litterfall and decomposition rates are correlated to canopy-related stand variables (LAI, BAREA, and DBH), whereas the larger fuels are related to environmental variables (SRAD) or surface fuel loadings (FUELLOAD). Basal area seems to be a variable that can be used for all fuel components.

Discussion

Litterfall

Litterfall rates in this study are slightly lower than those in other studies (compare Table 1 with Fig. 3), probably because the northern Rocky Mountain forests are less productive than the Pacific Northwest forests in Table 1 (Harmon et al. 1986). The low elevation moist sites of this study (CO-2, RM-2, SL-1, SL-2, SL-3, and KR-1) are probably the most ecologically similar to the Douglas-fir study sites reported in Table 1 and the foliage litterfall rates (0.12–0.15 kg·m⁻²·year⁻¹) are comparable with the minimum reported rates for Pacific Northwest Douglas-fir stands (0.17–0.50 kg·m⁻²·year⁻¹). Fine woody fuel litterfall rates measured in this study for those plots (0.001–0.139 kg·m⁻²·year⁻¹) also compare well with the Douglas-fir sites (0.005–0.129 kg·m⁻²·year⁻¹). Foliar litterfall rates of the lodgepole sites (TF, RR-3, RR-4, and CO-3 with rates of 0.12–0.15 kg·m⁻²·year⁻¹) are about one-half of those reported for lodgepole sites in Table 1 (0.362 kg·m⁻²·year⁻¹), whereas Table 1 subalpine fir sites have about double the rates (0.20–0.23 kg·m⁻²·year⁻¹) of the subalpine fir sites in this study (CO-3, SB-4, RM-4, and KR-4; 0.036–0.157 kg·m⁻²·year⁻¹). Large woody fuel (logs) rates are highly variable in this study (0.0001–0.207 kg·m⁻²·year⁻¹), but they also seem to agree with those reported for all studies in Table 1 (0.02–0.30 kg·m⁻²·year⁻¹).

Table 4. Results of the correlation analysis (coefficient r) of surface fuel litterfall rates ($\text{kg}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$) to both vegetation and environmental gradients.

Variable	Foliage	Twigs	Branches	Large branches	Total
Vegetation variables					
FUELLOAD	0.227	0.116	-0.032	-0.035	0.067
BAREA	0.845	0.777	0.555	0.371	0.634
SAPAREA	0.558	0.217	0.316	0.353	0.363
SNAGBA	0.653	0.497	0.467	0.464	0.651
TPH	0.224	0.392	0.075	0.060	0.125
SAPPH	-0.358	-0.187	-0.290	-0.100	-0.321
SPH	0.269	0.372	0.383	0.279	0.504
DOMDBH	0.491	0.280	0.385	0.137	0.271
AVEDBH	0.359	0.134	0.482	0.072	0.360
SNAGDBH	0.376	0.105	0.086	0.301	0.255
DOMHT	0.646	0.471	0.531	0.291	0.475
AVEHT	0.533	0.292	0.264	0.170	0.445
AGE	0.153	-0.003	-0.094	0.029	0.031
MAXAGE	0.065	0.000	-0.029	-0.056	-0.068
LAI	0.722	0.610	0.543	0.421	0.671
Environmental variables					
SOILDEPTH	-0.333	-0.048	-0.007	-0.079	-0.232
SAND	-0.014	-0.359	-0.159	-0.161	-0.113
SILT	-0.176	0.192	0.092	0.162	-0.017
CLAY	0.239	0.421	0.178	0.097	0.228
TMAX	0.340	0.082	0.310	0.094	0.258
TMIN	0.452	0.198	0.263	0.374	0.358
TDAY	0.383	0.116	0.310	0.171	0.294
PRCP	-0.044	0.136	0.053	0.319	-0.009
VPD	0.278	-0.009	0.262	-0.009	0.195
SRAD	-0.173	-0.118	-0.044	-0.503	-0.160
NPP	-0.269	-0.242	-0.045	0.055	-0.161
OUTFL	0.343	0.384	0.251	0.024	0.103

Note: Variables are defined in Table 3. Correlation coefficients $>|0.40|$ are given in boldface.

There are some limitations and shortcomings in this study that might influence the litterfall findings. Several times, it was impossible to empty litter traps on high-elevation plots in the autumn because of early snowfalls, so there may have been some decomposition losses because the summer's litter sat in the traps under the snow through the winter. Additionally, large snow banks on access roads sometimes delayed visits in the spring for weeks, allowing the litter to sit in traps under warm and moist conditions that were ideal for decomposition. Many conifer tree species shed their foliage during the late fall and early winter after the last trap visit so many of the fallen needles remained in the snow above the traps contributing to additional decomposition and wind losses. Several traps were vandalized during the summers causing gaps in the collection record for some plots. One ponderosa pine plot (KR-2) experienced an autumn prescribed fire that burned all but one of the traps. The sorting of foliage from other canopy material was a difficult and tedious task and was probably inconsistently done across the 12 field technicians involved in the project over the 10+ years of the study.

