

Changes in litter and dead wood loads following tree death beneath subalpine conifer species in northern Colorado

Christof Bigler and Thomas T. Veblen

Abstract: Litter and dead wood affect important processes in forest ecosystems such as nutrient and carbon cycling and are key influences on biodiversity and fire behavior. Increased tree mortality rates in western North America associated with climate trends and increased bark beetle activity highlight the need to better understand the dynamics of litter and dead wood following tree death. For eight old-growth stands in a subalpine forest landscape in northern Colorado (USA), we compared litter and dead wood loads beneath more than 200 dead and live Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), and lodgepole pine (*Pinus contorta* Douglas ex Loudon). The dynamics of litter and dead wood were analyzed using chronosequences of tree death dates over >100 years that we determined from tree rings. Immediately following tree death, high loads of litter accumulated, particularly for the biggest spruces, which accumulated 10 times more litter than live spruces (five times more for fir, two times more for pine). We estimated a higher decay rate of litter for spruce (half-life of four years) than for pine (15 years) and fir (19 years). The accumulation rates for dead wood following tree death were highly variable among trees, but maximum accumulation was attained during the first 50–60 years.

Résumé : La litière et le bois mort ont des effets sur d'importants processus dans les écosystèmes forestiers tels que le recyclage des nutriments et du carbone et ils ont une influence déterminante sur la biodiversité et le comportement du feu. L'augmentation du taux de mortalité des arbres dans l'ouest de l'Amérique du Nord, associée aux tendances climatiques et à l'augmentation de l'activité des scolytes, fait ressortir le besoin de mieux comprendre la dynamique de la litière et du bois mort après la mort des arbres. Nous avons comparé la charge de litière et de bois mort sous plus de 200 tiges, mortes et vivantes, d'épicéa d'Engelmann (*Picea engelmannii* Parry ex Engelm.), de sapin subalpin (*Abies lasiocarpa* (Hook.) Nutt.) et de pin tordu (*Pinus contorta* Douglas ex Loudon) dans huit vieux peuplements faisant partie d'un paysage de forêt subalpine du nord du Colorado, aux États-Unis. La dynamique de la litière et du bois mort a été analysée à partir de chronoséquences établies sur plus de 100 ans en utilisant la date de la mort des arbres déterminée grâce aux cernes annuels. Immédiatement après la mort des arbres, des charges importantes de litière se sont accumulées, particulièrement sous les plus gros épicéas qui accumulaient 10 fois plus de litière que les épicéas vivants (cinq fois dans le cas du sapin et deux fois plus dans le cas du pin). Nous avons estimé que le taux de décomposition de la litière était plus élevé sous les épicéas (demi-vie de quatre ans) que sous les pins (15 ans) et les sapins (19 ans). Le taux d'accumulation du bois mort après la mort des arbres variait énormément d'un arbre à l'autre mais l'accumulation maximum était atteinte durant les 50–60 premières années.

[Traduit par la Rédaction]

Introduction

Increased rates of noncatastrophic tree mortality (i.e., background mortality), as well as catastrophic tree mortality (i.e., disturbance-induced mortality) related to regional warming appear to be occurring in western North America and have important implications in terms of potential carbon releases into the atmosphere (Kurz et al. 2008; Running 2008). Longitudinal data from unmanaged old-growth forests in western North America show that background mortality rates have increased rapidly during the last decades of the 20th century (van Mantgem et al. 2009). This upward

trend in mortality rates has been documented for numerous conifer species in the Pacific Northwest, California, and the Interior West and is correlated with increasing water stress (van Mantgem et al. 2009). Elevated temperatures and (or) water stress also have been implicated in recent episodes of disturbance-induced tree mortality (i.e., pulses of mortality) in forests from Alaska to the Pacific Southwest (Bigler et al. 2007; Breshears et al. 2005; Raffa et al. 2008). There is a broad consensus that elevated tree mortality rates due to increased bark beetle activity in millions of hectares of forests across western North America are largely attributable to broad-scale warming and are likely to continue with pro-

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jected future warming (Bentz et al. 2009; Hicke et al. 2006; Romme et al. 2006).

Increased tree mortality rates have implications for forest structures and composition, as well as for the accumulation of litter and dead wood. Litter and dead wood contribute to important ecosystem processes such as nutrient and carbon cycling, soil respiration and acidification, and soil formation or stabilization (Herrmann and Prescott 2008; Kimmins 2004; Prescott 2005a). Downed leaves, needles, and woody material may facilitate or inhibit tree regeneration by storing water and nutrients, providing substrate for regeneration, or producing allelochemicals (Franklin et al. 1987). Litter and dead wood may enhance biodiversity by providing habitat, including shelter and food for vertebrates, invertebrates, plants, and fungi (Kimmins 2004; McComb and Lindenmayer 1999). High loads of litter and dead wood are considered an increased fire hazard in fire-prone forest ecosystems.

Litter and dead wood accumulate on the ground during various stages of tree growth and stand development (Baker 2003; Brown and See 1981; Kessell et al. 1978). Live trees recurrently shed leaves and needles because of limited life spans of these tissues. Pruning and breaking of twigs or branches and flaking of bark are caused by growth processes, impact of wind, precipitation, snow, and falling trees. High amounts of twigs and branches may accumulate on the ground, even in the absence of a discrete episode of catastrophic tree mortality. These accumulated loads of surface litter and dead wood decompose at different rates, depending on size and structural and chemical composition, as well as climatic conditions (McComb and Lindenmayer 1999). Decomposition is accomplished by invertebrates, which break down litter and dead wood into smaller pieces, which are further processed by soil microorganisms (Kimmins 2004). In old-growth stands or stands with closed canopies, accumulation of litter and dead wood may remain quite constant because of similar deposition and decomposition rates (Baker 2003; Brown and See 1981). However, litter and dead wood loads are expected to increase locally or regionally following background or disturbance-induced tree mortality affecting single trees, forest stands, or entire landscapes (Jorgensen and Jenkins 2010; Page and Jenkins 2007).

The objective of this study was to quantify changes in litter and dead wood loads following background mortality for three conifer species (Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), and lodgepole pine (*Pinus contorta* Douglas ex Loudon)) in a subalpine forest landscape in northern Colorado. We compared litter mass and different diameter classes of dead wood between individual dead and live trees and among tree species. The dynamics of litter and dead wood following tree death were investigated using chronosequences of tree death dates, which we determined from tree rings.

