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LITTER AND DEAD WOOD DYNAMICS IN PONDEROSA PINE FORESTS ALONG A 160-YEAR CHRONOSEQUENCE

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Abstract. Disturbances such as fire play a key role in controlling ecosystem structure. In fire-prone forests, organic detritus comprises a large pool of carbon and can control the frequency and intensity of fire. The ponderosa pine forests of the Colorado Front Range, USA, where fire has been suppressed for a century, provide an ideal system for studying the long-term dynamics of detrital pools. Our objectives were (1) to quantify the long-term temporal dynamics of detrital pools; and (2) to determine to what extent present stand structure, topography, and soils constrain these dynamics. We collected data on downed dead wood, litter, duff (partially decomposed litter on the forest floor), stand structure, topographic position, and soils for 31 sites along a 160-year chronosequence. We developed a compartment model and parameterized it to describe the temporal trends in the detrital pools. We then developed four sets of statistical models, quantifying the hypothesized relationship between pool size and (1) stand structure, (2) topography, (3) soils variables, and (4) time since fire. We contrasted how much support each hypothesis had in the data using Akaike's Information Criterion (AIC).

Time since fire explained 39–80% of the variability in dead wood of different size classes. Pool size increased to a peak as material killed by the fire fell, then decomposed rapidly to a minimum (61–85 years after fire for the different pools). It then increased, presumably as new detritus was produced by the regenerating stand. Litter was most strongly related to canopy cover ($r^2 = 77\%$), suggesting that litter fall, rather than decomposition, controls its dynamics. The temporal dynamics of duff were the hardest to predict. Detrital pool sizes were more strongly related to time since fire than to environmental variables. Woody debris peak-to-minimum time was 46–67 years, overlapping the range of historical fire return intervals (1 to >100 years). Fires may therefore have burned under a wide range of fuel conditions, supporting the hypothesis that this region's fire regime was mixed severity.

Key words: Colorado Front Range, USA; continuous time model; dead wood; duff; fire; litter; long-term dynamics; ponderosa pine forests; soils factors; stand structure; temporal patterns; topographic controls.

Introduction

Understanding the role of disturbance in controlling ecosystem structure offers a fundamental challenge to contemporary ecologists. Organic detritus in forested ecosystems can be a significant pool of carbon. Coarse dead wood alone accounts for 18% of total ecosystem carbon in temperate forests (Pregitzer and Euskirchen 2004). In fire-prone forests, detritus comprises the fuel bed (Van Wagner 1977), acting as a control over fire behavior (Nalder and Wein 1999). The role of fuels in controlling fire behavior (e.g., Schoennagel et al. 2004) in forests of the western United States makes understanding and quantifying the temporal dynamics of detritus in these forests critical.

Managers and policy makers are faced with decisions such as where and how to reduce fuel loads, whether to allow salvage logging after wildfires, or when and where to use prescribed fire. Past research has addressed specific consequences of such decisions at specific locations, including the effect of salvage logging on regeneration and fire hazard (e.g., Donato et al. 2006), and the importance of prescribed fire in fuel reduction (e.g., Stephens 1998). These studies can inform decisions at other landscapes and scales if there is a reference to relate the results to. Armed with knowledge of the dynamics of fuels and fire-killed trees, decision-makers can develop reasonable hypotheses of how those dynamics could change if a certain treatment is applied. Understanding the timing and magnitude of changes in detritus in fire-prone forests will provide this important link.

Historical and present disturbance regimes, as well as climate and resource availability, control ecosystem level carbon accumulation (Chapin et al. 2002). Fire suppression in forests in the western United States has likely

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contributed to an accumulation of fuels on the ground (Covington and Moore 1994). This has become an issue of concern in forests that historically had relatively short fire intervals, such as the ponderosa pine forests of the Colorado Front Range, because fire has been suppressed, on average, for longer than one fire cycle (mean fire intervals ranged from 9 to 43 years; Brown et al. 1999, Veblen et al. 2000). These unusually long fire-free intervals make them ideal for studying the long-term trends in accumulation of detrital material (Robertson and Bowser 1999), as well as the relative strength of other constraints on their temporal dynamics. Understanding and quantifying these detrital dynamics and their constraints would provide a detailed baseline against which to compare detritus in other dry, fire-prone forests, as well as potential changes in these dynamics through time. Temporal changes may be particularly important in semi-arid areas, such as these ponderosa pine forests, where water availability limits productivity, because climate change projections envision increases in water deficits (Lauenroth et al. 2004). Care must be taken, though, in using these studies to define the historical range of variability in pool sizes, because the disturbance regime has been altered (Bond-Lamberty et al. 2002).

The detrital pool comprises a set of sub-pools, each with different accumulation and decomposition dynamics (Perruchoud and Fischlin 1995), and with different effects on fire behavior (Rothermel 1972). We refer to the sum of downed dead wood in different size classes (twigs, branches, medium branches, logs), litter (fallen leaves and needles, cones and bark scales), and duff (partially decomposed but recognizable plant material on the surface of the mineral soil) generically as "detritus." There is a wealth of research on the long-term dynamics of coarse dead wood in coniferous forests of western North America, highlighting its importance for habitat and its effect on many ecological processes. This literature includes both theoretical and empirical studies (Harmon et al. 1986, Spies et al. 1988, Sturtevant et al. 1997, Clark et al. 1998, Hély et al. 2000, Janisch and Harmon 2002). Less information is available on the dynamics of fine dead wood, litter, and duff (Agee and Huff 1987, Nalder and Wein 1999, Wang et al. 2003, MacKenzie et al. 2004). Furthermore, none of these studies analyze both coarse and fine fuels (including litter) using a single, process-based framework.

The temporal dynamics of detrital pools are determined by the balance between inputs and outputs. Inputs are driven by processes such as tree mortality, litterfall, branch breakage, and, in the case of duff, fragmentation of fallen wood and litter. This last flux constitutes an output from the fresh detritus pools. However, the main flux from all pools is due to microbial decomposition.