The lack of strong correlations of litterfall and decomposition rates with vegetation or environmental variables (Tables 4–6) may reflect missing biophysical variables, low climate data quality and resolution, and the low number of

plots in this study. Important biophysical variables not included in this study are (i) morphological differences between tree species across the diverse sites, (ii) influence of disturbance history on litterfall rates, and (iii) ecophysiological controls on environmental conditions. For example, leaf longevity measurements differed across the species encountered on our plots ranging from 1–7 years on low-elevation sites to 1–14 years on high-elevation sites because of differences in species composition (Keane et al. 2002). Litterfall rates for all our plots were within a relatively small range ($0.057\text{--}0.136 \text{ kg}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$) indicating that the simulated and measured biophysical variables may have not had sufficient spatial and temporal resolution to consistently detect the subtle differences in litterfall rates across the sites in this study. In general, it appeared that litterfall was better correlated with vegetation characteristics, whereas decomposition seemed to be related to environmental variables (Tables 4 and 5). The low number of plots in each vegetation type by biophysical setting precluded a detailed investigation into the effect of species differences on fuel dynamics.

The number and size of litter traps used on the plot appears adequate for estimating litterfall for all components but the large woody fuel size classes (logs and large branches) (see Keane 2008). Results from an analysis of temporal and spatial variance using bootstrap methods show

Fig. 5. Scatterplots of foliage litterfall and decomposition rates for the 28 plots in the study plotted with the vegetation and environmental variables with the highest correlation: (a) and (b) leaf area index (LAI), (c) and (d) basal area, (e) and (f) dominant tree height, (g) and (h) soil depth, and (i) and (j) minimum temperature.