In this research, we addressed the following two questions. (i) Do surface loads of litter and dead wood differ between dead and live trees or among tree species? (ii) How do surface loads of litter and dead wood change over time following tree death? We expected to observe more litter and dead wood beneath dead than live trees and also higher loads beneath tree species dead and trees with larger crowns and

more foliage. Because needle fall is highest shortly before and after tree death, we assumed that pulses of increased litter loads were followed by decreasing litter loads due to decomposition.

Materials and methods

Study area and tree species

We selected a study area in Roosevelt National Forest in the Colorado Rocky Mountains (USA), which encloses the Trap Park and Corral Park valleys (Table 1). The study area extends over 5.6 km × 4 km, and elevations range from 3080 to 3400 m. As a result of past stand-replacing fires, the forest landscape consists of a spatial mosaic of stands that vary in species composition, structure, and stand age. The characteristic tree species are Engelmann spruce, subalpine fir, lodgepole pine, and quaking aspen (*Populus tremuloides* Michx.). The sampled stands are unmanaged and dominated by conifers that established following fires ca. 230 to >700 years ago (Table 1). A continental climate prevails in the study area, with estimated mean temperatures ranging from -10.1 °C in January to 10.8 °C in July, and annual precipitation amounting to 697 mm (based on climate interpolations from 1910–2004; Bigler et al. 2007).

The sampled tree species included Engelmann spruce, subalpine fir, and lodgepole pine. Both Engelmann spruce and subalpine fir are shade-tolerant tree species dominating old-growth stands in the central Rocky Mountains (Veblen 1986). These two species co-exist, with subalpine fir being more abundant in the understory and the longer-lived Engelmann spruce being more abundant in the canopy (Peet 2000). Subalpine fir has a long, narrow crown with high needle density and reaches heights of up to 14–30 m in old-growth stands. Engelmann spruce has a relatively narrow, conical crown and attains heights of up to 24–40 m. Lodgepole pine is a light-demanding species that often establishes even-aged stands following stand-replacing fires (Peet 2000). The trees have relatively narrow crowns and reach heights of 18–25 m.

Field sampling

The field sampling was conducted in 2004 (Bigler et al. 2007). Eight sample sites were selected in stands dominated by Engelmann spruce, subalpine fir, or lodgepole pine (Table 1). In each of the two valleys, we selected four sites with two sites at each elevation (lower or upper) on both slopes of the valley (left or right). At each site, all standing dead trees ≥20 cm DBH (diameter at breast height) were sampled in transects of 10–50 m width and variable length. Only dead trees were selected that had not been killed by blowdown, insect outbreaks, avalanches, fire, or mechanical damage such as rockfall. Thus, the dead trees represent background mortality rather than catastrophic mortality. For each dead tree, we matched a live tree of the same species and of similar DBH. Matching increases the efficiency of tests with paired samples, if the matching variables (here tree species and size) are assumed to be associated with the response variables (here loads of litter and dead wood) (Breslow and Day 1989).

We removed two increment cores at breast height (ca. 1.30 m) from opposite sides of the stem from each dead

Table 1. Description of sample sites and number of sampled trees per species and tree status (live or dead).

Site	Coordinates (easting/northing)	Elevation (m)	Aspect (°)	Slope (°)	DBH (cm)	Stand initiation (year)	Number of sampled trees				Total
							Subalpine fir (live/dead)	Lodgepole pine (live/dead)	Engelmann spruce (live/dead)		
Corral Creek, L, A	434588/4485840	3111	164	13	29.1	1584	1/1	7/7	3/3		22
Corral Creek, L, B	433785/4486799	3250	149	17	34.7	1731	0/0	8/8	6/6		28
Corral Creek, R, A	433552/4485498	3082	352	16	36.8	1505	1/1	2/3	12/11		30
Corral Creek, R, B	432435/4485332	3225	6	10	34.5	1288	7/7	0/0	7/7		28
Trap Creek, L, A	429740/4488366	3180	71	10	29.6	1700	8/7	0/1	3/4		23
Trap Creek, L, B	429628/4488649	3220	100	23	32.6	1771	5/5	0/1	5/4		20
Trap Creek, R, A	430115/4488128	3198	300	13	29.6	1516	9/9	0/0	4/4		26
Trap Creek, R, B	429935/4487247	3265	276	7	29.8	1710	12/13	0/0	0/0		25
Total							43/43	17/20	40/39		202

Note: Subalpine fir, *Abies lasiocarpa*; lodgepole pine, *Pinus contorta*; Engelmann spruce, *Picea engelmannii*. Site is the name of the sample site followed by L or R (orographic left side or right side of the valley) followed by A or B (A for lower site, B for upper site). The values for coordinates (measured in Universal Transverse Mercator coordinates), elevation, aspect, slope, and DBH (diameter at breast height) are mean values calculated from dead and live trees. The values differ slightly from those reported in Bigler et al. (2007), because different tree samples were considered. Stand initiation is the approximate year of stand initiation based on the earliest establishment date of dead and live trees measured at breast height.

and live tree and measured different tree-specific variables (elevation, aspect, slope steepness, coordinates, DBH). Eroded or decaying stem sections were avoided when taking increment cores, which was particularly important for the sampling of dead trees.