Aboveground biomass accumulates in predictable patterns after a disturbance (Bormann and Likens 1979). Variations in forest biomass (either dependent or independent of post-disturbance successional changes) would modify inputs and, consequently, be the driver of detrital dynamics, though other factors may be affecting the magnitude of output fluxes from the detrital pool. Moisture and temperature can affect both the inputs and outputs from detrital pools, through their effect on net primary production and decomposition (Chapin et al. 2002). At broad scales, these controls have been quantified using mean annual precipitation, temperature, and actual evapotranspiration (Whittaker 1970, Meentemeyer 1978). In the Rocky Mountains, altitude and orientation of a particular site affect its radiative load, precipitation, and temperature, thereby determining its water balance (Peet 2000). Soil characteristics, such as depth and texture, may also play a role (Peet 2000). Topographic or soil conditions could therefore control detrital pool size, through their influence on net primary production and decomposition. Our objectives in this study were (1) to quantify the long-term temporal dynamics of detrital pools (downed dead wood in different size classes, litter, duff) using a single, process-based framework; and (2) to determine to what extent present stand structure and environmental characteristics (topography, soils) constrain these temporal dynamics.

Methods

Study area and data

We selected 31 sites in the Colorado Front Range of the Rocky Mountains, USA, between 39°7′ and 40°2′ N (Fig. 1), obtaining a chronosequence of time since fire from 1 to 159 years. Fire history information was obtained from published work (Brown et al. 1999, Veblen et al. 2000, Huckaby et al. 2001), and from USDA Forest Service staff. All sites were dominated by ponderosa pine (*Pinus ponderosa* Dougl. ex Laws), with secondary components of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), and Rocky Mountain juniper (*Juniperus scopulorum* L). Within each fire year or fire perimeter, we randomly selected one or two sites (depending on the extent) with different aspects. These sites covered a range of soils, topographic positions, and stand structure conditions. Fire severity was high at all the sites that burned since 1963 (sites 15 to 31), except one (site 15), where many large trees survived (see Plate 1). Burn severity at the older sites is unknown. Some of these older sites may have also burned more recently than the date we considered for this study, though there was no clear evidence of such burnings in the field or in the fire history information.

Each site was a relatively homogeneous stand (approximately 100 × 50 m). We randomly selected 10 points along the stand's main axis. At each point, we began a 15-m planar transect (sensu Brown et al. 1982) in a random direction, along which we counted downed wood pieces in four diameter classes (twigs, <0.6 cm; branches, 0.6–2.5 cm; medium branches, 2.5–7.6 cm; and logs, >7.6 cm; Brown 1974). We collected litter

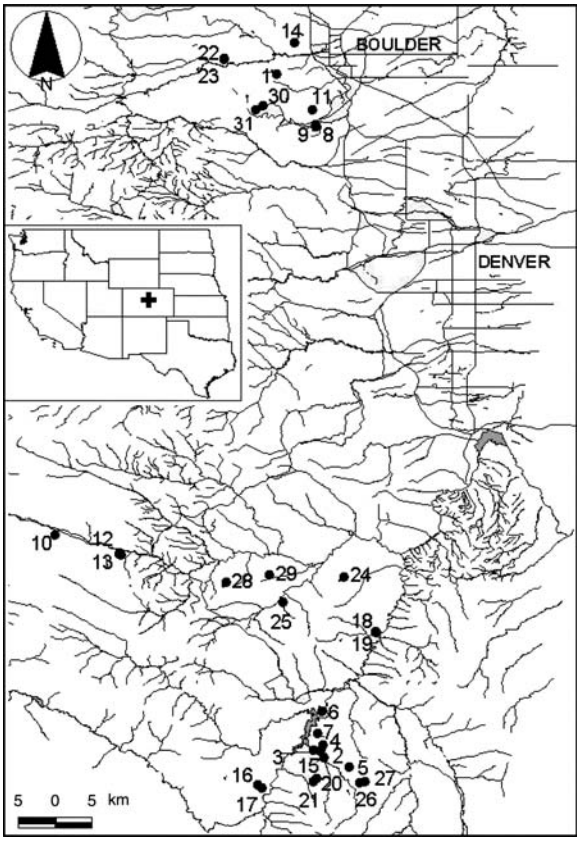

FIG. 1. Sites in the Colorado Front Range, USA, that comprised the 160-year chronosequence of time since fire, and location of the study area within the Western states (inset). Numbers were used to identify each site, with site 1 having the longest time since fire, and site 31 having the shortest time since fire. Note that there are groups of sites that burned in the same year, so site numbers do not directly reflect a chronology.

(obtaining air-dried masses) and measured duff depth in four 0.25-m^2 circular plots along the transect. At each point, we selected four trees, following the point-centered quarter method (Cottam and Curtis 1956). These trees are the closest individuals in each quadrat, defined by the transect and a perpendicular line at the sample point (Cottam and Curtis 1956). We measured their height (with a PM-5/360 clinometer, Suunto, Vantaa, Finland), diameter at breast height (dbh), and the distance from the point to each tree. We estimated canopy cover at each point with 12 densitometer readings taken every 5 m in a 15 × 10 m grid, as well as aspect (compass bearing from north), slope (clinometer reading), geographical coordinates, and elevation (Garmin III+ handheld Global Positioning System, Garmin International, Olathe, Kansas, USA).

For each site, we combined the measurements from all 10 points to estimate dead wood and duff masses using published algorithms (Brown 1974, Brown et al. 1982). We used the 40 point-to-tree distances to estimate tree density, and combined it with the trees' dbh to estimate basal area (Cottam and Curtis 1956). We used published species-specific allometric equations (Brown 1978, Gholz et al. 1979, Edminster et al. 1980, Ter-Mikaelian and Korzukhin 1997) to estimate mean tree total, branch and foliage biomass (for actual equations used, see Table 2 in Hall et al. 2005), and multiplied these by tree density to obtain per hectare values.