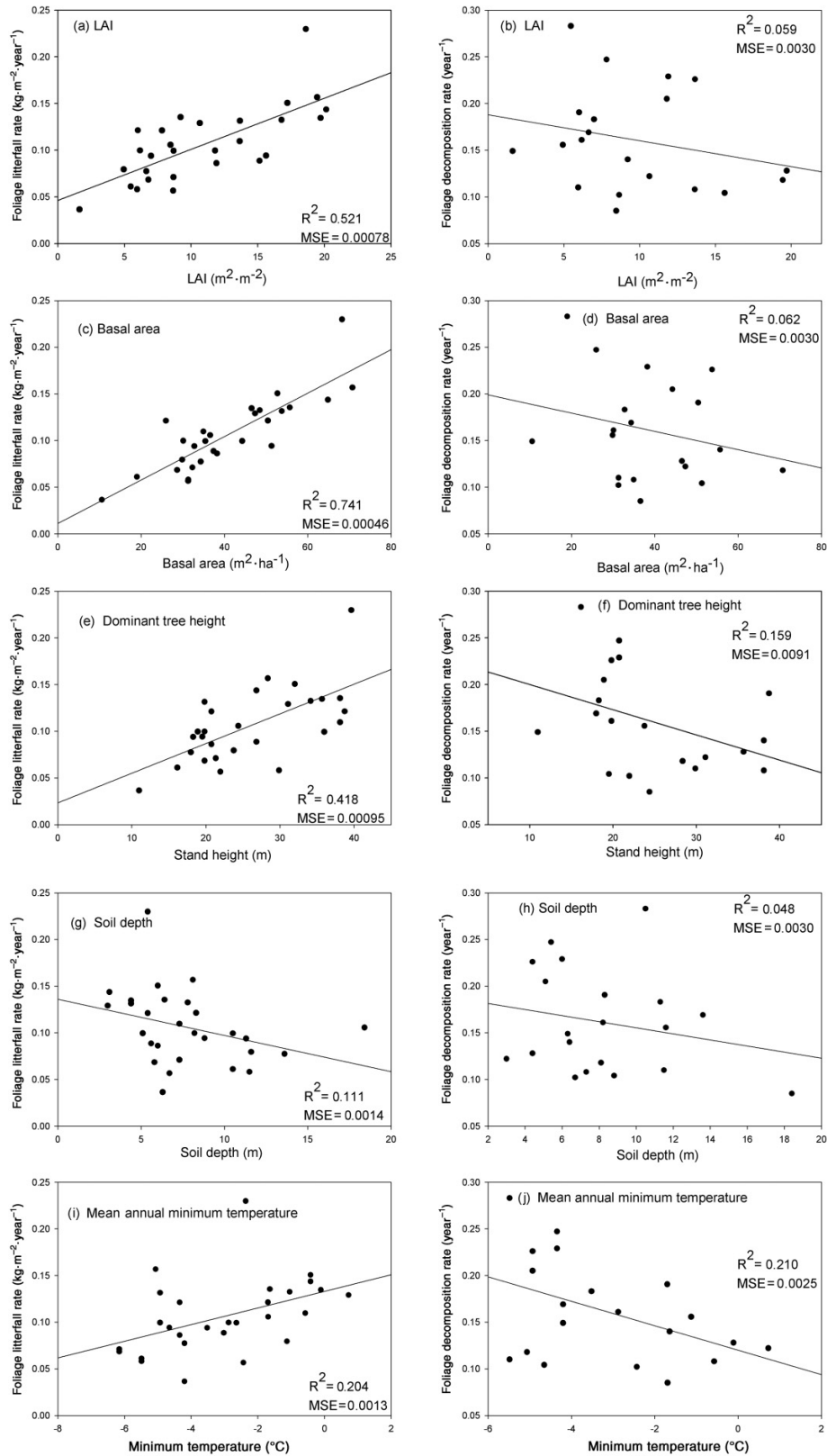


Table 5. Results of the correlation analysis (coefficient *r*) of surface fuel decomposition rates (*k* values, year⁻¹) to both vegetation and environmental gradients.

Variable	Foliage	Twigs	Branches	Large branches
Vegetation variables				
FUELLOAD	-0.230	-0.269	0.431	0.359
BAREA	-0.248	-0.392	-0.009	-0.055
SAPAREA	-0.146	-0.450	-0.021	0.573
SNAGBA	-0.015	-0.231	0.045	0.162
TPH	0.055	0.020	0.020	-0.339
SAPPH	0.015	0.259	-0.244	-0.218
SPH	0.004	-0.037	-0.065	-0.203
DOMDBH	-0.388	-0.505	-0.291	0.144
AVEDBH	-0.263	-0.614	-0.049	0.443
SNAGDBH	-0.287	-0.564	-0.234	0.025
DOMHT	-0.398	-0.424	-0.081	0.042
AVEHT	-0.164	-0.388	0.136	0.187
AGE	0.121	-0.102	0.160	0.393
MAXAGE	0.024	0.021	0.099	0.177
LAI	-0.243	-0.579	0.017	-0.235
Environmental variables				
SOILDEPTH	-0.219	0.064	-0.213	-0.101
SAND	-0.060	-0.256	-0.171	0.330
SILT	-0.106	0.303	0.141	-0.218
CLAY	0.276	0.085	0.147	-0.369
TMAX	-0.496	-0.549	-0.031	0.448
TMIN	-0.458	-0.391	-0.049	0.468
TDAY	-0.493	-0.518	-0.036	0.458
PRCP	0.052	0.297	0.372	-0.111
VPD	-0.473	-0.593	-0.043	0.441
SRAD	-0.109	-0.110	-0.198	-0.069
NPP	-0.275	-0.007	0.216	0.438
OUTFL	-0.222	-0.207	0.257	-0.078

Note: See Table 3 for variable abbreviations. Correlation coefficients $>|0.40|$ are given in boldface.

that, although the collection design was sufficient (seven traps capturing 90% variance) for fallen foliage and fine woody fuels, the larger woody material was inadequately sampled, because the traps were too few and too small to capture the phenomenon of tree fall (Keane 2008). In retrospect, I probably should have sampled fallen logs and branches across the entire plot and used the litter traps to collect only the foliage and branchwood smaller than 25 mm, but this would have required extensive monitoring of logs both inside and outside plot boundaries. Another alternative would have been to sample the logs across a longer time span (>10 years), but this is problematic because staffing, funding, and transportation can be quite variable over the ≥ 10 years of sampling. In an extension of this statistical analysis (Keane 2008), it was determined that >30 plots of 7–9 traps each (>210 traps total) would be needed to achieve a probability of detection >0.9 for logs for the entire ≥ 10 year record. Obviously, this large number of traps would be quite costly and time consuming to install and maintain. The tree life table and mortality rate approaches used by other studies (e.g., Harmon and Hua 1991) appear to be more effective, especially in ecosystems with large, long-lived trees.

Fuel decomposition

The decomposition measurements of this study did not

match the rigor, detail, and scale of the litterfall measurements. Decomposition was only measured over a 3 year time span, which was probably not long enough to adequately describe decay for the larger woody fuels. Decomposition was also only measured on five sites, and it did not include logs and other canopy material. There were only three sets of litterbags installed at each site, so a comprehensive analysis of variance such as that done for the litterfall data was not possible with such a small sample. Moreover, it was difficult to remove the material that had fallen on the litterbags over the 3 years while they were in the field. Needles and small materials sometimes worked their way into the bags through the coarse mesh, and decomposing material below and on the top of the bags appeared to be brought into the bag by soil macrofauna. Some bags were chewed or torn apart by rodents and ungulates, and others were actually carried off site by unknown factors. These limitations only affected around 16% of the samples.