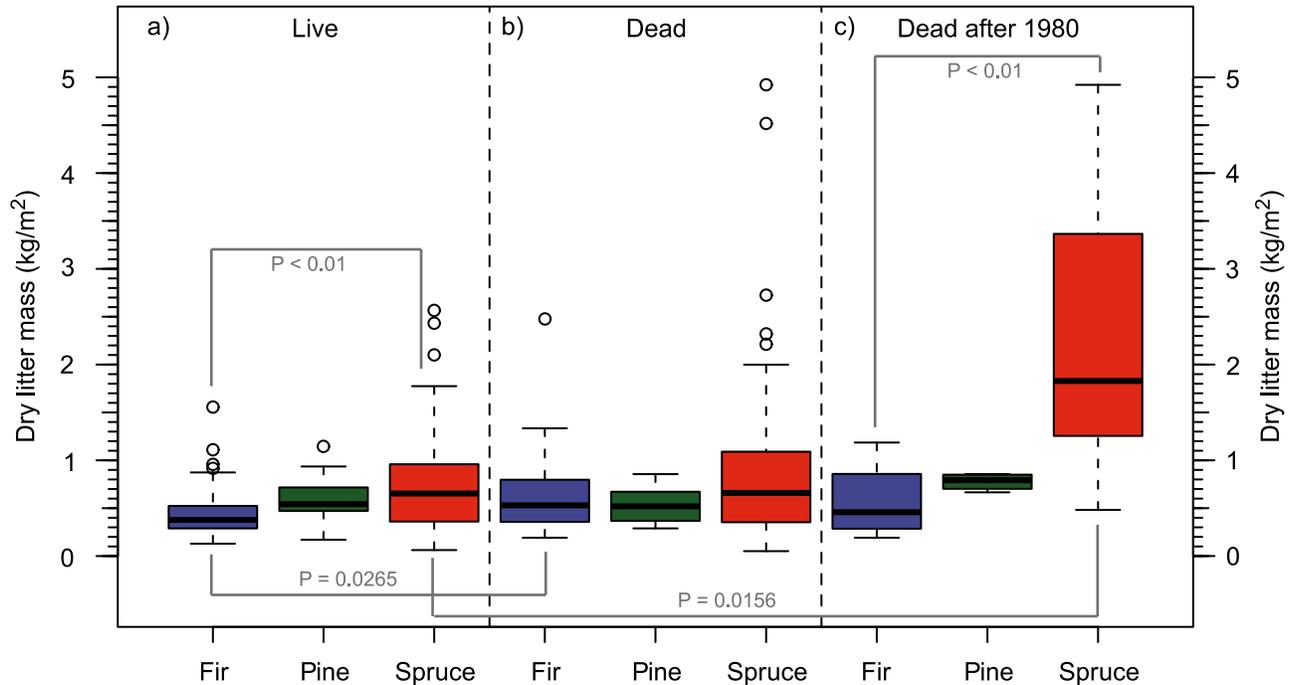
From each dead and live tree, we collected litter and counted the number of pieces of dead wood in different size classes (Brown et al. 1982). Litter was sampled within a 0.3 m × 0.3 m plot with the plot center 0.5 m south of the tree trunk. We collected only fallen litter such as needles, bark flakes, seeds from trees, or cones and cone scales (i.e., duff, herbs, moss, lichens, and shrubs were not included in the samples). The litter samples were stored in paper bags. We sampled dead wood using a planar intersect oriented in a southerly direction; numbers of intersections of pieces of dead wood with the vertical sampling plane were counted. The sampling plane reached from the stem to the outer part of the crown projection. For dead trees, we estimated the crown projection based on remaining twigs and branches and (or) stem diameter. The length of the sampling planes was 1.22 ± 0.34 m (mean ± standard deviation for dead and live trees) and correlated with DBH of the trees (Spearman rank correlation, $\rho = 0.33$, $P < 1.3 \times 10^{-6}$). Counts for dead wood (including fallen twigs, branches, stems, and tree boles in and above the litter) were made for different diameter classes: <0.6 cm, 0.6–<2.6 cm, 2.6–<7.6 cm, ≥7.6 cm. We calculated dead wood densities for each diameter class as number of pieces of dead wood per metre and converted the densities to oven-dried mass per square metre (Brown et al. 1982). Conversion for diameter class ≥7.6 cm requires measurements of diameters according to stage of decay (sound or rotten) of the single pieces of dead wood, which we did not measure in the field. Instead, we assumed mean diameters of 10 cm and moderately rotten dead wood. For the estimation of both litter mass and dead wood densities, we applied no slope correction, because slope steepness was only measured in the direction of the steepest slope (which is not necessarily the direction used for litter and dead wood sampling). Based on these values, litter and dead wood loads were underestimated by a maximum of <0.1% to 15.5% per tree (Brown et al. 1982).

Lab procedures

The litter samples were dried at room temperature for a few days and then oven-dried at 70 °C for 96 h. We measured the dry mass with a precision of 0.1 g and converted the resulting values to kilograms per square metre.

We applied standard procedures used in dendrochronology to process the increment cores (Stokes and Smiley 1996). Tree-ring widths were measured with a precision of 0.01 mm, and we performed visual and quantitative cross-dating of the tree rings (Grissino-Mayer 2001). Cross-dating compares and matches growth patterns among trees, which guarantees that each tree ring is assigned to the correct calendar year. We first developed tree-ring chronologies from live trees, which were subsequently used to cross-date the tree rings of the dead trees (for details, see Bigler et al. 2007). If, for the dead trees, the last tree ring in the two cores showed different dates, we assumed the year of tree death to be the more recent year. We further noted whether cores showed evidence of eroded tree rings at the outermost

Fig. 1. Comparison of dry litter mass for subalpine fir (*Abies lasiocarpa*), lodgepole pine (*Pinus contorta*), and Engelmann spruce (*Picea engelmannii*): (a) live trees, (b) dead trees (regardless of death date), and (c) dead trees that died after 1980. The boxes of the boxplots include the first, second, and third quartiles; values beyond the whiskers are shown as circles. Groups differing significantly ($P < 0.1$) are based on a multiple comparison test after Kruskal–Wallis (P values indicate significance levels); braces pointing downward (in the upper part of the plot area) are based on a paired Wilcoxon’s signed rank test (exact P values are shown). Sample sizes in (a) and (b): see Table 1; sample sizes in (c): fir, $n = 14$; pine, $n = 4$; spruce, $n = 7$.



ring. To estimate the date of stand initiation (Table 1), we determined for each site the earliest year of the innermost tree rings. For those cores that missed the pith, we used a geometric method to estimate the number of missing rings between pith and first complete tree ring (Duncan 1989). No correction was applied for the number of years between ground level and coring height.

