

Wildfire alters belowground and surface wood decomposition on two national forests in Montana, USA

Deborah S. Page-Dumroese^{A,C}, Martin F. Jurgensen^B, Chris A. Miller^B, James B. Pickens^B and Joanne M. Tirocke^A

^AUSDA Forest Service, Rocky Mountain Research Station, 1221 S Main, Moscow, ID 83843, USA.

^BSchool of Forestry and Environmental Science, Michigan Technological University, Houghton, MI 49931, USA.

^CCorresponding author. Email: debbie.dumroese@usda.gov

Abstract. Wildfires can drastically alter belowground processes such as organic matter (OM) decomposition. We used wood stakes of two different tree species, trembling aspen (*Populus tremuloides* Michx.) and loblolly pine (*Pinus taeda* L.), placed at three soil locations (soil surface, forest floor–mineral soil interface, mineral soil), as an index of the long-term (5-year) effects of wildfire on OM decomposition in two forest stands after high-severity wildfire and in an unburned control. Wood stake mass loss was generally higher for aspen, especially in the mineral soil of burned plots, than in control plots after 5 years. Soil surface and interface (unburned stands only) stakes showed few significant differences for either species on the Bitterroot National Forest. On the Gallatin National Forest, both pine and aspen stakes had significantly greater mass loss at the interface (unburned stand) at the end of 5 years, and also decayed significantly faster at the 10–20-cm depth in the wildfire area. Using wood stakes as an index of soil microsite properties in burned and unburned plots, we show that fire increased both OM decomposition and mineral soil microsite variability. These results strengthen our understanding of soil-surface and belowground ecosystem responses to wildfire.

Additional keywords: Bitterroot National Forest, Gallatin National Forest, organic matter, *Pinus taeda*, *Populus tremuloides*, soil microsite.

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Introduction

In the western USA, many Rocky Mountain forests have evolved with wildfire (Quigley and Arbelbide 1997; Keane *et al.* 2002). However, after the large fires of 1910, the USDA Forest Service began a successful campaign to suppress or exclude wildfires from many national forests (Pyne 1982). Removing fire from these ecosystems resulted in a gradual accumulation of forest-floor material and both fine and coarse woody debris on the soil surface. With the change in frequency of large-scale fires, forest stand growth and structure have gradually moved from early seral, shade-intolerant species to late seral, shade-tolerant species (Mutch *et al.* 1993). The resulting forests contain trees with large canopies in multiple layers; concomitantly severe summer droughts have increased forest wildfire occurrence and severity (Westerling *et al.* 2006). Because of fire exclusion, wildfires in the western USA generally burn with high intensity, resulting in deep soil heating, destruction of organic matter (OM) and loss of soil microbes (Keane *et al.* 2002).

In addition to having higher-severity fires, the western USA fire weather seasons have lengthened by nearly 19% since 1979 (Jolly *et al.* 2015), and current climate change models predict that angiosperm tree dominance will be favoured within forest ecosystems, particularly those at the southern edge of the boreal forest (Intergovernmental Panel on Climate Change (IPCC)

2007). The greater incidence of wildfire coupled with higher decomposition rates of angiosperm OM has the potential to influence carbon (C) storage in mineral soils across large areas (Weedon *et al.* 2009). Over the past several decades, large wildfires in the western USA have increased in both frequency and duration owing to changes in temperature, number of rain-free days and humidity (Jolly *et al.* 2015). All of these factors will likely influence C storage and decomposition rates in this region with the potential to lead to a decrease in forest soil C stocks. For example, Page-Dumroese and Jurgensen (2006) estimate that up to 80% of C contained in the forest floor, coarse and fine woody residue, and surface (0–30-cm) mineral horizons could be lost during high-severity fires in the north-western USA. Soil nitrogen (N), which is volatilised at temperatures ranging from 300 to 500°C (Hungerford *et al.* 1991; Esquilin *et al.* 2007), was depleted by 500–700 kg ha⁻¹ and up to 23 Mg ha⁻¹ of C during the Biscuit Fire in OR, USA (Bormann *et al.* 2008). In addition, high-intensity fires also produce large amounts of recalcitrant pyrogenic C (charcoal), which is highly resistant to decomposition and can affect soil nutrient availability and leaching losses (Schmidt and Noack 2000; Gundale and DeLuca 2006). However, exact estimates of C and N losses depend on fire severity, soil erosion and the amount of surface OM remaining on site after the fire (Murphy *et al.* 2006; Johnson *et al.* 2007).

Assessing the impacts of high-severity fires on wood decomposition can be difficult because of highly variable soil properties and processes (Fons *et al.* 1997). This also holds true for microbial biomass, community composition and metabolic activity (Bissett and Parkinson 1980). For example, fire may change soil microsite pH variability, which can alter the bacteria: fungi ratio and affect subsequent decomposition (Oliver *et al.* 2015). To assess changes in microbial processes after wild or prescribed fire, litter bags have often been used to assess decomposition, but OM used in the litter bags is usually site-specific, making it difficult to compare results and soil impacts in cross-site comparisons (Knorr *et al.* 2005a). For example, litter decomposition was slower after a low-intensity underburn in ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) stands (Monleon and Cromack 1996) or after stands were clearcut-harvested and prescribed-burned (White 1986). In contrast, Grigal and McColl (1977) noted no changes in *Populus tremuloides* Michx. and *Aster macrophyllus* L. leaf litter decomposition after a low-severity wildfire (lower litter layers remained intact) as compared with an adjacent unburned forested area.

Changes in soil and microclimatic conditions (e.g. soil temperature and moisture) from forest floor loss and overstorey tree removal by fire have a large impact on subsequent OM decomposition, the extent of which depends on various factors, especially fire severity and soil type (Donnelly *et al.* 1990; Neary *et al.* 1999). Fire can affect many soil properties, and produces complex soil and site changes that occur in a short period of time (Neary *et al.* 1999). Depending on intensity and duration, fire can alter soil structure by removing stable aggregates and decreasing hydrologic function (Mataix-Solera *et al.* 2011), combust OM on and near the soil surface (Anderson 1991), volatilise soil nutrients (Neary *et al.* 1999), kill or alter soil microbial populations (Dunn *et al.* 1985; Covington and DeBano 1990; DeBano *et al.* 1998), and decrease soil acidity (Certini 2005). Slower mineral soil OM decomposition rates can result from a higher soil C:N ratio (Parr and Papendick 1978), which increases after forest fires owing to higher losses of soil N than soil C (Johnson and Curtis 2001). These factors interact with altered temperature and moisture regimes (Reichstein *et al.* 2005; Bradford *et al.* 2014) to potentially alter both surface and belowground OM decomposition rates.