We cosine-transformed the mean aspect readings for each site into a relative sun exposure range (0, north-facing; 1, south-facing slopes; McCune and Keon 2002). In addition, we calculated two composite exposure indices from mean slope, aspect, and latitude. The topographic index (TI) is the cosine of the incidence angle of solar radiation at solar noon of the summer solstice (Bonan 2002); the heat load index (HLI) is based on an empirical function (McCune and Keon 2002). Finally, we obtained coarse-scale soils data for each site on the A horizon's permeability (centimeters per hour), organic matter (grams per 100 g of soil) and clay content (percentage), soil profile mean available water content (percentage), and rock depth (centimeters) (STATSGO Data Base; USDA 1994).

Temporal dynamics of detrital pools

To quantify the temporal dynamics of detritus, we developed a model of detrital turnover using linked differential equations that portrayed the dynamics of live aboveground biomass (AB), standing dead biomass (SD) and detritus (Det); all measured in megagrams per hectare (Fig. 2). We modeled net primary productivity (NPP) as a Gompertz function (Winsor 1932), in which the relative growth rate decreases exponentially through time. Mortality, fall, and decomposition were modeled as first-order functions of the source pool (Fig. 2). We refer to this as the compartment model:

$$\frac{d\mathrm{AB}}{dt} = \mathrm{NPP} - \mathrm{mortality} = r_{\max}\mathrm{AB}\left(1 - \frac{c}{r_{\max}}\ln\frac{\mathrm{AB}}{\mathrm{AB}_0}\right) - m\mathrm{AB}$$

$$\frac{d\mathrm{SD}}{dt} = \mathrm{mortality} - \mathrm{fall} = m\mathrm{AB} - f\mathrm{SD}$$

$$\frac{d\mathrm{Det}}{dt} = \mathrm{fall} - \mathrm{decomposition} = f\mathrm{SD} - k\mathrm{Det}.$$

AB_0 is the initial size of the AB pool, t is time (years), $r_{\max}$ is the maximum relative growth rate of the live biomass pool (yr^{-1}); and c is the exponential decay rate of the relative growth rate (yr^{-1}), m, f, and k are the rate constants of the corresponding fluxes (yr^{-1}). We used a nonlinear steepest gradient search (applied with the Solver Add-In in Microsoft Excel) to estimate the parameters that minimized the residual sums of squares, solving the system of differential equations by numerical integration (using a fourth-order Runge-Kutta method applied through Visual Basic for Applications).

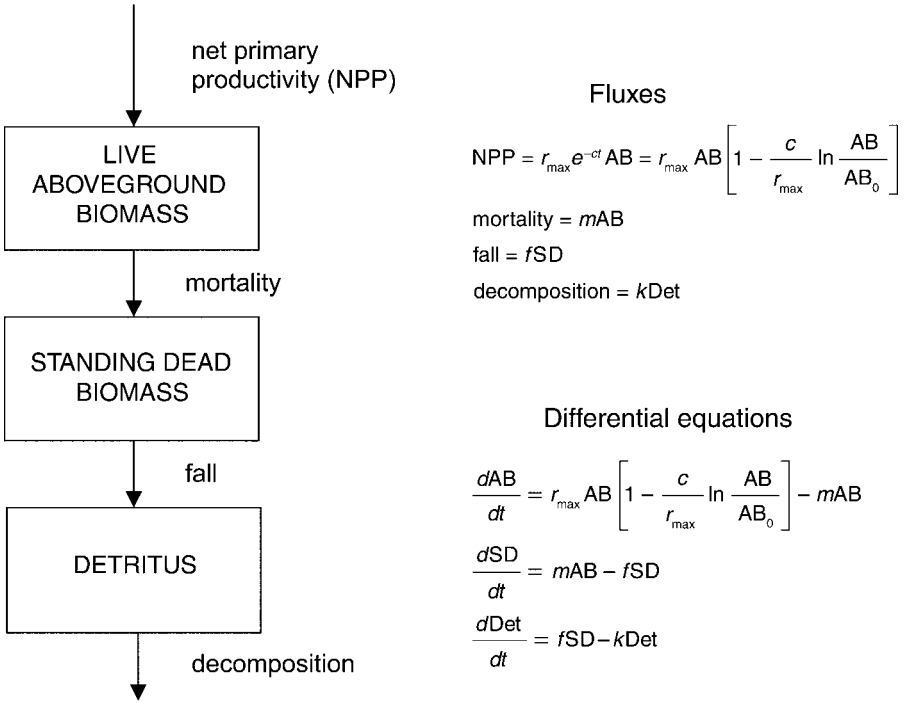

FIG. 2. Diagram and equations of the compartment model describing the temporal dynamics of each detrital pool (Det). Detrital pools (Mg/ha) are litter, twigs (0–0.6 cm diameter), branches (0.6–2.5 cm), medium branches (2.5–7.6 cm), logs (>7.6 cm), and total dead wood. Live aboveground biomass (AB; Mg/ha) and standing dead biomass (SD; Mg/ha) components correspond to the tissue types found in the analogous detrital pool. AB_0 (initial aboveground biomass; Mg/ha), r_{max}, c, m, f, and k (rate constants; yr^{-1}) are parameters that were fit separately for each detrital pool, and t is time (years). A similar compartment model was developed for duff, adding a new pool called DUFF, with a "fragmentation" flux (a first-order function of the source pool) between the DETRITUS pool and the DUFF pool, and the "decomposition" flux as an output from the DUFF pool (not shown in figure for simplicity).

Stand structure and environmental constraints

The underlying assumption of our first objective was that time since fire determines the patterns of variation in detritus in these ponderosa pine forests. To evaluate whether other, nontemporal constraints had equal or greater influence on the variability in detrital pool size, we hypothesized that three types of variables could explain the observed variability in detrital pool size: (1) overstory stand structure, as the source of detrital material; (2) topographic characteristics, through their effect on temperature and moisture, would control net primary productivity and decomposition rates; and (3) soil characteristics, key controls over a site's water balance, and therefore also determining net primary productivity and decomposition rates, and, consequently, detrital pool size.