Despite the limitations of the decomposition measurements, the measured rates seemed to compare quite well with those measured in other studies (Table 1). The range of *k* values for foliage decomposition measured in this study for the Douglas-fir sites (0.085–0.205) are similar to those in Table 1 (0.005–0.56). Similar results are found in the lodgepole sites (foliage: 0.104–0.247 in this study and 0.09–0.14 in Table 1) and subalpine fir sites (0.110–0.169 in this study

Table 6. Results of the regression analysis of surface fuel litterfall ($\text{kg}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$) and decomposition rates (k , year^{-1}) to both the vegetation gradients and environmental gradients at the plot level using two variables (defined in Table 3) at most.

Dependent variable	Equation	df (error)	R^2
Accumulation rates ($\text{kg}\cdot\text{m}^{-2}$)			
Foliage	$\hat{y} = 0.0173 + 0.00129 \text{ SNAGBA} + 0.0019 \text{ BAREA}$	25	0.779
Twigs	$\hat{y} = 0.0144 + 0.00077 \text{ BAREA} - 0.00037 \text{ SAND}$	25	0.694
Branches	$\hat{y} = \exp(-6.962 + 0.0364 \text{ BAREA} + 0.0358 \text{ AVEDBH})$	25	0.504
Large branches	$\hat{y} = \exp(5.907 + 0.0034 \text{ SPH} - 0.040 \text{ SRAD}) - 0.001$	25	0.420
Total	$\hat{y} = \exp(-2.668 + 0.0267 \text{ BAREA})$	25	0.500
Decomposition rates (k)			
Foliage	$\hat{y} = \exp(-1.525 - 0.0076 \text{ DOMDBH})$	18	0.167
Twigs	$\hat{y} = 0.146 - 0.0017 \text{ AVEDBH} - 0.0023 \text{ LAI}$	13	0.571
Branches	$\hat{y} = \exp(-3.312 + 0.017 \text{ FUELLOAD})$	13	0.166
Large branches	$\hat{y} = \exp(-3.734 - 0.0077 \text{ MAXAGE} + 0.0172 \text{ AGE})$	14	0.370

Note: Significant correlation coefficients are given in boldface ($p < 0.05$).

and 0.09–0.17 in Table 1). This would indicate that the values calculated from this study should be useful for future modeling efforts.

There are many reasons for the lack of strong correlation between site factors and decomposition rates (Table 5), and they are summarized in Prescott (2005). Decomposition is a complex process that is highly influenced by local factors acting at fine scales, such as tree spatial distribution, soil type, and microclimate, and these fine scale influences and associated variability may swamp effects of the coarse-scale environmental variables used in this study to predict decay rates (Kaarik 1974; Millar 1974; Moorhead and Sinsabaugh 2006). Moreover, the exponential function introduced by Olson (1963) does not seem to fit long-term trends of decomposition in many forests, so the k value may be inappropriate for comparing decay rates across ecosystems. I found that the exponential function used to determine k often did not always fit the collected decomposition data collected in this study because of the short time period (3 years), slow rate of decomposition, and high variability within a plot.

Conclusions

The correlation analysis shows that litterfall is related to canopy characteristics, whereas decomposition is somewhat related to biophysical site conditions. However, the low correlation coefficients suggest that there are many other environmental variables important to litterfall and decomposition, such as disturbance, species morphology, and ecophysiological characteristics. The log woody fuel deposition and decomposition estimates measured in this study contain high error rates, but the fine fuel dynamics, which is critically lacking in the literature, appear useful for most models and management applications. The regression analysis results provide a means to dynamically model the measured fuel processes across landscapes using vegetation and environmental variables. For example, the LAI spatial product computed from MODIS imagery could be used to map litterfall rates across the landscape using our regression results (Table 6). These data can provide managers with valuable estimates of litterfall and decomposition rates that can be used to determine the longevity of fuel treatments and prioritize fuel treatment areas by calculating how long it

would take to accumulate enough surface fuels to ignite or support a crown fire or kill overstory trees using the fire behavior models.

Acknowledgements

I acknowledge all those field technicians who spent countless hours collecting, sorting, and weighing litter: Todd Carlson, Kirsten Schmidt, Wayne Lynholm, Courtney Couch, Laurie Dickinson, Myron Holland, Curtis Johnson, Micha Krebs, Eric Aplan, Daniel Covington, Amy Rollins, and Ben McShan of the Rocky Mountain Research Station Missoula Fire Sciences Laboratory. I also thank Joseph White of Baylor University; Ceci McNicoll, USDA Forest Service Gila National Forest; Wendel Hann, USDA Forest Service Washington Office; Dan Fagre, USGS Glacier Field Station; Dave Peterson, USDA Forest Service Pacific Northwest Research Station; Matt Rollins, Russell Parsons, Helen Smith, Denny Simmerman, and Kathy Gray, USDA Forest Service Rocky Mountain Research Station Missoula Fire Sciences Laboratory; for field work, technical support, assistance in the analysis, and invaluable advice. Lastly, I thank Roger Ottmar and Tom Spies, USDA Forest Service, Pacific Northwest Research Station; Elizabeth Reinhardt, Rocky Mountain Research Station; Jan van Wagtenonk, Yosemite National Park; and four anonymous journal reviewers for insightful and helpful reviews. This work was partially funded by the USGS National Biological Service and Glacier National Park's Global Change Research Program under Inter-agency Agreements 1430-1-9007 and 1430-3-9005 and the USGS CLIMET project.