Despite the important role of woody material in C budgets and C sequestration, very little is known on the effects of fire on wood decomposition. Although decay rates of standing fire-killed trees have been studied (Harmon 1982), we could find only one study of wood decomposition in the soil literature, which reported wood dowels decayed faster in the fire-impacted mineral soil of a burned tallgrass prairie than in an unburned soil (O'Lear *et al.* 1996). In addition, vegetation and climate models often use generalised OM decomposition rates taken from litter bag studies (Blanco *et al.* 2011), but decomposition of surface woody material and fine roots may be a better predictor of tree growth within ecosystem models (Gárate and Blanco 2013) or subsequent soil function recovery.

In the summers of 2000 and 2001, numerous wildfires burned more than 3 000 000 ha in the western USA (Rorig and Ferguson 2002), many of which at high severity, and resulted in the loss of most, if not all, surface OM (Robichaud *et al.* 2008). With such increased incidence and intensity of fire in forest ecosystems,

more information is needed on how fire-induced changes in soil properties and microclimate affect subsequent OM decomposition, and possible implications of these changes on forest management, C sequestration and modelling soil C turnover.

Therefore, the objective of our study was to assess the effects of wildfire on OM decomposition in two forest stands with different climate regimes and soil types in the northern Rocky Mountains, USA. We used wood stakes as an index of OM decomposition changes after wildfires, in which wood quality is held constant, and mass loss (decomposition) becomes a function of soil abiotic (e.g. moisture, temperature, pH, available N) and biotic (e.g. microbial biomass, functional diversity) conditions. Wood was selected as the OM substrate because it is a normal component of forest soils (surface residue, stumps, roots), and its decomposition is affected by changes in soil properties and climatic conditions over long time periods (Chen *et al.* 2000). Wood stakes have been used to measure the effect of a soil temperature gradient, land-use changes and timber harvesting on OM decomposition (Jurgensen *et al.* 2006; Risch *et al.* 2013; Finér *et al.* 2016). Stakes of two tree species were used, trembling aspen (*Populus tremuloides* Michx.) and loblolly pine (*Pinus taeda* L.), that have different wood properties (e.g. lignin type, lignin to cellulose ratio, N content), and would favour the development of different wood-decomposing microbial communities (Blanchette 1984). We hypothesised that wood decomposition would be more rapid at the soil surface and in the mineral soil after a wildfire than in an adjacent unburned stand owing to: (1) higher soil temperatures caused by forest floor loss, overstorey removal, and the grey–black colour of the mineral soil surface, and (2) higher soil moisture contents from more precipitation reaching the soil surface, and decreased soil water uptake by roots.

Methods

Site description

Our study was conducted in stands on the Bitterroot and Gallatin National Forests, Montana, USA (Fig. 1), which had wildfires that destroyed nearly all the forest floor and downed woody residue over large areas. Plots were established in locations that experienced high fire severity (Robichaud *et al.* 2008, 2009), and in adjacent unburned (control) stands that were as similar as possible in slope, aspect, soil, elevation and tree species to the burned stands. On both sites, high-severity burn conditions (i.e. loss of all pre-fire ground cover and surface OM, charred visible roots, extensive soil charring (black colour), grey mineral soil colour; Parsons *et al.* 2010) extended for at least 2 ha around our study plots.

Bitterroot National Forest

One series of study plots was located on the Bitterroot National Forest (BNF) in western Montana, USA (45.91°N 114.03°W) within the area burned by the Valley Complex Fire that started on 31 July 2000. Soil at this site is a sandy-skeletal, mixed, frigid, Typic Haplustept in a granitic colluvium parent material (Soil Survey Staff 2009), and has a gravelly loam texture with a rock fraction of 44–51%. Plot elevations are ~2410 m, with mean annual precipitation and air temperature of 915 mm and 20°C (Robichaud *et al.* 2008). A majority of the