Analysis

The study included litter and dead wood samples collected beneath 102 dead and 100 live trees (Table 1). We compared litter mass between live and dead trees regardless of death dates, as well as between live and dead trees that died after 1980 (i.e., within the last 25 years), within each species using a nonparametric two-sample test. A paired Wilcoxon’s signed rank test of the differences in medians between tree pairs was performed (Zar 1999). The motivation behind selecting trees that died after 1980 was to detect pulses of litterfall of relatively recent tree death. Similar results were obtained when the 1980 threshold date was varied by ± 5 years. The analysis of dead trees that died after 1980 included only dead trees without eroded tree rings so that cross-dated dates of the outermost ring were reliable estimates of the actual year of death. We compared dead wood densities between live and dead trees within each species and within each class of dead wood using the same two-sample test. Because of the lack of an obvious temporal trend in dead wood densities, no separate tests were performed for dead trees that died after a specific date. For the

analysis of both litter and dead wood, we included only matched pairs of live and dead trees that were of similar size and the same species.

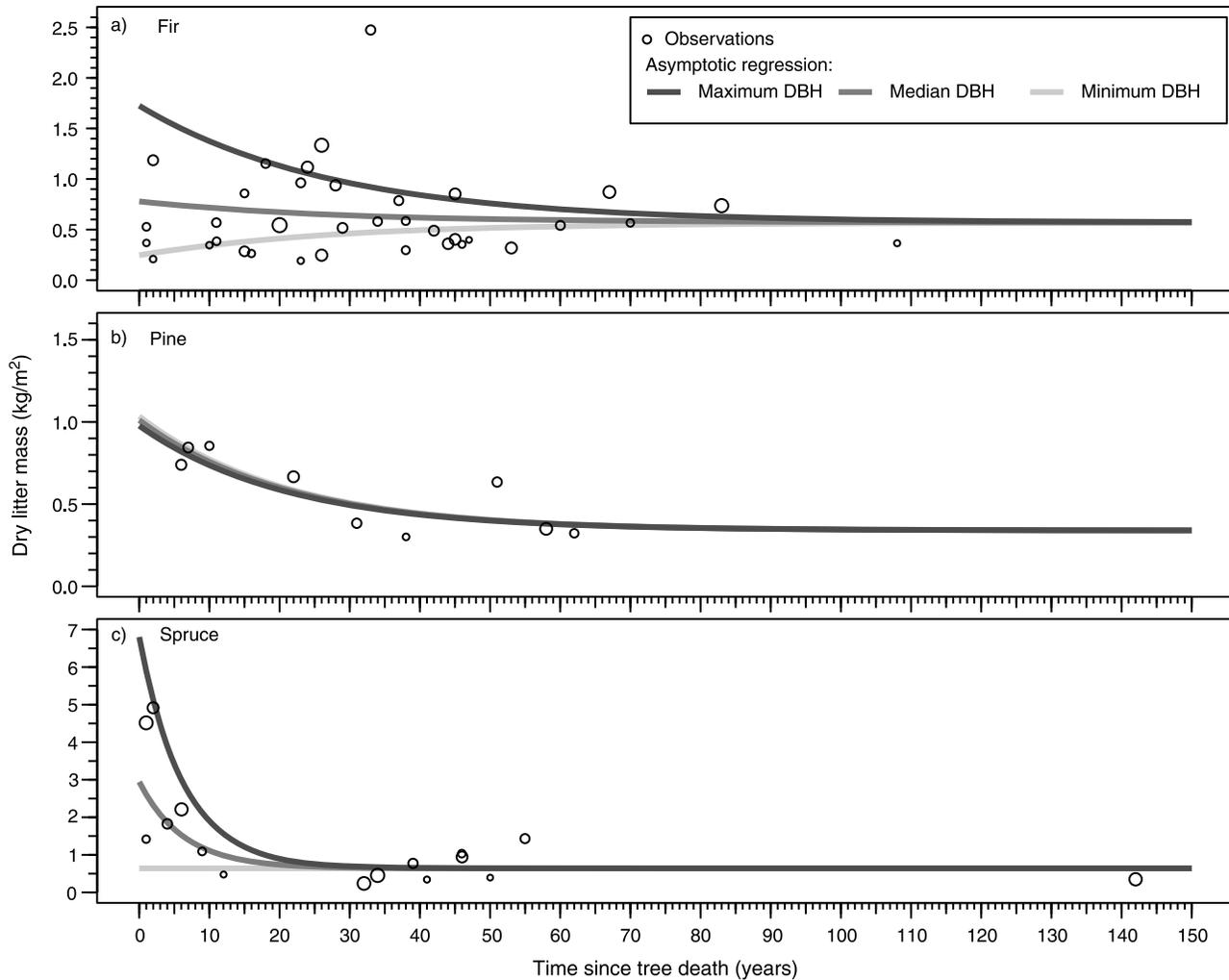
We compared litter mass and dead wood densities among tree species within live trees, within dead trees, and within dead trees that died after 1980 (for litter only) using a nonparametric multisample test. A Kruskal–Wallis rank sum test was initially performed to test for difference in medians among species, followed by a multiple comparison test after Kruskal–Wallis for pairwise tests of difference in medians between species (Zar 1999).

We examined changes in litter mass following tree death using a nonlinear function that was applied only to cross-dated dead trees lacking eroded tree rings. An asymptotic regression model was selected that included parameters that describe (i) litter mass in the year of tree death, (ii) litter mass many years after tree death related to litter input from neighboring trees (assuming constant and equal rates of litter deposition and decomposition), and (iii) the decay rate of litter. Litter mass in the year of tree death was assumed to be affected by tree size (DBH), which correlates with foliage biomass. The asymptotic regression model is defined as

$$[1] \quad L_t = L_{\text{Asym}} + (L_0 - L_{\text{Asym}}) \cdot \exp(-\exp(k') \cdot t)$$

where the variable L_t (in kg/m^2) is litter mass t years after tree death, the coefficient L_{Asym} (in kg/m^2) is the asymptotic litter mass as t converges to ∞ (i.e., corresponding to the accumulation of litter from neighboring trees), and the coefficient L_0 (in kg/m^2) is litter mass in the year of tree death,