References

- Alexander, R.R. 1954. A comparison of growth and morality following cutting in old-growth mountain spruce stands. USDA For. Serv. Rocky Mountain For. Range Exp. Stn. Res. Note RN-11.
- Avery, C.C., Larson, F.R., and Schubert, G.H. 1976. Fifty-year records of virgin stand development in southwestern ponderosa pine. USDA For. Serv. Gen. Tech. Rep. RM-22.
- Berg, B., and Ekbohm, G. 1993. Decomposing needle litter in *Pinus contorta* (lodgepole pine) and *Pinus sylvestris* (Scots pine) monocultural systems—is there a maximum mass loss? Scand. J. For. Res. 8: 457–465.

- Botkin, D.B. 1993. *Forest dynamics: an ecological model*. Oxford University Press, New York.
- Brais, S., Sadi, F., Bergeron, Y., and Grenier, Y. 2005. Coarse woody debris dynamics in a post-fire jack pine chronosequence and its relation with site productivity. *For. Ecol. Manage.* **220**: 216–226. doi:10.1016/j.foreco.2005.08.013.
- Bray, J.R., and Gorham, E. 1964. Litter production in forests of the world. *Adv. Ecol. Res.* **2**: 101–157.
- Brown, J.K. 1970. A method for inventorying downed woody fuel. USDA For. Serv. Gen. Tech. Rep. INT-16.
- Busse, M.D. 1994. Downed bole-wood decomposition in lodgepole pine forests of central Oregon. *Soil Sci. Soc. Am. J.* **58**: 221–227.
- Carlton, D.W., and Pickford, S.G. 1982. Fuelbed changes with aging of slash from ponderosa pine thinnings. *J. For.* **86**: 91–101.
- Christiansen, E.C., and Pickford, S.G. 1991. Natural abatement of fire hazard in Douglas-fir blowdown and thinning fuelbeds. *Northwest Sci.* **65**: 141–147.
- Dimock, E.J. 1958. Litter fall in a young stand of Douglas-fir. *Northwest Sci.* **32**: 19–29.
- 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. doi:10.1139/x79-030.
- Edmonds, R.L. 1987. Decomposition rates and nutrient dynamics in small-diameter woody litter in four forest ecosystems in Washington, U.S.A. *Can. J. For. Res.* **17**: 499–509. doi:10.1139/x87-084.
- Edmonds, R.L. 1991. Organic matter decomposition in western United States forests. *In Proceedings, Management and Productivity of Western-Montane Forest Soils, 10–12 Apr. 1990, Boise, Idaho. Compiled by A.E. Harvey and L.E. Neuenschwander.* USDA For. Serv. Gen. Tech. Rep. INT-280. pp. 118–125.
- Edmonds, R.L., Vogt, D.J., Sandberg, D.H., and Driver, C.H. 1986. Decomposition of Douglas-fir and red alder wood in clear-cuttings. *Can. J. For. Res.* **16**: 822–831. doi:10.1139/x86-145.
- Edmonds, R.L., and Eglitis, A. 1989. The role of the Douglas-fir beetle and wood borers in the decomposition of and nutrient release from Douglas-fir logs. *Can. J. For. Res.* **19**: 853–859. doi:10.1139/x89-130.
- Fernandes, P.M., and Botelho, H.S. 2003. A review of prescribed burning effectiveness in fire hazard reduction. *Int. J. Wildland Fire*, **12**: 117–128. doi:10.1071/WF02042.
- Ferry, G.W., Clark, R.G., Montgomery, R.E., Mutch, R.W., Leenhouts, W.P., and Zimmerman, G.T. 1995. Altered fire regimes within fire-adapted ecosystems. *In Our living resources: a report to the nation on the distribution, abundance, and health of U.S. plants, animals, and ecosystems.* U.S. Department of the Interior, National Biological Service, Washington, D.C. pp. 222–224.
- 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. doi:10.1139/b77-190.
- Fosberg, M.A. 1970. Drying rates of heartwood below fiber saturation. *For. Sci.* **16**: 57–63.
- US General Accounting Office (GAO). 2002. Severe wildland fires: leadership and accountability needed to reduce risks to communities and resources. Report to Congressional Requesters GAO-02-259. US General Accounting Office, Washington, D.C.