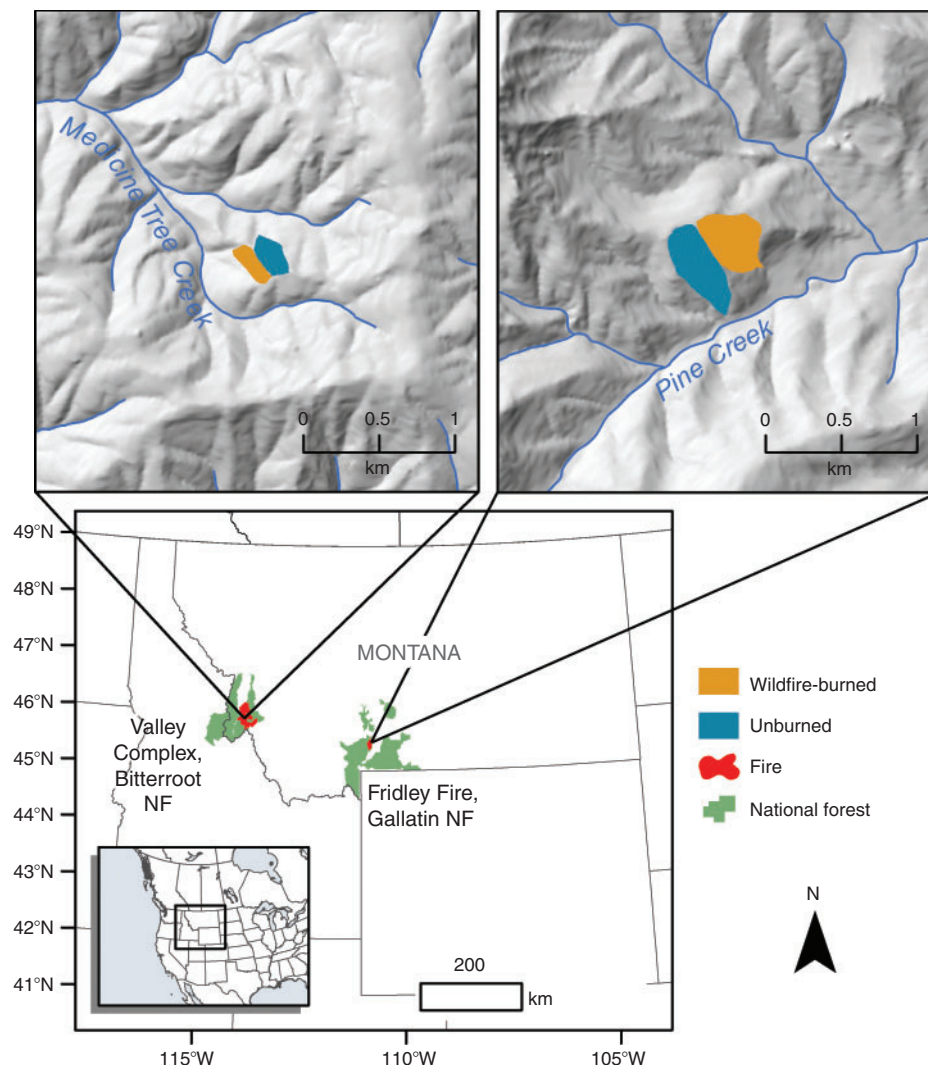


Fig. 1. Study site location and extent of the wildfires on the Bitterroot and Gallatin National Forests (NF).

yearly precipitation occurs as snowfall, but rainfall in the months of April–October ranged from a high of 185 mm in 2003 to a low of 71 mm in 2004 during our study (Table 1). Air temperature from 2003 to 2006 during these months ranged from 8 to 13°C. The adjacent control plots were in a late succession Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) stand with a few scattered ponderosa pines. Historically, the fire frequency in this area averages 16 years (range 4–29 years), but fire suppression has extended that range and this site had not burned for over 50 years (Arno 1976).

Gallatin National Forest

Another series of plots was located on the Gallatin National Forest (GNF) in south-central Montana, USA (45.51°N 110.78°W) within the burned area of the Fridley Fire, which started on 19 August 2001. Soil is a loamy-skeletal, mixed, Typic Agriboroll with volcanic parent material, and has a gravelly silt loam texture with a rock fraction of 34–47% (Soil Survey Staff 2009). Plot elevations are ~2090 m, with mean

annual precipitation and air temperature of 755 mm and 24°C (Robichaud *et al.* 2008). In general, rainfall and air temperatures were higher on this forest than on the BNF (Table 1). The adjacent, unburned control stand was predominately Douglas-fir. The historic fire frequency for this site is ~75 years (Fischer and Clayton 1983), but our study site had not burned for at least 200 years (Pfister *et al.* 1977).

Wood stakes

Wood stakes placed on the soil surface (2.5 × 2.5 × 15 cm), and stakes inserted into mineral soil (2.5 × 2.5 × 20 or 30 cm) were cut from kiln-dried, knot-free aspen and loblolly pine ‘mother’ stakes (2.5 × 2.5 × 50 cm). Two field ‘daughter’ stakes were cut from each mother stake, and the remaining centre sections were used to determine initial mass (t_0) of all field stakes.

In early June 2002, loblolly pine and aspen stakes were installed on the surface of the forest floor, at the forest floor–mineral soil interface (if both present), and in the mineral soil of two burned and adjacent control plots in each forest following the

Table 1. Average precipitation and air temperature at wildfire study plots on the Bitterroot and Gallatin National Forests: 1 April–31 October 2003 to 2006

Location	Year			
	2003	2004	2005	2006 ^A
Bitterroot National Forest				
Rainfall (mm)	185.4	71.1	152.8	113.5
Temperature (°C)	12.8	11.6	9.9	7.7
Gallatin National Forest				
Rainfall (mm)	112.3	319.0	169.7	156.7
Temperature (°C)	15.2	14.8	14.5	16.1

^AThe weather station on the Bitterroot National Forest was removed in mid-June 2006 and therefore precipitation and temperature means for this year only include data through 4 June.

protocol outlined in [Jurgensen *et al.* \(2006\)](#). Twenty-five surface stakes of both species were placed horizontally on the mineral soil surface (no forest floor), and 25 mineral soil stakes were installed vertically in all burned plots: GNF – $2.5 \times 2.5 \times 20$ cm; BNF – $2.5 \times 2.5 \times 30$ cm. The GNF mineral soil stakes were only 20 cm long because of high rock content in the shallow to bedrock soil. In the unburned control plots, 25 surface stakes of both species were placed on top of the forest floor, 25 stakes at the forest floor–mineral soil interface and 25 stakes inserted into mineral soil, for a study wood stake total of 500 ($n = \text{fire: } 2 \text{ plots} \times 2 \text{ tree species} \times 2 \text{ stake locations} \times 25 \text{ replicates}$; control: $2 \text{ plots} \times 2 \text{ species} \times 3 \text{ stake locations} \times 25 \text{ replicates}$). To minimise soil compaction at the wood stake–mineral soil interface and damage to the stakes during installation, all mineral soil stakes were placed into 2.5-cm^2 holes ~ 30 cm apart made by a square 2.5-cm soil-coring tool, so that the stake tops were flush with the mineral soil surface. The top of each stake was sealed to prevent water from wicking through the stake. Every June for the next 5 years, five stakes of both tree species were randomly removed from each soil location in all burned and unburned plots, weighed in the field to obtain wood stake moisture content at extraction, and sent to the School of Forest Resources and Environmental Science, Michigan Technological University, Houghton, Michigan, for processing.

Owing to periodic erosion events on the GNF fire site (see [Robichaud *et al.* 2008](#) for details), a complete set of 10 aspen stake samples could not be obtained from the burned mineral soil in 3 of the 5 years: 2004 – three stakes, 2005 – two stakes, 2007 – three stakes. The GNF experienced several large rain events in 2002–05 that resulted in significant runoff (0–4.7 mm) and sediment production (0–5.8 mm) during the study period ([Robichaud *et al.* 2008](#)). Large rain events also occurred on the BNF, but less runoff (0–2.5 mm) and sediment production (0–0.33 mm) were measured.