We had collected data on a number of variables to analyze each of these hypotheses (Fig. 3). We fit statistical models based on each set of independent variables with each of the detrital sub-pools as dependent variables. If more than one variable was included in a particular model, we tested the independent variables for multicollinearity, and eliminated any combination with variance inflation factor >2, or tolerance <0.6. All statistical models were fit using PROC NLIN (SAS Institute 2003). We log-transformed dead medium branches, logs, total dead wood, and litter to fulfill normality and constant variance assumptions.

From each set that responded to each of the three hypotheses posed, we ranked the statistical models we had developed a priori using Akaike's Information Criterion (AIC_c; Burnham and Anderson 2002). We selected all models from each set that explained at least 10% of the variability in the dependent variable, had similar support in the data as the top model (i.e., were within six AIC units of the best model), and had coefficients whose 95% confidence intervals did not overlap zero. We calculated the coefficient of determination (r^2) for each model as the correlation between observed and predicted values, in logarithmic space for those variables we log-transformed. We visually analyzed the plots of residuals for each of the selected models to detect violation of the regression assumptions or the performance of the models we fit.

We compared the best models selected from the stand structure, topography, and soils sets to determine what was the main driver of the variability in each detrital pool (Fig. 3). To this comparison we added a statistical model based on time since fire, which reproduced the trends delineated by the compartment model developed

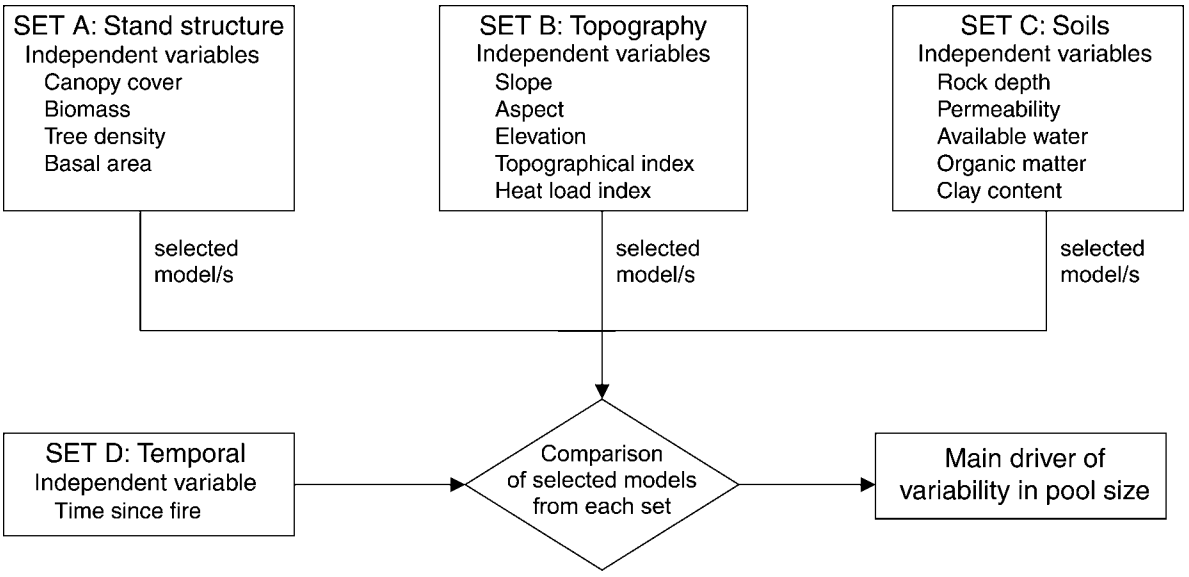

FIG. 3. Flow diagram showing the types of statistical models tested and ranked to determine the main drivers of the variability in pool size. These steps were repeated independently for each detrital pool (litter, duff, twigs [0–0.6 cm diameter], branches [0.6–2.5 cm], medium branches [2.5–7.6 cm], logs [>7.6 cm], and total dead wood). Selected models, and the AIC_c values used to compare them, are shown in Table 2.

to fulfill our first objective. We did not use the compartment model in this comparison for two reasons. First, the methodology used to parameterize the compartment model was different to that used to fit the statistical models, which would obscure the comparison. Second, the compartment model had significantly more parameters that the statistical models, for which it would have been strongly penalized in the calculation of AIC_c (Burnham and Anderson 2002).

RESULTS

Temporal dynamics of the detrital pools

All dead wood classes showed a peak in pool size between 10 and 19 years after fire, which decreased to a minimum (at 61–85 years) before increasing nonlinearly (except for medium branches, which stabilized) (Fig. 4). The compartment model captured the temporal dynamics of the dead wood pools, explaining between 39% and 80% of the variability (Table 1). Litter increased monotonically with time since fire, and our model explained 69% of the variability (Table 1, Fig. 5a). The dynamics of duff were more complex than any of the other pools', which affected model fit: the compartment model explained 35% of the variability in duff. In all cases, modeled live biomass followed a sigmoidal curve, and standing dead decreased monotonically for 10 to 60 years, increasing slowly toward a maximum thereafter (results not shown). The estimated rate constants for detrital fall were similar to those found in the literature (Table 1), while those for mortality and decomposition were, respectively, lower and higher than published values (Table 1).

Stand structure and environmental constraints

Topographic position partially explained the variability in dead wood classes (except branches) and litter (Table 2). Pool size was positively related to variables reflecting exposure (aspect, TI, and HLI), and negatively related to elevation (Table 2). Soils variables explained 10–54% of the variability in total dead wood, medium branches, logs, litter, and duff (Table 2). Dead wood pools were related to rock depth (negatively) and available water content (positively), as well as clay content (negatively) (Table 2). Total dead wood and logs were positively related to organic matter content, and the former was positively related to permeability (Table 2). Litter was positively related to available water content (Table 2). Rock depth and permeability explained 30% of the variability in duff. The direction of these correlations was opposite to those for the dead wood pools (Table 2). Litter was the only detrital pool that was related to stand structure. Linear functions of canopy cover and basal area explained over 70% of the variability (Table 2, Fig. 5b). The canopy cover model seemed to underestimate litter pools in stands with high canopy cover. However, no trend was found in model residuals, since this model was fit in logarithmic space, which shrinks the spread at larger values. Both canopy cover and basal area were strongly correlated with time since fire ($r^2 = 83\%$ and 63%, respectively).