Fig. 2. Changes in dry litter mass following tree death for (a) subalpine fir (*Abies lasiocarpa*), (b) lodgepole pine (*Pinus contorta*), and (c) Engelmann spruce (*Picea engelmannii*). The circles represent observed litter mass of dead trees; the size of the circles is scaled to maximum and minimum tree sizes (DBH) within each species. Lines show the fit of the asymptotic regression models (eq. 1; Table 2) for trees with maximum DBH (fir, 45 cm; pine, 50 cm; spruce, 56.6 cm), median DBH (fir, 29 cm; pine, 34.25 cm; spruce, 34 cm), and minimum DBH (fir, 20 cm; pine, 23.5 cm; spruce, 20.5 cm). Sample sizes: fir, $n = 36$; pine, $n = 9$; spruce, $n = 16$.



which changes linearly with the variable DBH ($L_0 = L_{0,\text{intercept}} + L_{0,\text{DBH}} \times \text{DBH}$). The coefficient k' (year^{-1}) is the log-transformed decay rate k (i.e., $\exp(k') = k$); the transformation $\exp(k')$ bounds this term to positive values. The half-life of litter was calculated as $t_{1/2} = \log(2)/k$. The models were fit using the “gnls” function (“nonlinear model using generalized least squares”; package “nlme”, version 3.1-96) in the R software (version 2.10.1) for statistical computing (R Development Core Team 2009).

The asymptotic regression model was applied to the litter data, but not to the dead wood data, because patterns of accumulation following tree death differ between litter and dead wood. Changes in litter mass may be appropriately modeled by this regression model, because litterfall occurs rapidly within a few years before and after tree death, followed by decomposition. Fall of dead wood, however, may occur episodically over several decades. Because of these differing processes, we assessed changes in dead wood over time only graphically.

Results

Changes in litter loads following tree death

Dry litter mass beneath trees ranged from 0.06 to 2.57 kg/m^2 for live trees (Fig. 1a), from 0.05 to 4.92 kg/m^2 for dead trees (Fig. 1b), and from 0.19 to 4.92 kg/m^2 for dead trees that had died after 1980 (Fig. 1c). Dead fir showed a 40% higher amount of litter than live fir ($P = 0.0265$, $n = 42$ pairs). Spruce that died after 1980 had accumulated 2.8 times more litter than live spruce ($P = 0.0156$, $n = 7$ pairs). Within live trees, there was >70% more litter beneath spruce than beneath fir ($P < 0.01$; for sample sizes of Kruskal–Wallis tests, see Table 1 and Fig. 1). Analogous for trees that died after 1980, almost four times more litter was found beneath spruce than beneath fir ($P < 0.01$).

The asymptotic regression models showed a significant decay of litter mass with time since tree death for all species (Fig. 2; coefficient k in Table 2). Half-life of litter ($t_{1/2}$) decreased from fir (19.2 years) to pine (14.6 years) to spruce

Table 2. Model description of the asymptotic regression models (eq. 1).

Species	<i>n</i>	L_{Asym}		$L_{0,intercept}$		$L_{0,DBH}$		k'		$t_{1/2}$	
		Estimate ± SE [kg/m ²]	Estimate ± SE [year ⁻¹]	log(2)/ <i>k</i> [year]							
Subalpine fir	36	0.570±0.151 (0.001)	-0.936±1.222 (0.449)	0.059±0.047 (0.221)	0.059±0.047 (0.221)	-3.320±1.104 (0.005)	0.036	19.2			
Lodgepole pine	9	0.340±0.204 (0.157)	1.085±1.610 (0.530)	-0.002±0.043 (0.962)	-0.002±0.043 (0.962)	-3.050±1.172 (0.048)	0.047	14.6			
Engelmann spruce	16	0.641±0.194 (0.006)	-2.858±1.648 (0.109)	0.171±0.043 (0.002)	0.171±0.043 (0.002)	-1.840±0.413 (0.001)	0.159	4.4			

Note: Subalpine fir, *Abies lasiocarpa*; lodgepole pine, *Pinus contorta*; Engelmann spruce, *Picea engelmannii*. For each species, the following parameters are shown: number of observations (*n*), estimate ± standard error (SE), *P* value (in parentheses), and half-life ($t_{1/2}$). Units are indicated in brackets. Values for *k* and $t_{1/2}$ were calculated using the nonrounded raw data.

(4.4 years). Only for spruce was there a significant and positive effect of tree size on the amount of litter in the year of tree death (coefficient $L_{0,DBH}$ in Table 2). For a tree of 35 cm DBH, expected litter loads in the year of tree death decreased from spruce (3.11 kg/m²) to fir (1.13 kg/m²) to pine (1.01 kg/m²) (Table 2). Over the long term, litter mass converged at 0.57 kg/m² for fir, at 0.34 kg/m² for pine, and at 0.64 kg/m² for spruce (Fig. 2; coefficient L_{Asym} in Table 2).

Changes in dead wood loads following tree death

Dead wood densities beneath live and dead trees generally decreased from the smallest (<0.6 cm) to the largest diameters (≥7.6 cm) (Fig. 3), with the distributions for the two larger diameter classes skewed to zero (Figs. 3c and 3d). Median mass of dead wood (kg/m²) increased from the smallest to the next diameter class, and maximum values generally increased from the smallest to the largest diameter class (Fig. 3). Within the <0.6 cm diameter class (Fig. 3a), there was a >40% higher dead wood density beneath live spruce than beneath dead spruce, which was marginally significant ($P = 0.0723$, $n = 36$ pairs). Both live fir and spruce had higher densities than live pine ($P < 0.01$ for fir and pine, $P < 0.001$ for spruce and pine; for sample sizes of Kruskal–Wallis tests, see Table 1). Live spruce had a >40% higher density than live fir, which was marginally significant ($P < 0.1$). Within diameter class 0.6–<2.6 cm (Fig. 3b), a more than two times higher dead wood density occurred beneath dead fir than beneath live fir ($P = 0.0027$, $n = 42$ pairs), and a >90% higher density was found beneath dead than live pine, which was marginally significant ($P = 0.073$, $n = 17$ pairs). Live spruce accumulated a >90% higher density of dead wood than live fir ($P < 0.01$). For the 2.6–<7.6 cm diameter class (Fig. 3c), there were no significant differences among species or between dead and live trees. For diameters ≥7.6 cm (Fig. 3d), live trees tended to show higher densities than dead trees, but only pine approached being statistically different ($P = 0.0625$, $n = 17$ pairs). For the two largest diameter classes (Figs. 3c and 3d), 65%–82% of the live and dead trees did not accumulate any dead wood.