Stake analyses

All wood stakes were dried at 105°C for 48 h and weighed. A 2.5-cm-long block was cut from the 5- and 15-cm soil depth from each GNF mineral soil stake to assess the effect of soil depth on wood decomposition. Similar blocks were cut from the 5-, 15- and 25-cm depth from mineral soil stakes on the BNF.

Wood decomposition (mass loss) during each year of the study was measured by comparing dry weight of each field stake with the weight of its corresponding control section (t_0). Mass loss averages for each plot were used as a treatment observation in the statistical analyses.

Soil sampling

Adjacent to the wildfire and unburned control plots on each National Forest, we randomly selected three sampling points for forest floor and mineral soil collection. Forest floor depth was measured and collected within a 30-cm circle and placed in a paper bag. After the forest floor was removed, soil bulk density was determined by excavating 10-cm increments to a depth of 20 cm on the GNF and to a 30-cm depth on the BNF, filling the holes with polyurethane expanding foam covered with a weighted cardboard plate, and letting the foam cure overnight ([Page-Dumroese *et al.* 1999](#)). All soil samples and foam cores were taken to US Forest Service (USFS) Soil Analytical Laboratory in Moscow, Idaho, to determine soil physical and chemical properties, and to measure foam core volume for bulk density calculations.

Soil samples were weighed after drying to 105°C for 24 h, sieved through a 2-mm mesh screen to remove rocks, and weighed again to calculate soil fine fraction bulk density ([Page-Dumroese *et al.* 1999](#)). The sieved soil was analysed for C and N (LECO CN analyser), OM by weight loss on ignition at 375°C for 8 h, and pH in a 2 : 1 water–soil slurry. Soil chemical properties (C and N) and OM were corrected for fine-fraction bulk density and expressed on a per hectare basis. Soil temperatures were measured at the 10-cm mineral soil depth every 4 h on one burned and control plot at each study site using Hobo temperature loggers (Onset Computer Corp). Temperature degree days were calculated as the proportion of a day above threshold temperatures (2 and 10°C) by adding the hours above the temperature threshold value in each year, and then averaging the values over 5 years. We also attempted to collect soil moisture values every 4 h, but owing to instrument malfunction and animal damage, much of this information was lost. However, rainfall and air temperature data from April to October were collected for a majority of the study period ([Table 1](#)), and data collection methods are detailed in [Robichaud *et al.* \(2008\)](#).

Statistical analyses

The five stakes removed from each subplot at each sampling date were analysed for weight loss and the results averaged before analysis. Only this average was used as an observation for each combination of treatments in the statistical analyses. An analysis of variance (ANOVA) was conducted with *SAS* (ver. 9.2) using a factorial design, and the factors in the ANOVA model were treatment (wildfire burned and unburned control), forest (BNF and GNF), subplot (two subplots within each treatment and forest), extraction date (5 years), and depth (0–10, 10–20, and 20–30 cm). Within this model, subplots were treated as nested effects within the wildfire-burned and control treatment for each forest. The nested effects were estimated by their own means instead of the mean across all subplots. The initial model employed was the standard ‘effects model’ with factors and their interactions included ([Milliken and Johnson 1984](#)).

Table 2. Mean forest floor and mineral soil properties for the Bitterroot and Gallatin National Forests

Values in parentheses are standard error of the mean. Bold numbers indicate significant differences between the control and wildfire

Forest	Variable	Control	Wildfire	<i>P</i>
Bitterroot	Forest floor			
	Depth (cm)	6.8		
	Organic matter (Mg ha ⁻¹)	122 (23)	–	
	Carbon (Mg ha ⁻¹)	56 (18)	–	
	Nitrogen (kg ha ⁻¹)	127 (9)	–	
	C : N ratio	44 (0.3)	–	
	Mineral soil ^A			
	Organic matter (Mg ha ⁻¹)	101 (12)	67 (18)	0.06
	Carbon (Mg ha ⁻¹)	31 (9)	26 (10)	0.02
	Nitrogen (kg ha ⁻¹)	962 (21)	1025 (16)	0.13
	C : N ratio	16 (0.2)	18 (1.3)	0.02
	Bulk density (Mg m ⁻³)	1.3 (0.2)	1.2 (0.3)	0.21
	pH	4.5 (0.1)	5.2 (0.2)	0.05
	Soil temperature at 10 cm (°C)	6.5 (0.5)	7.8 (0.4)	0.005
	5-year average degree days >2°C	207	215	
	5-year average degree days >10°C	125	158	
Gallatin	Forest floor			
	Depth (cm)	2.7		
	Organic matter (Mg ha ⁻¹)	65 (8)	–	
	Carbon (Mg ha ⁻¹)	33 (10)	–	
	Nitrogen (kg ha ⁻¹)	78 (16)	–	
	C : N ratio	42 (0.4)	–	
	Mineral soil ^B			
	Organic matter (Mg ha ⁻¹)	102 (15)	83 (8)	0.07
	Carbon (Mg ha ⁻¹)	28 (5)	26 (5)	0.07
	Nitrogen (kg ha ⁻¹)	1372 (10)	1612 (11)	0.06
	C : N ratio	10.9 (0.1)	15 (1.2)	0.03
	Bulk density (Mg m ⁻³)	1.5 (0.2)	1.3 (0.3)	0.32
	pH	5.3 (0.2)	5.5 (0.2)	0.41
	Soil temperature at 10 cm (°C)	7.0 (0.4)	9.8 (0.4)	0.001
	5-year average degree days >2°C	224	227	
	5-year average degree days >10°C	137	194	

^ABitterroot National Forest mineral soil data are for the 0–30-cm depth.^BGallatin National Forest mineral soil data are for the 0–20-cm depth.

When significant interactions were detected, the ‘means model’ was used to clarify the relationships. All analyses were conducted at $\alpha = 0.05$ significance level.

Surface stakes were analysed similarly to the mineral stakes, but stake location was used to denote differences among stakes on the surface of the burned soil and surface of the forest floor and interface in the unburned soil. Within this model, subplots were treated as nested effects within each forest and stake location. Differences in standard deviations among mineral stakes at the BNF were evaluated with a two-sample *t* test utilising either pooled or unpooled variance statistics based on the results of a preliminary *F* test for homogeneity of variance. Fire effects on soil properties (burned vs control) were evaluated with a *t* test.