The statistical models describing the temporal dynamics of dead wood pools ranked above (i.e., better represent the patterns in the data) all the topographic and soils models (Table 2). The linear function of canopy cover best described variations in litter (Table 2).

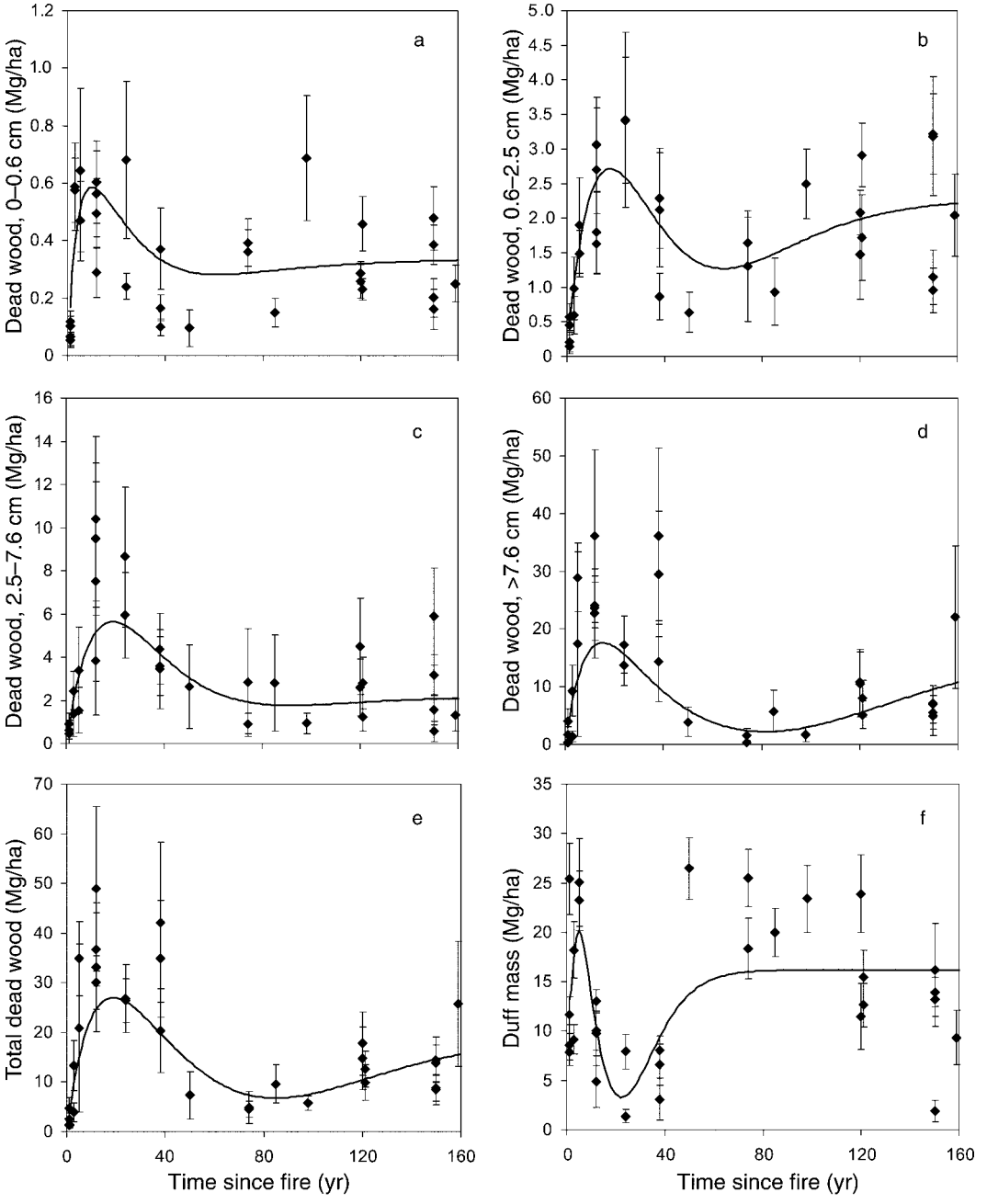

FIG. 4. Temporal dynamics of detrital pools: (a) twigs, (b) branches, (c) medium branches, (d) logs, (e) total dead wood, (f) duff. Solid diamonds represent the data, with bars showing standard errors. Black lines represent trends predicted by the compartment models (Fig. 2, Table 1).

Soil characteristics were the best predictors of duff, as indicated by the selected models (Table 2).

DISCUSSION

Temporal dynamics of the detrital pools

Our results quantify the dynamics described by Harmon et al.'s (1986) conceptual model of dead wood dynamics: low initial amounts, followed by a distinct peak at 10 (twigs) to 19 (total dead wood) years after fire, presumably as the material killed by the fire accumulated on the ground. This peak decomposed more quickly than expected based on results of other studies (Table 1), and the different dead wood pools reached a minimum between 61 and 85 years after fire, except for medium branches, where it leveled off. The time it took pool sizes to reach peak and minimum values were similar to those found in mountain hemlock

TABLE 1. Rate constants and model fit for single exponential terms in the compartment model (yr^{-1}) and in examples from the published literature.

Flux and references	Detrital pool						
	Twigs	Branches	Medium branches	Logs	Total dead wood	Litter	Duff
Rate constants (yr^{-1})							
Mortality, *m*							
This study	0.0014	0.00036	0.010	0.0028	0.0029	0.059	0.079
Harmon et al. (1986), Harrington (1996)	|←———	(0.012–0.073)	———→|		···	···	···
Fall, *f*							
This study	0.026	0.055	0.059	0.066	0.052	0.57	0.21
Harrington (1996), Everett et al. (1999)	···	0.151	|←———	(0.069–0.19)	———→|	NA†	···
Decomposition, *k*							
This study	0.26	0.057	0.047	0.065	0.053	0.041	1.3
Harmon et al. (1986), Hart et al. (1992), Yin (1999)	···	|———	(0.004–0.017)	———→|	···	0.07–0.19	···
Fragmentation‡	···	···	···	···	···	···	0.27
NPP‡							
r_{max}	1.29	0.93	0.75	0.45	0.64	0.38	0.11
c	0.08	0.06	0.06	0.03	0.04	0.06	0.08
Model fit							
r^2	0.39	0.68	0.63	0.62	0.80	0.69	0.35

Note: Abbreviations are: NPP, net primary productivity; r_{max}, maximum relative growth rate; *c*, temporal decay rate of the maximum relative growth rate.