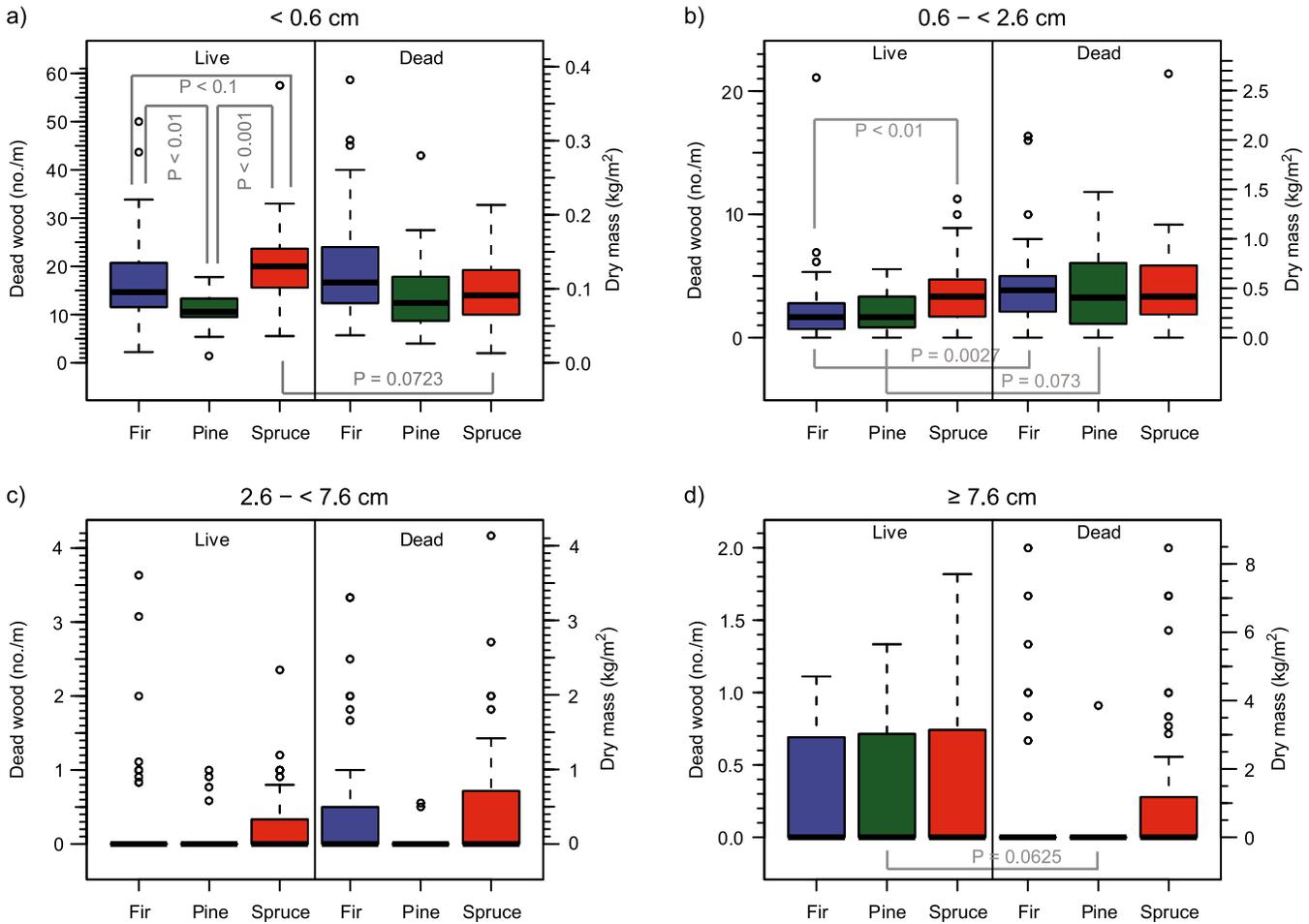
Although the variability in the dead wood densities was too great to allow development of predictive temporal models, some general patterns were evident. For all four diameter classes, the maximum dead wood densities were attained during the first 50 to 60 years after tree death as opposed to >60 years after tree death (Fig. 4).

Discussion

Changes in litter loads following tree death

Litter mass between live and dead (regardless of death date) trees differed only for fir, with dead trees having accumulated more litter (Fig. 1). However, for spruce, trees that died within the last 25 years (i.e., post-1980) had almost three times higher litter loads than live trees. There were higher litter loads for live spruce than for live fir, and for trees that died within the last 25 years, there were almost four times higher litter loads for spruce than for fir. The higher amount of litter for spruce may be related to the larger tree size and the higher foliar mass compared with fir

Fig. 3. Comparison of dead wood for live and dead subalpine fir (*Abies lasiocarpa*), lodgepole pine (*Pinus contorta*), and Engelmann spruce (*Picea engelmannii*) shown for diameter classes: (a) <0.6 cm, (b) 0.6–<2.6 cm, (c) 2.6–<7.6 cm, and (d) ≥7.6 cm. The left y axes show densities (number of pieces of dead wood per metre), and the right y axes show dry mass (kg/m²). For sample sizes, see Table 1.