Results

Bitterroot National Forest

Soil properties

On the BNF, virtually all the forest floor was removed by the high-intensity wildfire, resulting in C and N losses of

56 Mg ha⁻¹ and 127 kg ha⁻¹ respectively (Table 2). Appreciable losses of C and OM were also found in the surface mineral soil, but it appears that some forest floor N moved into the mineral soil, as it was higher post-burn than in the control. As expected from such a high-severity fire, soil acidity decreased (pH increased) in the surface mineral soil.

Soil temperature

Averaged over the 5 years of our study, soil temperature was 1.3°C higher in the burned than in the unburned plots (Table 2), which resulted in 8 more 2°C degree days each year and 33 additional 10°C degree days each year in the burned soil than in the control soil. Warmer soil conditions during the growing seasons of 2003 through 2005 on the burned plots are clearly shown by the number of degree days >10°C in the early spring and late fall (Table 3).

Wood stake decomposition

As expected, aspen stakes decomposed faster than pine stakes in both the burned and unburned plots ($P \leq 0.0001$).

Table 3. Average number of 2°C and 10°C degree days on the Bitterroot and Gallatin National Forests during the 2003 through 2005 growing seasons

Forest	Month	Unburned		Wildfire	
		2°C	10°C	2°C	10°C
Bitterroot	March	6	0	16	10
	April	19	0	29	6
	May	31	7	31	14
	June	29	27	31	30
	July	31	31	31	31
	Aug	31	31	31	31
	Sept	29	21	31	23
	Oct	28	8	31	10
Total degree days		204	125	231	155
Gallatin	March	5	2	13	4
	April	22	6	24	3
	May	28	10	31	13
	June	26	22	31	31
	July	31	31	31	31
	Aug	31	29	31	31
	Sept	27	17	31	23
	Oct	24	6	30	10
Total degree days		194	123	222	146

The removal of the litter layer by the wildfire did not have a significant effect on aspen surface stake mass loss in each year sampled (Fig. 2a), but when averaged over the 5 years, aspen mass loss on the wildfire soil surface (29.6%) was significantly greater ($P = 0.027$) than on the unburned litter surface (17.2%) and the litter layer–mineral soil interface in the unburned control stand (20.6%). Surface pine wood stakes decomposed much more slowly than aspen (Fig. 2b), and no significant mass loss differences were found among pine stakes on the wildfire-burned surface and those on the unburned soil surface ($P = 0.09$).

In contrast to the surface stakes, fire had a major effect on wood decomposition in the mineral soil. Aspen stakes decayed significantly faster in the burn-affected soil than in the unburned stand (Fig. 2c), so at the end of our 5-year study (6 years after the fire), aspen mass loss was 55% in burned soil and only 27% in the unburned control. A similar pattern was found with the more slowly decomposing pine stakes (Fig. 2d), which had a 5-year mass loss of 34% in burned soil and only 12% in the unburned soil.

Mineral soil depth had little impact on decomposition of the 30-cm aspen stakes in either the burned and unburned plots ($P = 0.867$), but had a small, but significant, effect when averaged across treatment and years sampled ($P = 0.04$). Mass loss from the top 10 cm of the stakes was ~6% higher than from the bottom 10 cm (Fig. 3a). Soil depth had no effect on pine stake decomposition ($P = 0.89$).

Gallatin National Forest

Soil properties

The forest floor on the GNF was thinner than on the BNF, so forest floor C and N losses from the wildfire were lower

(Table 2). Surface mineral soil N content on the GNF was slightly higher than on the BNF, but forest floor N was lower. Similarly to the BNF, post-fire soil N was higher than in the undisturbed stand, indicating that some forest floor N also moved into the mineral soil during or after the fire. Although both the BNF and the GNF were categorised as high severity (Robichaud *et al.* 2008), soil OM and C losses were lower and the pH change less on the GNF, indicating there was likely a lower-severity fire at the GNF plot locations.

Soil temperature

The average 5-year temperature in the burned soil on the GNF was also higher than in unburned soil (nearly 3°C), which amounted to only 3 more 2°C degree days each year, but an additional 57 degree days above the 10°C threshold (Table 2). The burned GNF soil was also warmer (~3°C) and had greater number of degree days than on BNF, especially above 10°C. The average 5-year soil temperature in the GNF unburned soil was only 0.5°C higher than in the BNF, but resulted in 15 and 12 additional 2°C ($P = 0.03$) and 10°C degree days each year ($P = 0.05$; Table 2). Similar to the BNF, soil temperatures in 2003 did not go above 2°C until March and dropped below this threshold in October (Table 3).

Wood stake decomposition

In contrast to the BNF, the decomposition of both aspen and pine surface stakes after the fire was faster at the forest floor–mineral soil interface in the unburned stand than on the surface of the burned mineral soil and on top of the litter layer (Fig. 4a and 4b). At the end of 5 years, aspen stake mass loss at the forest floor–mineral soil interface was 42%, as compared with ~16% on the wildfire-burned soil and on top of the unburned litter layer. Pine stake decomposition was much slower than aspen, with a 5-year pine stake mass loss of 21% at the forest floor–mineral soil interface and only ~7% on the surface of the wildfire-affected soil and on the unburned stand litter layer.

Owing to soil erosion on the aspen plots, fewer mineral soil stakes were sampled in 3 of the 5 years, so we did not compare yearly differences in mass loss between stakes in the burned and unburned soils (Fig. 4c). However, aspen decomposition was quite fast, with a 5-year mass loss of 61% in wildfire-affected soil and 48% in the unburned soil. When averaged over all years, aspen mass loss was significantly greater in the burned mineral soil ($P = 0.0005$). Pine mass loss was also faster in the burned mineral soil ($P \leq 0.0001$), but again much slower than aspen (Fig. 4d).

Soil depth had a significant effect on decomposition of the 20-cm pine stakes, but only in the burned soil ($P = 0.017$). Average stake mass loss for the top 10 cm was 22%, but increased to over 40% for the bottom 10 cm (Fig. 3b). Aspen stake mass loss was also higher at the 10–20-cm soil depth (41.6%) than at 0–10 cm (21.4%) in the burned soil ($P = 0.088$).