- Gottfried, G.L. 1978. Five-year growth and development in a virgin Arizona mixed conifer stand. USDA For. Serv. Rocky Mountain For. Range Exp. Stn. Res. Pap. RM-203.
- Graham, R.L. 1982. Biomass dynamics of dead Douglas-fir and western hemlock boles in mid-elevation forests of the Cascade Range. Ph.D. dissertation, Oregon State University, Corvallis, Ore.
- Grier, C.C., and Logan, R.S. 1977. Old-growth *Pseudotsuga menziesii* communities of a western Oregon watershed: biomass distribution and production budgets. *Ecol. Monogr.* **47**: 373–400. doi:10.2307/1942174.
- Hagan, J.M., and Grove, S.L. 1999. Coarse woody debris: humans and nature competing for trees. *J. For.* **97**: 6–11.
- Hann, W.J., Jensen, M.E., and Keane, R.E. 1988. *Ecosystem management handbook*. Ch. 4. ECODATA methods and field forms. Northern Region Handbook, USDA Forest Service, Northern Region, Missoula, Mont.
- Harmon, M.E., and Hua, C. 1991. Coarse woody debris dynamics in two old-growth ecosystems. *Bioscience*, **41**: 604–610. doi:10.2307/1311697.
- Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Lienkaemper, G.W., Cromack, K., and Cummins, K.W. 1986. Ecology of coarse woody debris in temperate ecosystems. *Adv. Ecol. Res.* **15**: 133–302.
- Hart, S.C., Firestone, M.K., and Paul, E.A. 1992. Decomposition and nutrient dynamics of ponderosa pine needles in a Mediterranean-type climate. *Can. J. For. Res.* **22**: 306–314. doi:10.1139/x92-040.
- Huebschmann, M.M., Lynch, T.B., and Wittwer, R.F. 1999. Needle litterfall prediction models for even aged natural shortleaf pine (*Pinus echinata* Mill.) stands. *For. Ecol. Manage.* **117**: 179–186. doi:10.1016/S0378-1127(98)00466-6.
- Jenkins, M.A., Webster, R., Parker, G.R., and Spetich, M.A. 2004. Coarse woody debris in managed central hardwood forests of Indiana, USA. *For. Sci.* **50**: 781–792.
- Johansson, M.-B. 1994. Decomposition rates of Scots pine needle litter related to site properties, litter quality, and climate. *Can. J. For. Res.* **24**: 1771–1781. doi:10.1139/x94-229.
- Kaarik, A.A. 1974. Decomposition of wood. *In Biology of plant litter decomposition. Edited by C.H. Dickinson and G.J.F. Pugh.* Academic Press, London. pp. 129–174.
- Keane, R.E. 2008. Surface fuel litterfall and decomposition in the northern Rocky Mountains, USA. USDA For. Serv. Res. Pap. RMRS-RP-70.
- Keane, R.E., Ryan, K.C., and Running, S.W. 1996. Simulating effects of fire on northern Rocky Mountain landscapes with the ecological process model Fire-BGC. *Tree Physiol.* **16**: 319–331.
- Keane, R.E., McNicoll, C., and Rollins, M.G. 2002. Integrating ecosystem sampling, gradient modeling, remote sensing, and ecosystem simulation to create spatially explicit landscape inventories. USDA For. Serv. Gen. Tech. Rep. RMRS-GTR-92.
- Keenan, R.J., Prescott, C.E., Kimmins, J.P., Pastor, J., and Dewey, B. 1996. Litter decomposition in western red cedar and western hemlock forests on northern Vancouver Island, British Columbia. *Can. J. Bot.* **74**: 1626–1634. doi:10.1139/b96-197.
- Klemmedson, J.O. 1992. Decomposition and nutrient release from mixtures of Gambel oak and ponderosa pine leaf litter. *For. Ecol. Manage.* **47**: 349–361. doi:10.1016/0378-1127(92)90284-G.
- Klemmedson, J.O., Meier, C.E., and Campbell, R.E. 1990. Litter fall transfers of dry matter and nutrients in ponderosa pine stands. *Can. J. For. Res.* **20**: 1105–1115. doi:10.1139/x90-146.
- Kueppers, L.M., Southon, J., Baer, P., and Harte, J. 2004. Dead wood biomass and turnover time, measured by radiocarbon, along a subalpine elevation gradient. *Oecologia (Berl.)*, **141**: 641–651. doi:10.1007/s00442-004-1689-x.
- Laiho, R., and Prescott, C.E. 1999. The contribution of coarse woody debris to carbon, nitrogen, and phosphorus cycles in