† Published values of litter fall are expressed in $Mg \cdot ha^{-1} \cdot yr^{-1}$, not as a rate constant (our mean values [0.015 $Mg \cdot ha^{-1} \cdot yr^{-1}$] are an order of magnitude lower than published values [0.5 $Mg \cdot ha^{-1} \cdot yr^{-1}$; Vogt et al. 1986]).

‡ All values are from this study.

forests (Boone et al. 1988). Coarse woody debris (>7.6 cm diameter) was still accruing after 159 years, a result that is consistent with studies of old-growth forests in this area (Robertson and Bowser 1999).

The compartment model reproduced these temporal trends, explaining over half the variability in most cases. This model was based on our understanding of the mechanisms that control detrital accumulation, and provided insights into pool turnover times and dynamics. The model can be used as a tool to increase our understanding of detrital dynamics, and can be applied to other systems, or can be expanded to address more complex issues (e.g., modeling all detrital pools simultaneously; or develop a spatially explicit variant). The estimated values of the rate constants (Table 1) can also be used independently of the model itself.

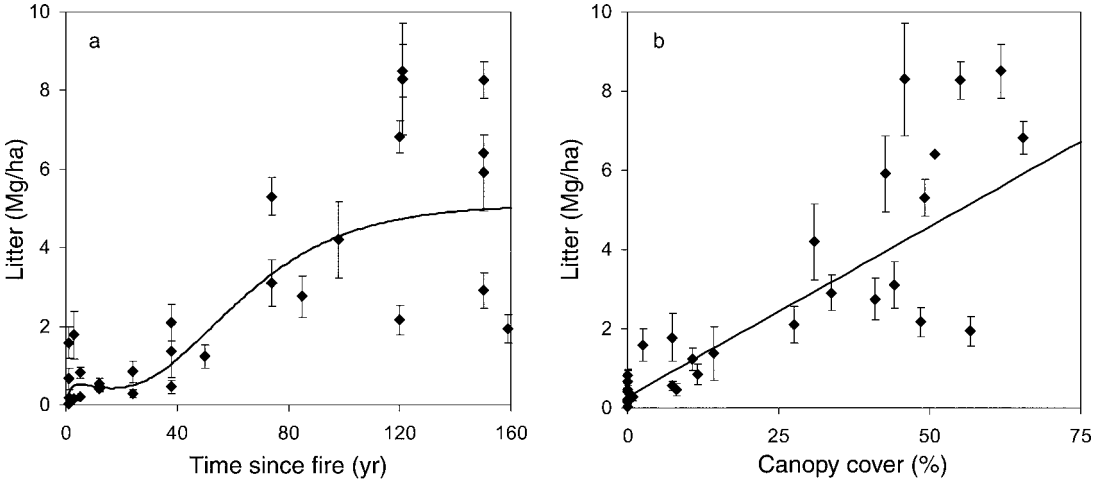

FIG. 5. Dynamics of litter accumulation: (a) temporal dynamics of the litter pool and (b) litter as a linear function of canopy cover. Solid diamonds represent the data, with bars showing the standard errors. Black lines represent values predicted by the (a) compartment or (b) statistical models. Models were fit in logarithmic space to satisfy regression assumptions.

TABLE 2. Selected statistical models from each set (structure, topography, soils, temporal), predicting each detrital pool.