Cross-site fire comparison

Decomposition

By using a standard wood substrate on both forests, we anticipated being able to conduct cross-site comparisons. Although the patterns of aspen and pine stake decomposition

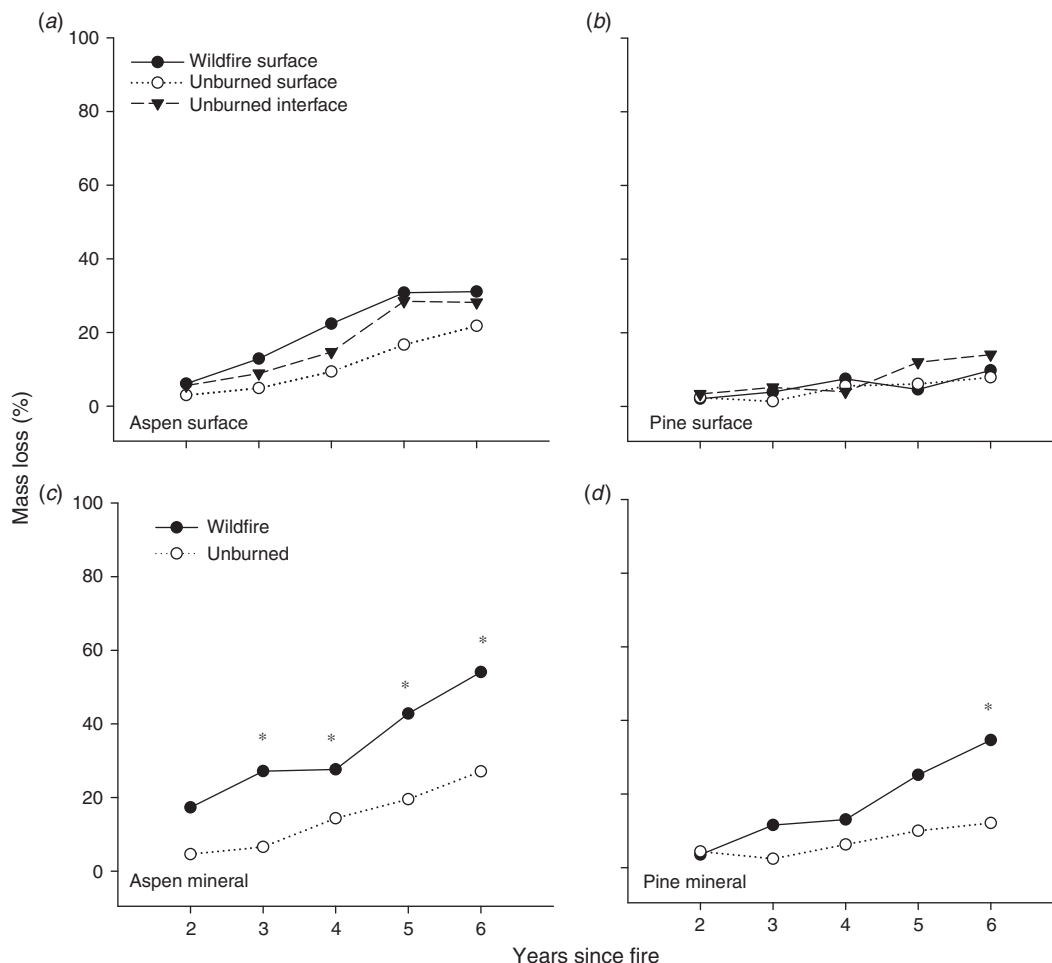


Fig. 2. Mass loss of aspen and pine stakes in burned and adjacent unburned control plots on the Bitterroot National Forest for: (a) surface aspen; (b) surface pine; (c) mineral aspen; and (d) mineral pine. For each year after the fire, wildfire stake mass loss values with an asterisk are significantly different from the control plots for that year ($P \leq 0.0001$).

were generally similar on both National Forests, a comparison of mass loss timelines after the wildfires will give some insight into possible soil and climate factors affecting the decomposition process on each forest. However, such forest comparisons were confounded by mineral soil stake length differences (GNF – 20 cm; BNF – 30 cm), the erosion loss around aspen mineral soil stakes on the GNF, and the BNF Valley Complex Fire occurring 1 year earlier (2001) than the Fridley fire (2002) on the GNF. Therefore, mass loss patterns of aspen and pine surface and mineral soil stakes from the 0–20-cm soil depth on each forest were compared 2 to 5 years after each fire (Figs 2 and 4). There was very little yearly difference in aspen and pine mass loss between the two forests at the three surface stake locations on the burned or unburned plots. However, when averaged over the 4 years, mass loss at the unburned forest floor–mineral soil interface was significantly higher on the GNF than the BNF for both aspen ($P = 0.001$) and pine ($P = 0.014$).

Mass loss of pine stakes in the burned mineral soil on the GNF was higher than on the BNF for all 4 years, but the difference was only significant 2 years after the fire (Table 4). Although we could not compare the difference in aspen

decomposition in burned mineral soil between the two forests, mass loss of aspen stakes in unburned mineral soil on the GNF was much larger than on the BNF. Surprisingly, pine stake decomposition in the burned or unburned mineral soil on the two forests was not significantly different 3–5 years after the fire ($P = 0.365$).

Soil microsite conditions

As the decomposition process reflects the biotic and the abiotic properties in and around the individual wood stake, we assessed the effect of wildfire on soil microsite conditions by comparing the variability (standard deviations) of surface and mineral soil stake mass loss for 5 years in both the burned and unburned plot. As shown in Table 5, microsite mass loss variability generally increased as wood decay increased, but reflects differences between wildfires, stake location, wood species and forests. Except for aspen on the BNF, mass loss variability of surface stakes on the burned soil was much less than at the unburned forest floor–mineral soil interface. However, when averaged across all 5 years, the differences were not significant.