- three Rocky Mountain coniferous forests. *Can. J. For. Res.* **29**: 1592–1603. doi:10.1139/cjfr-29-10-1592.
- Laverty, L., and Williams, J. 2000. Protecting people and sustaining resources in fire-adapted ecosystems—a cohesive strategy. Forest Service response to GAO Report GAO/RCED 99-65. USDA Forest Service, Washington, D.C.
- Mackensen, J., Bauhus, J., and Webber, E. 2003. Decomposition rates of coarse woody debris—a review with particular emphasis on Australian tree species. *Aust. J. Bot.* **51**: 27–37. doi:10.1071/BT02014.
- Maguire, D.A. 1994. Branch mortality and potential litterfall from Douglas-fir trees in stands of varying density. *For. Ecol. Manage.* **70**: 41–53. doi:10.1016/0378-1127(94)90073-6.
- Means, J.E., Cromack, K., Jr., and MacMillan, P.C. 1985. Comparison of decomposition models using wood density of Douglas-fir logs. *Can. J. For. Res.* **15**: 1092–1098. doi:10.1139/x85-178.
- Meentemeyer, V. 1978. Macroclimate and lignin control of litter decomposition rates. *Ecology*, **59**: 465–472. doi:10.2307/1936576.
- Millar, C.S. 1974. Decomposition of coniferous leaf litter. In *Biology of plant litter decomposition*. Edited by C.H. Dickinson and G.J.F. Pugh. Academic Press, London. pp. 105–129.
- Moorhead, D.L., and Sinsabaugh, R.L. 2006. A theoretical model of litter decay and microbial interaction. *Ecol. Monogr.* **76**: 151–174. doi:10.1890/0012-9615(2006)076[0151:ATMOLD]2.0.CO;2.
- Nackaerts, K., Coppin, P., Muys, B., and Hermy, M. 2000. Sampling methodology for LAI measurements with LAI-2000 in small forest stands. *Agric. For. Meteorol.* **101**: 247–250. doi:10.1016/S0168-1923(00)00090-3.
- Olson, J.S. 1963. Energy storage and the balance of producers and decomposers in ecological systems. *Ecology*, **44**: 322–331. doi:10.2307/1932179.
- Pastor, J., and Post, W.M. 1985. Development of a linked forest productivity – soil process model. Martin Marietta Energy Systems, Inc. for the US Department of Energy, Environmental Sciences Division, Oak Ridge, Tenn. Environ. Sci. Div. Publ. 2455.
- Pfister, R.D., Kovalchik, B.L., and Arno, S. F., and Presby, R.C. 1977. Forest habitat types of Montana. USDA For. Serv. Gen. Tech. Rep. INT-34.
- Pearson, J.A., Knight, D.H., and Fahey, T.J. 1987. Biomass and nutrient accumulation during stand development in Wyoming lodgepole pine forests. *Ecology*, **68**: 1966–1977. doi:10.2307/1939887.
- Prescott, C.E. 2005. Do rates of litter decomposition tell us anything we really need to know? *For. Ecol. Manage.* **220**: 66–74. doi:10.1016/j.foreco.2005.08.005.
- Prescott, C.E., Taylor, B.R., Parsons, W.F.J., Durall, D.M., and Parkinson, D. 1993. Nutrient release from decomposing litter in Rocky Mountain coniferous forests: influence of nutrient availability. *Can. J. For. Res.* **23**: 1576–1586. doi:10.1139/x93-198.
- Prescott, C.E., Zabek, L.M., Staley, C.L., and Kabzems, R. 2000. Decomposition of broadleaf and needle litter in forests of British Columbia: influences of litter type, forest type, and litter mixtures. *Can. J. For. Res.* **30**: 1742–1750. doi:10.1139/cjfr-30-11-1742.
- Prescott, C.E., Hope, G.D., and Blevins, L.L. 2003. Effect of gap size on litter decomposition and soil nitrate concentrations in a high-elevation spruce–fir forest. *Can. J. For. Res.* **33**: 2210–2220. doi:10.1139/x03-152.
- Reinhardt, E., and Keane, R.E. 1998. FOFEM—a first order fire effects model. *Fire Manage. Notes*, **58**: 25–28.
- Robertson, G.P., and Paul, E.A. 2000. Decomposition and soil organic matter dynamics. In *Methods in ecosystem science*. Edited by O.E. Sala, R.B. Jackson, H.A. Mooney, and R.W. Howarth. Springer, New York. pp. 104–116.
- Rollins, M.G., Keane, R.E., and Parsons, R.A. 2004. Mapping fuels and fire regimes using remote sensing, ecosystem simulation, and gradient modelling. *Ecol. Appl.* **14**: 75–95. doi:10.1890/02-5145.
- Rothermel, R.C. 1972. A mathematical model for predicting fire spread in wildland fuels. USDA For. Serv. Pac. Intermountain For. Range Exp. Stn. Res. Pap. INT-115.
- Running, S.W., and Hunt, E.R., Jr. 1993. Generalization of a forest ecosystem process model for other biomes, BIOME-BGC, and an application for global-scale models. In *Scaling physiological processes: leaf to globe*. Edited by J.R. Ehrlinger and C.B. Field. Academic Press, Inc. New York. pp. 141–157.
- Sanchez-Flores, E., and Yool, S.R. 2004. Site environment characterization of downed woody fuels in the Rincon Mountains, Arizona: regression tree approach. *Int. J. Wildland Fire*, **13**: 467–477. doi:10.1071/WF04015.
- Sollins, P. 1982. Input and decay of coarse woody debris in coniferous stands in western Oregon and Washington. *Can. J. For. Res.* **12**: 18–28. doi:10.1139/x82-003.
- Sollins, P., Cline, S.P., Verhoeven, T., Sachs, D., and Spycher, G. 1987. Patterns of log decay in old growth Douglas-fir forests. *Can. J. For. Res.* **17**: 1585–1595. doi:10.1139/x87-243.
- Spies, T.A., Franklin, J.F., and Thomas, T.B. 1988. Coarse woody debris in Douglas-fir forests of western Oregon and Washington. *Ecology*, **69**: 1689–1702. doi:10.2307/1941147.
- Stohlgren, T.J. 1988. Litter dynamics in two Sierran mixed conifer forests. II. Nutrient release from decomposing litter. *Can. J. For. Res.* **18**: 1136–1144. doi:10.1139/x88-175.
- Stump, L.M., and Binkley, D. 1993. Relationships between litter quality and nitrogen availability in Rocky Mountain forests. *Can. J. For. Res.* **23**: 492–502. doi:10.1139/x93-067.
- Taylor, B.R., Prescott, C.E., Parsons, W.F.J., and Parkinson, D. 1991. Substrate control of litter decomposition in four Rocky Mountain conifer forests. *Can. J. Bot.* **69**: 2242–2250. doi:10.1139/b91-281.
- Thornton, P.E., Running, S.W., and White, M.A. 1997. Generating surfaces of daily meteorological variables over large regions of complex terrain. *J. Hydrol.* **190**: 214–251. doi:10.1016/S0022-1694(96)03128-9.
- Thornton, P.E., Law, B.E., Gholz, H.L., Clark, K.L., Falge, E., Ellsworth, D.S., Goldstein, A.H., Monson, R.K., Hollinger, D.Y., Falk, M., Chen, J., and Sparks, J.P. 2002. Modeling and measuring the effects of disturbance history and climate on carbon and water budgets in evergreen needleleaf forests. *Agric. For. Meteorol.* **113**: 185–222. doi:10.1016/S0168-1923(02)00108-9.
- Trofymow, J.A., Barclay, H.J., and McCullough, K.M. 1991. Annual rates and elemental concentrations of litter fall in thinned and fertilized Douglas-fir. *Can. J. For. Res.* **21**: 1601–1615. doi:10.1139/x91-223.
- Turner, J., and Long, J.N. 1975. Accumulation of organic matter in a series of Douglas-fir stands. *Can. J. For. Res.* **5**: 681–690. doi:10.1139/x75-094.
- Venables, W.N., and Ripley, B.D. 1999. *Modern applied statistics with SPLUS*. Springer, New York.
- Vogt, K.A., Grier, C.C., and Vogt, D.J. 1986. Production, turnover, and nutrient dynamics of above- and belowground detritus of world forests. *Adv. Ecol. Res.* **15**: 303–377.
- Webster, C.R., and Jenkins, M.A. 2005. Coarse woody debris dynamics in the southern Appalachians as affected by topographic