Detrital pool and variable set	Model †	AIC_c	r^2	SE‡
Dead twigs				
Temporal§	$DP = \left(\frac{TSF}{\lambda}\right)^{\alpha-1}\frac{e^{-TSF/\lambda}}{\lambda} + bTSF^c$	−104.2	0.39	0.16
	$\alpha = 3.84$ (0.21), $\lambda = 2.29$ (0.26), $b = 0.14$ (0.068), $c = 0.17$ (0.11)			
Topographic	DP = 0.56 (0.15) − 0.01 (0.006) SLOPE + 0.01 (0.11) ASPECT	−96.8	0.15	0.19
Dead branches				
Temporal§	$DP = \left(\frac{TSF}{\lambda}\right)^{\alpha-1}\frac{e^{-TSF/\lambda}}{\lambda} + bTSF^c$	−15.4	0.56	0.68
	$\alpha = 5.48$ (0.14), $\lambda = 4.23$ (0.36), $b = 0.47$ (0.22), $c = 0.29$ (0.10)			
Dead medium branches‖				
Temporal§	$DP = \left(\frac{TSF}{\lambda}\right)^{\alpha-1}\frac{e^{-TSF/\lambda}}{\lambda} + bTSF^c$	−25.7	0.60	0.57
	$\alpha = 6.24$ (0.16), $\lambda = 3.51$ (0.32), $b = 0.92$ (0.25), $c = 0.17$ (0.067)			
Topographic	DP = 4.36 (4.12) + 8.67 (4.15) TOPOGRAPHY − 0.004 (0.002) ELEVATION	−7.2	0.18	0.80
Soils	DP = 3.82 (0.86) − 0.095 (0.044) CLAY	−7.1	0.10	0.82
Soils	DP = −0.41 (1.23) − 0.015 (0.007) DEPTH + 0.51 (0.18) WATER	−6.4	0.16	0.81
Logs‖				
Temporal¶	$DP = \left\{\frac{h}{\pi}\left[h^2 + (TSF - a)^2\right]\right\}m + b_0 + b_1TSF$	−2.3	0.65	0.81
	$a = 22.07$ (1.63), $h = 17.24$ (6.78), $s = 2802$ (905), $b_0 = -19.42$ (7.99), $b_1 = 0.205$ (0.068)			
Topographic	DP = 38.29 (16.0) + 25.91 (11.19) TOPOGRAPHY − 0.023 (0.007) ELEVATION	16.5	0.19	1.18
Soils	DP = −2.45 (0.98) − 0.097 (0.019) DEPTH + 2.26 (0.41) WATER	−0.5	0.54	0.89
Soils	DP = 16.24 (3.22) − 0.56 (0.12) CLAY	3.4	0.42	0.98
Soils	DP = −0.68 (0.55) + 5.90 (1.26) ORGANIC	3.8	0.42	0.98
Total dead wood				
Temporal¶	$DP = \left\{\frac{h}{\pi}\left[h^2 + (TSF - a)^2\right]\right\}m + b_0 + b_1TSF$	−26.1	0.72	0.56
	$a = 22.87$ (1.52), $h = 17.22$ (5.84), $s = 3776$ (1158), $b_0 = -24.44$ (10.34), $b_1 = 0.29$ (0.083)			
Soils	DP = −4.86 (3.38) − 0.11 (0.031) DEPTH + 3.17 (0.66) WATER	−3.1	0.29	0.86
Soils	DP = 21.30 (4.49) − 0.63 (0.20) CLAY	−1.7	0.19	0.90
Soils	DP = 5.64 (2.32) + 0.38 (0.16) PERMEABILITY	−1.0	0.17	0.91
Soils	DP = 2.95 (2.34) + 5.94 (2.00) ORGANIC	0.3	0.13	0.93
Litter‖				
Temporal#	$DP = \frac{DP_{ss}}{1 + fe^{-aTSF}}$	−6.8	0.68	0.81
	$DP_{SS} = 5.41$ (1.85), $f = 16.79$ (6.63), $a = 0.040$ (0.013)			
Temporal	DP = 0.25 (0.09) + 0.03 (0.007) TSF	−6.6	0.65	0.83
Structure	DP = 0.28 (0.061) + 0.086 (0.015) COVER	−19.2	0.77	0.68
Structure	DP = 0.39 (0.078) + 0.19 (0.040) BA	−13.3	0.72	0.75
Topographic	DP = 4.03 (2.41) + 5.20 (1.77) HEAT LOAD − 0.003 (0.001) ELEVATION	20.8	0.22	1.26
Topographic	DP = 2.91 (2.90) + 7.39 (2.62) TOPOGRAPHY − 0.004 (0.001) ELEVATION	23.1	0.16	1.31
Soils	DP = −1.98 (0.44) + 0.45 (0.097) WATER	13.6	0.33	1.15
Duff				
Soils	DP = 19.73 (2.04) − 0.31 (0.086) PERMEABILITY	119.6	30	6.37
Soils	DP = 8.03 (1.99) − 0.094 (0.027) DEPTH	119.8	30	6.39

Notes: The models are ranked by AIC_c, the best model having the lowest value (Burnham and Anderson 2002). Abbreviations are: DP, detrital pool; BA, basal area; CLAY, clay content; COVER, canopy cover; DEPTH, rock depth; ELEVATION, meters above sea level; TOPOGRAPHY and HEAT LOAD, composite topographic indices; ORGANIC, organic matter content; PERMEABILITY, hydraulic conductivity of the A horizon; TSF, time since fire; WATER, available water content; α, λ, a, b, b_0, b_1, c, h, and s are statistical parameters.

† Models and parameters (with standard errors in parentheses).

‡ Standard error of estimates. Values are in Mg/ha for non-transformed variables, and in natural log space for log-transformed variables.

§ Combination of a Gamma distribution (parameters α, λ) and a power function (base b and exponent c).

‖ Log-transformed variables (medium branches, logs, total dead wood, litter).

¶ Combination of a Cauchy distribution (parameters a, h, scaling factor s) and a linear function (slope b_1 and intercept b_0).

Logistic function with maximum DP_{SS}, exponential rate a, and multiplier f.

PLATE 1. A stand that burned in 1963. Large surviving trees remain among patches of small, dense saplings (site 15). Photo credit: S. Hall.

We found that a single exponential function within the compartment model was sufficient to describe the fall and decomposition of dead wood in this system, in contrast to Everett et al. (1999) and Bond-Lamberty et al.'s (2002) conclusion that multiple exponential models are needed to describe the dynamics of dead wood. This is particularly important in view of the range of time since fire that we analyzed, covering a period during which stand structure has changed. The disturbance regime in these forests may well be altered by fire suppression; however, our results suggest that this alteration has not (yet) affected decomposition, fall, and mortality rates significantly, given that assuming that these parameters are temporally invariant allowed us to successfully model the dynamics of coarse and fine dead wood pools.

Time since fire was a better predictor of large-diameter dead wood dynamics than it was for smaller diameter classes. Finer material turns over faster than coarse wood, which can stay on the ground for over a century (McFee and Stone 1966), and twigs are therefore more responsive to interannual variations in inputs than logs. Though large wood may be spatially more variable (e.g., Manies et al. 2005), fine wood varies more through time. Finally, time since fire explained a greater proportion of the variability in total dead wood dynamics than those of any of the diameter classes, even though we expected the accumulation and decomposition rates of the different size classes to be significantly different. The values of the rate constants of the compartment model indicated that, with the possible exception of twigs, the dynamics of woody debris were relatively independent of diameter, as seen in other studies (Bond-Lamberty et al. 2002, Manies et al. 2005, but see Harmon et al. 1986).

Litter did not show an initial peak of residual material because all the young sites we sampled were in high-severity burns, where the foliage was consumed in the fire, leaving little material to then accumulate on the ground. The litter pool stabilized after ~120 years, as seen in other temperate coniferous forests (Boone et al. 1988). Variability in litter pool size was greater in older stands (Fig. 5). This is likely related to spatial variation in environmental conditions, as well as variation in fire severity or pre-fire stand structure, which reflect historical legacies of past conditions on ecosystem structure (Veblen 2003). Litter accumulation was strongly related to canopy cover dynamics, showing how stand development (which is a temporal phenomenon) likely controlled the size of this detrital pool. This suggests that litter fall was more important (or more variable across the age sequence) than decomposition in controlling these dynamics. The relation to canopy cover was stronger than to time since fire, suggesting that there was time-independent variability in canopy cover that affected litter pool size.