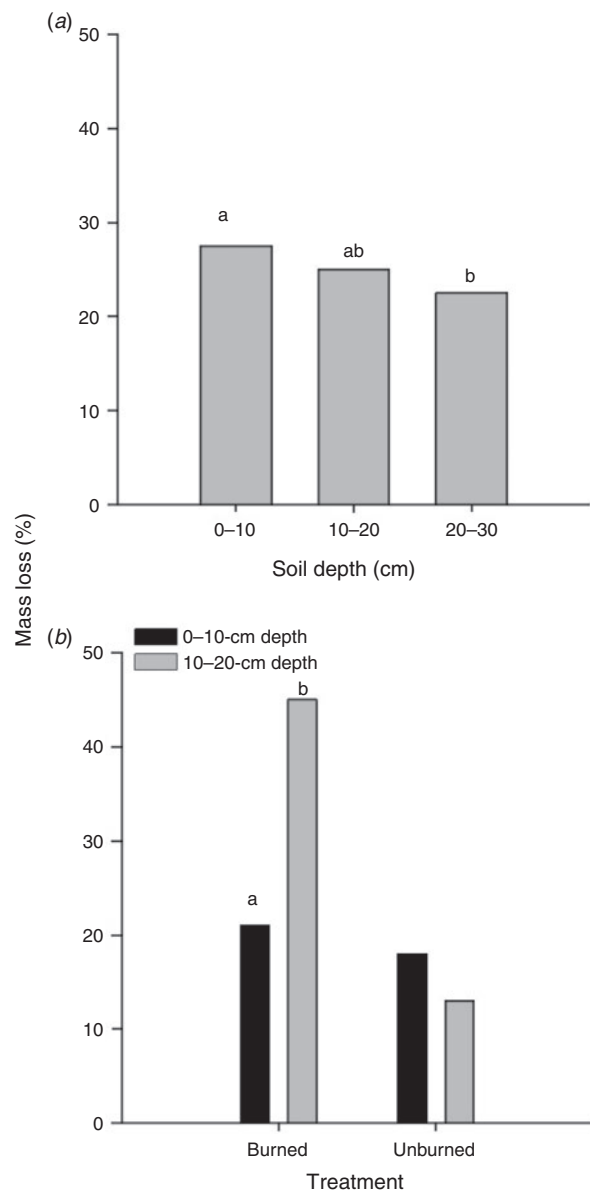


Fig. 3. Mass loss of wood stakes at different soil depths for: (a) aspen stakes averaged across wildfire, unburned plots and sampling years on the Bitterroot National Forest; and (b) pine stakes in wildfire and unburned plots averaged across sampling years on the Gallatin National Forest. Different letters indicate significant differences among or between soil depths at $P \leq 0.05$.

In contrast, wood stake mass loss variability was considerably greater in burned mineral soil. Aspen mass loss variability on the BNF was greater in burned than in unburned mineral soil in the first 2 years ($P = 0.015$ and $P = 0.009$ respectively) and for pine stakes in the last 2 years of the study ($P = 0.009$ and $P = 0.033$). When averaged across the 5 years, mass loss standard deviations in burned mineral soil were significantly greater for aspen stakes on the BNF ($P = 0.016$) and for pine stakes on the GNF ($P = 0.026$). We did not estimate mineral soil aspen mass loss variability on the GNF owing to the low number of stakes sampled in 3 of the 5 years.

Stake moisture content

Unfortunately, we were unable to obtain adequate information on mineral soil water content during the study, but wood stake moisture content is an indicator of soil moisture levels before the stake extractions. As shown in Table 6, both aspen and pine stakes on the GNF burned soil surface were drier than on the BNF. As expected, the stakes at the unburned litter layer–mineral soil interface had the highest moisture content. In contrast, both the aspen and pine stakes in the burned mineral soil of both forests were significantly wetter than stakes in the adjacent unburned soil. Although wood stake water contents are a function of the precipitation and temperature regimes in each forest (Table 1), they also reflect mass loss differences, as faster stake decomposition in burned mineral soil would increase wood porosity and water-holding potential.

Discussion

Decomposition

Wood stakes

As we hypothesised, the results of our study showed that wood decomposition was more rapid in the mineral soil after wildfire than in adjacent unburned stands. However, contrary to our expectations, decomposition of wood stakes placed on the surface of burned soils was less than or similar to stakes on the litter surface or at the litter layer–mineral soil interface in the unburned stands. Similarly to our study, O'Lear *et al.* (1996) showed that wood dowels decayed faster in the mineral soil of a burned tallgrass prairie than in an unburned soil. However, as noted earlier, we could find little else describing fire impacts on wood decomposition on the soil surface or in mineral soil.

In contrast, many fire–OM decomposition studies have been conducted using surface litter bags, which have given widely differing results. For example, Stark (1977) and O'Connell and Menage (1983) reported tree litter (leaves and needles) decomposed faster after fire, which was attributed to warmer soil conditions and changes in soil chemical properties, particularly N cycling. Meanwhile, Springett (1976), Raison *et al.* (1983, 1986), and Monleon and Cromack (1996) found prescribed fires lowered decomposition rates owing to a thinner forest floor and higher aridity.

Decomposition of OM is generally controlled by the interactions of soil physical, chemical and biological properties, and any one or more of these may constrain or enhance decay (Lavelle *et al.* 1993; Sollins *et al.* 1996). As we predicted, increased mineral soil temperatures after fire were a major factor in wood decomposition on both forests, but it was more pronounced on the GNF, where fire increased degree days $>10^{\circ}\text{C}$ by 42%, as compared with a 25% increase on the BNF. Such temperature-dependent decomposition results are consistent with pine wood stake mass loss in a temperature gradient study from northern Finland to southern Poland (Jurgensen *et al.* 2006). There has been much discussion on the importance of temperature on the decomposition of soil OM (e.g. Davidson *et al.* 2000; Giardina and Ryan 2000; Thornley and Cannell 2001; Bellamy *et al.* 2005). However, the focus of many studies has been on soil respiration or turnover rates of different mineral soil OM fractions (e.g. Reynolds and Hunter 2001; Knorr *et al.* 2005b; Waldrop and Harden 2008), which are