- position and anthropogenic disturbance history. *For. Ecol. Manage.* **217**: 319–330. doi:10.1016/j.foreco.2005.06.011.
- White, D.E., Atzet, T., and Martinez, P.A. 2004. Relationship of historic fire regimes to dead wood components in white fir forests of southwestern Oregon. *Proc. Tall Timbers Fire Ecol. Conf.* **22**: 117–124.
- White, J.D., Running, S.W., Thornton, P.E., Keane, R.E., Ryan, K.C., Fagre, D.B., and Key, C.H. 1998. Assessing simulated ecosystem processes for climate variability research at Glacier National Park, USA. *Ecol. Appl.* **8**: 805–823. doi:10.1890/1051-0761(1998)008[0805:ASEPFC]2.0.CO;2.
- White, M.A., Thornton, P.E., Running, S.W., and Nemani, R.R. 2000. Parameterization and sensitivity analysis of the BIOME-BGC terrestrial ecosystem model: net primary production controls. *Earth Interact.* **4**: 1–85. doi:10.1175/1087-3562(2000)004<0003:PASAOT>2.0.CO;2.
- Wright, K.H., and Lauterback, P.G. 1958. A 10-year study of mortality in a Douglas-fir sawtimber stand in Coos and Douglas Counties, Oregon. *USDA For. Serv. Pac. Northwest For. Range Exp. Stn. Res. Pap. PNW-27*.
- Yavitt, J.B., and Fahey, T.J. 1982. Loss of mass and nutrient changes of decaying woody roots in lodgepole pine forests, southeastern Wyoming. *Can. J. For. Res.* **12**: 745–752. doi:10.1139/x82-113.