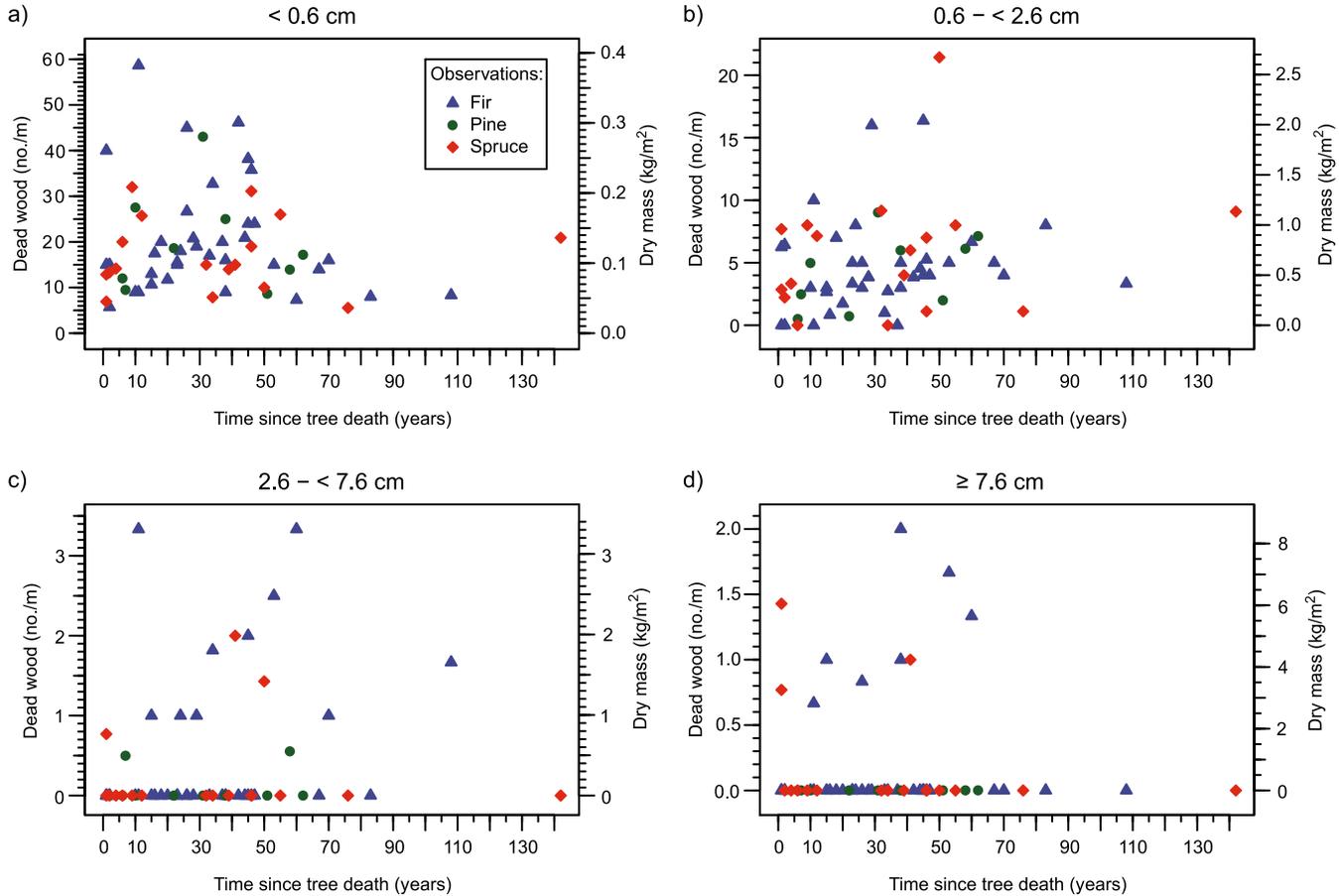
or pine. Furthermore, spruce tends to shed bark flakes more frequently than fir or pine. Page and Jenkins (2007) compared litter loads from lodgepole pine stands in Utah and Idaho during endemic and current epidemic stage of mountain pine beetle outbreak, as well as 20 years following an outbreak. They reported mean litter mass for lodgepole pine that varied between 0.29 and 0.38 kg/m² in endemic stands, between 0.52 and 0.68 kg/m² in epidemic stands, and 0.37 kg/m² in post-epidemic stands. The loads in our study show a similar temporal pattern but are almost twofold higher. Our results were 0.54 kg/m² for live lodgepole pine (Fig. 1a), corresponding to the endemic stands in Page and Jenkins (2007), 1.01 kg/m² in the year of tree death (based on a tree with 35 cm DBH in the asymptotic regression model; Fig. 2b), corresponding to epidemic stands, and 0.60 kg/m² 20 years after tree death or 0.38 kg/m² 60 years after tree death (Fig. 2b), corresponding to post-epidemic stands. For Engelmann spruce, mean litter mass was shown in Jenkins et al. (2008), which amounted to ca. 0.65 kg/m² in endemic stands, ca. 0.5 kg/m² in epidemic stands, and ca. 0.4 kg/m² 20 years after outbreaks. The corresponding values from spruce in our study showed that live trees accumulated 0.65 kg/m² (Fig. 1a) and dead trees accumulated 3.11 kg/m² in the year of death (tree with 35 cm DBH),

0.74 kg/m² 20 years after tree death, and 0.64 kg/m² 60 years after tree death (Fig. 2c). For subalpine fir, we did not find any longitudinal data in the literature.

The effect of tree size (DBH) on litter mass in the year of tree death was particularly strong for spruce (Table 2). In the year of tree death, the largest dead trees accumulated 4.6 times (fir), 1.8 times (pine), and 10.4 times (spruce) more litter compared with the median litter mass of live trees (Figs. 1 and 2). Both dead spruce and fir had similar asymptotic litter loads (Table 2), probably a result of litter input from neighboring spruce and fir, which co-exist in these forest stands. We assume that the crowns of live fir prevent high litter input from neighboring trees, particularly from recently dead and live spruce with their relatively high litter mass (Figs. 1 and 2). Similar effects may apply to the smallest dead fir and spruce included in the sample, where expected litter loads increased following tree death and levelled off at a higher level several decades after tree death (Fig. 2).