Temporal trends of duff were complex and hard to capture. Possibly, our point measures of duff, which is spatially very heterogeneous, were not as accurate or representative of area-based values as measurements of the other detrital pools. These trends, however, seemed to mirror those of dead wood: as one increased, the other decreased (Fig. 4). Outputs from the dead wood pools (fragmentation and partial decomposition) provide inputs into the duff pool, which could explain these mirrored dynamics.

Stand structure and environmental constraints

Detrital pool sizes were more strongly related to time since disturbance than to environmental factors. Similar conclusions were reached in studies in fire-prone subboreal spruce forests (Clark et al. 1998) and secondary growth ponderosa pine–Douglas-fir forests (MacKenzie et al. 2004), but environmental variables better explained fuel loads in mixed conifer forests with varying species composition (Sánchez-Flores and Yool 2004). This difference could be because the soils data available to us were at a very coarse scale (USDA 1994), or because our study focused on ponderosa pine forests, limiting the range of topographic conditions studied.

The direction of the relationships observed between detrital pool sizes (except duff) and topography consistently indicated that sites that were more exposed to radiation had greater debris loads. We would expect more exposed, warmer sites to have less detritus if temperature were controlling decomposition, or moisture was controlling inputs by enhancing net primary productivity. Our results suggest that topographic controls were expressed through the effect of moisture on decomposition, as has been found in other dry forests (Klopatek et al. 1998). Dead wood pools were generally greater where the soil A horizon characteristics indicated that soils were less able to retain moisture: more permeable soils and soils with lower clay content. This supports the hypothesis that surface moisture limited dead wood decomposition. However, mean available soil water content, a variable that integrates the whole soil profile, was positively related to dead wood amounts. Deeper water sources unavailable for surface detrital decomposition can stimulate tree productivity, particularly given ponderosa pine's deep roots (Oliver and Ryker 1990). As happened with the temporal trends of duff, the response of this detrital pool to environmental variables mirrored the response of the dead wood pools: variables that were positively correlated with dead wood were negatively correlated with duff, and vice versa.

Ecological insights and management implications

In the ponderosa pine forests of the Colorado Front Range, dead wood accumulated on the ground following predictable temporal patterns. Variations in stand structure or environmental conditions did not appear to constrain these dynamics. This is key to linking such long-term studies to what occurs on the ground: quantifying fire hazard and prioritizing treatment areas should not ignore variations in fire history, given that fuel loads were more strongly related to time since fire than to environmental or structural characteristics. The temporal signal was strong enough to overcome the main disadvantage of the chronosequence approach: confounded spatial and temporal sources of variability. Furthermore, as we selected this chronosequence to reflect variations in time since fire, our results support the hypothesis that it is lack of fire, rather than other changes that occurred after Euro-American settlement (grazing, logging, or climatic variability; Covington and Moore 1994, Veblen et al. 2000) that is driving the observed dynamics. The portion of the variability in pool sizes that was unexplained could be related to a variety of temporal and nontemporal factors that we were unable to examine in this study. Examples of these are medium-term climatic oscillations, logging, mountain pine beetle outbreaks (such as occurred in the 1970s; M. R. Kaufmann, *personal communication*), and mistletoe infestation.

The time between maximum and minimum dead wood pools sizes varied between 46 and 67 years, depending on the diameter class. Overlapping the historical fire return intervals (1 to >100 years; Brown et al. 1999, Veblen et al. 2000) with the time frames of maximum variation in dead wood suggests that fires may have burned under a large range of fuel conditions, presumably even where the fire regime has not been altered, supporting the characterization of the fire regime of these forests as mixed severity (Brown et al. 1999, Veblen et al. 2000). A necessary caveat is that this study was not designed to address whether the range of historical fire return intervals was due to variations in how long it takes fuels to accumulate to a minimum fire-bearing threshold, or to other factors such as weather (see Veblen et al. 2000). The range of detrital pool sizes we observed affected fire behavior at some of our sites when they burned during the Hayman fire (2002; Hall and Burke 2006). The magnitude and timing of variations in detritus provide a quantitative baseline against which future long-term studies in dry forests may be compared, to determine whether climate change is affecting these pools, either directly or through changes in the disturbance regime.

Litter pool size was strongly related to canopy cover, highlighting the importance of litter fall, rather than decomposition, as controls over pool size. Cover in relatively sparse forests, such as these ponderosa pine systems (Peet 2000), can be estimated from remotely sensed data (Spanner et al. 1994). Spatially heterogeneous litter pools could then be modeled using remotely sensed canopy cover values. These data could be used to estimate carbon sequestered in litter, or as inputs to fire behavior models. Similar relationships between litter and canopy cover could be developed in other dry, fire-prone forests, where the need to obtain spatially explicit estimates of litter distribution is critical. The duff pool was the hardest to model, and there is need for greater understanding of the processes and variables that control its dynamics, as duff can comprise a large pool of carbon, which may be affected by fire or climate change.

We were able to satisfactorily model the dynamics of woody debris and litter using a single, process-based compartment model. This model, and the plausible turnover rate constants we estimated, can be used to make projections of detritus, aboveground biomass, and standing dead biomass accumulation. There is a wealth of research and management applications that would benefit from these estimates, particularly given that they are provided through a single, quantitative framework. These model estimates would quantify carbon sequestration in ponderosa pine forests. The spatial distribution of these pools on a landscape can have important implications for fire behavior and fuel reduction strategies, as well as ecological implications for our understanding of the role of disturbance in controlling ecosystem structure. Model predictions of snag (standing dead) dynamics may be useful for addressing wildlife habitat concerns, and for determining the effect salvage

logging practices could have on downed fuels. The compartment model is intuitive and easy to implement, which makes it ideal for providing insights into the biomass, snag, and detritus dynamics in similar forests around the world.

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