Many studies have quantified decomposition of litter and typically have been based on litterbag experiments. However, the time frame in these studies is commonly restricted to several months or years (Kimmins 2004). Because mass loss of litter becomes very slow with advanced decomposi-

Fig. 4. Changes in dead wood following tree death. Dead wood is shown for subalpine fir (*Abies lasiocarpa*) (triangles), lodgepole pine (*Pinus contorta*) (circles), and Engelmann spruce (*Picea engelmannii*) (diamonds) within diameter classes: (a) <0.6 cm, (b) 0.6–<2.6 cm, (c) 2.6–<7.6 cm, and (d) ≥ 7.6 cm. The left y axes show densities (number of pieces of dead wood per metre), and the right y axes show dry mass (kg/m²). For sample sizes, see Fig. 2.



tion, early decay rates probably overestimate the complete decomposition process, resulting in unreliable long-term projections (Prescott 2005b). In our study, we applied a chronosequence approach by relating time since tree death to measured litter loads (Fig. 2). The estimated decay rate for spruce in our study was more than three times higher than for pine and more than four times higher than for fir (Table 2). The faster decomposition of spruce litter may be partially explained by higher initial accumulation of litter beneath spruce, which is generally positively related to decay rates (Kimmins 2004). Decay rates reported for conifer needles in the literature agree with the estimate for spruce in our study but are 1.9–3.6 times higher for pine and 2.5–4.7 times higher for fir (Keane 2008; Kueppers and Harte 2005; Taylor et al. 1991). The litter samples in our study included not only conifer needles, but also bark and cones that have lower decay rates than conifer needles (Taylor et al. 1991), which may explain the lower decay rates estimated for pine and fir in our study. The accuracy and precision of the estimated decay rate for pine might have been greater if more trees of different sizes that had died <20 years ago had been sampled (Fig. 2b).

Changes in dead wood loads following tree death

Within the smallest diameter class of dead wood

(<0.6 cm), both live fir and spruce accumulated more dead wood than live pine (Fig. 3a). For spruce, more small dead wood accumulated beneath live trees than following tree death. Within the second smallest diameter class (0.6–<2.6 cm), dead wood loads beneath live spruce were almost twofold higher than beneath live fir, and loads beneath dead fir were more than twofold higher than beneath live fir (Fig. 3b). Dead wood between 0.6 and <2.6 cm in diameter contributed the highest median loads to the overall biomass of dead wood on the ground (Fig. 3). However, because of the high spatial variability within the two largest diameter classes (≥ 2.6 cm; Figs. 3c and 3d), large dead wood was often only locally an important element of the surface dead wood (Brown and Bevins 1986). Minimum, median, and maximum values of dead wood loads for fir, pine, and spruce for all diameter classes in our study agreed relatively well with those reported in other studies (Brown and Bevins 1986; DeRose and Long 2009; Jenkins et al. 2008; Jorgensen and Jenkins 2010; Page and Jenkins 2007). Discrepancies may be explained by different climates, stand ages, and sampling schemes. Sampling along several planar intersects per tree would have certainly decreased the variability in estimated dead wood loads in our study.

The time-series data on dead wood did not reveal a predictable pattern of accumulation after tree death (Fig. 4),

supporting previous findings from spruce–fir stands in Utah affected by spruce beetles (Jorgensen and Jenkins 2010). Maximum values occurred for some species 40 or more years following tree death. Many trees did not accumulate any dead wood ≥ 2.6 cm, even decades after tree death, whereas a smaller number of trees recorded relatively high loads (Figs. 4c and 4d). These results imply that the accumulation of dead wood on the ground occurred irregularly over a time frame of ca. 50–60 years. Contrary to the temporal dynamics of litter, where we observed high accumulation immediately following tree death with subsequent decomposition (Fig. 2), there was a lack of a predictable, temporal pattern in dead wood loads following tree death.

There are at least two possible explanations for this lack of predictable relationship of dead wood loads and time since tree death. First, the higher spatial variability in dead wood (Fig. 3), particularly for diameters ≥ 2.6 cm, may partially explain this lack of relationship. High variability in dead wood loads beneath individual trees is consistent with high variabilities in coarse dead wood among stands of varying age, composition, and associated abiotic site factors (Fahey and Knight 1986; Peet 2000). A denser sampling scheme with longer planar intersects around each tree might have taken into account this high spatial variability in dead wood. Second, deposition of dead wood does not necessarily occur immediately following tree death, but rather takes place over several decades and is mostly driven by wind and snow storms. Retrospective reconstructions of treefall events in nearby stands have shown that there are pulses of tree falls driven by wind events and synchronized over areas of 1000s of square kilometres (Veblen et al. 1991). These are wind events that at some localities may result in enough tree fall to be recognized as a stand-level blowdown killing most canopy trees over a hectare or more, but over larger areas, the same wind events cause the fall of standing and dead trees in relatively small groups (Veblen et al. 1991). The importance of decadal-scale variation in wind-driven deposition of dead wood is consistent with our observations in the current study that a majority of trees that died >20 years ago were still standing and still had twigs and branches in the crown (Bigler et al. 2007).

Conclusions

In subalpine forests of northern Colorado, the dating of tree death and measurement of litter and dead wood beneath trees that died over a time span of more than 100 years presents a novel approach that yields some important insights into how tree death may influence the dynamics of litter and dead wood. Litter accumulated shortly after tree death, with litter mass beneath large, dead trees increasing by twofold (pine), fivefold (fir), or 10-fold (spruce) compared with live trees. Based on chronosequences over more than 100 years, we estimated litter to decompose fastest for spruce (half-life four years), followed by pine (half-life 15 years) and fir (half-life 19 years). The accumulation of dead wood following tree death was highly variable among trees. Rather than the smooth and predictable accumulation of dead wood over time intuitively expected as dead trees decompose and fall, patterns of accumulation of dead wood were highly irregular and appeared to be driven by wind and

snow storms. The recently increased mortality rates of different conifer species across western North America may not only affect forest structures and composition, but may also have far-reaching implications for various ecosystem processes by affecting the temporal and spatial dynamics of litter and dead wood.

Our findings imply that the consequences of tree death for the dynamics of the fuel complex and the resulting fire hazard are not as easily predicted as previously believed. In the current study, the higher litter loads (i.e., recently cast needles) present in the first few years following the death of lodgepole pine and Engelmann spruce are consistent with predicted higher rates of surface fire spread following bark beetle outbreaks (Jenkins et al. 2008; Page and Jenkins 2007). However, the accumulation rates for dead wood following tree death are highly variable among trees, and accumulation rates over time could not be predicted from regression models. Our results reinforce the need for caution in assuming predictable rates of surface dead wood accumulation following tree death (Jorgensen and Jenkins 2010). Fire history studies in subalpine forests in our study area have emphasized the importance of interannual climate variation, and associated short-term fire weather, as the primary limitation to extreme fire behaviour (Schoennagel et al. 2007; Sibold et al. 2006). Analogously, the current study implies that fuel-defined fire hazard related to accumulation of surface dead wood following tree death is also partially driven by climate events.

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