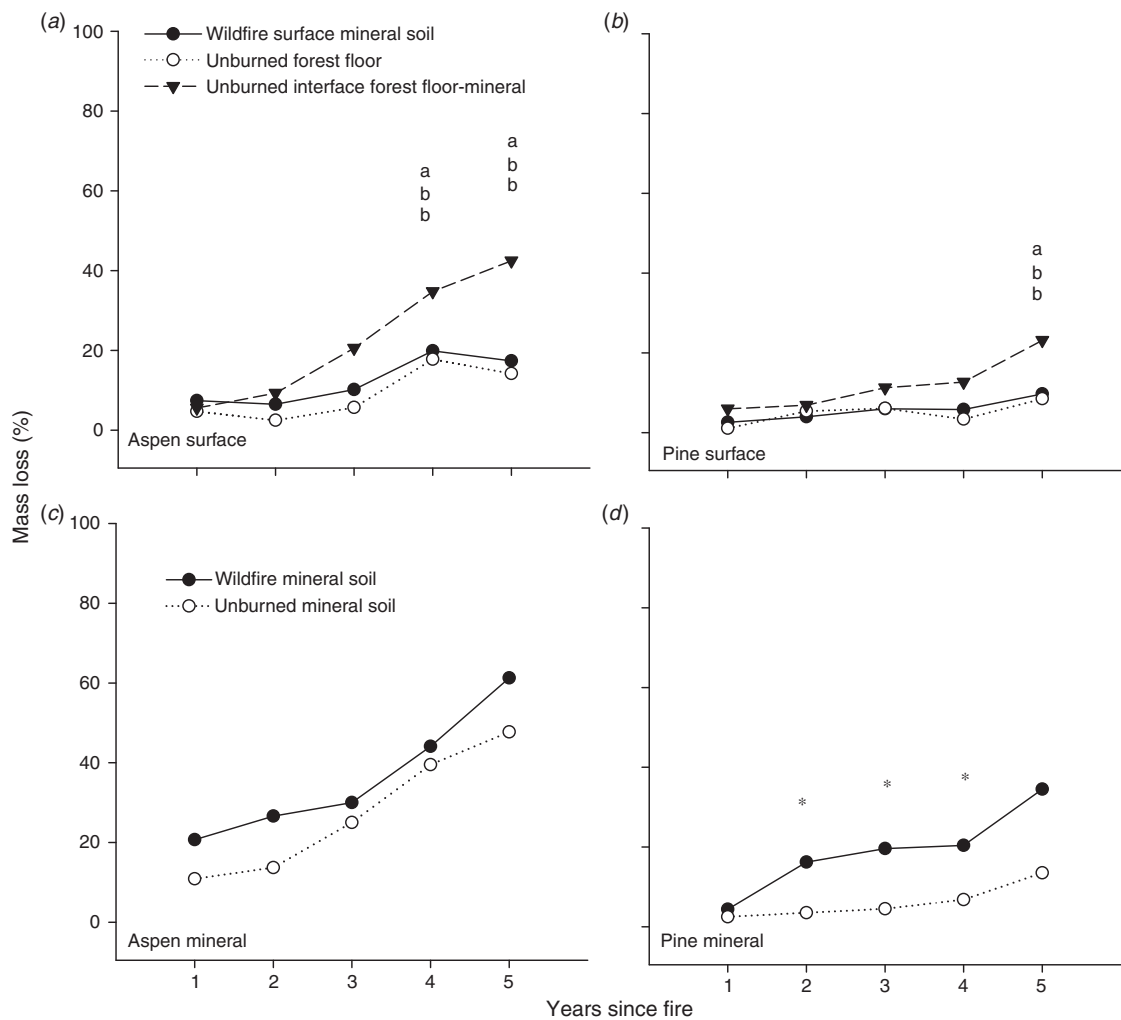


Fig. 4. Mass loss of aspen and pine wood stakes in burned and unburned adjacent plots on the Gallatin National Forest for: (a) surface aspen; (b) surface pine; (c) mineral aspen; and (d) mineral pine. For each year after the fire, wildfire stake mass loss values with letters (surface stakes) or asterisks (mineral stakes) are significantly different from the control stake weight loss at $P \leq 0.05$.

Table 4. Aspen and pine wood stake mass loss in burned and unburned mineral soil (0–20-cm depth) 2 to 5 years after wildfires on the Bitterroot and Gallatin National Forests (NFs)
Values followed by an asterisk are significantly different ($\alpha \leq 0.02$) between the Bitterroot and Gallatin National Forests

Years after fire	Treatment	Aspen mineral		Pine mineral	
		Bitterroot NF	Gallatin NF	Bitterroot NF	Gallatin NF
		Percentage			
2	Wildfire	— ^A	—	3.5	15.6*
	Unburned	5.7	12.7	5.0	3.5
3	Wildfire	—	—	11.0	19.6
	Unburned	7.5	2.0*	2.4	4.5
4	Wildfire	—	—	13.9	20.4
	Unburned	14.4	39.5*	6.7	6.8
5	Wildfire	—	—	23.4	31.5
	Unburned	21.1	47.2*	10.2	13.5

^ANo comparison owing to erosion loss of aspen stakes on the Gallatin NF.

Table 5. Changes in standard deviation of aspen and pine surface and mineral soil stake mass loss in burned and unburned plots over the 5-year study: (a) Bitterroot National Forest (NF); (b) Gallatin National Forest

Asterisks indicate a significant difference at $\alpha = 0.05$ between stakes in the burned and unburned soil within years

(a) Bitterroot NF surface stakes						
Species	Treatment	Years after fire				
		2	3	4	5	6
Aspen	Wildfire – surface	0.049	0.107	0.173	0.173	0.220
	Unburned – interface	0.025	0.048	0.054	0.168	0.201
Pine	Wildfire – surface	0.020	0.026	0.062	0.028	0.077
	Unburned – interface	0.031	0.076	0.056	0.131	0.150
Mineral soil stakes						
Species	Treatment	Years after fire				
		2	3	4	5	6
Aspen	Wildfire	0.100*	0.175*	0.205	0.187	0.181
	Unburned	0.035	0.024	0.063	0.107	0.157
Pine	Wildfire	0.033	0.079	0.097	0.216*	0.252*
	Unburned	0.037	0.046	0.044	0.050	0.104
(b) Gallatin NF surface stakes						
Species	Treatment	Years after fire				
		1	2	3	4	5
Aspen	Wildfire – surface	0.040	0.054	0.064	0.078	0.046
	Unburned – interface	0.054	0.065	0.182	0.201	0.229
Pine	Wildfire – mineral	0.015	0.008	0.026	0.022	0.048
	Unburned – interface	0.041	0.054	0.101	0.096	0.177
Mineral soil stakes						
Species	Treatment	Years after fire				
		1	2	3	4	5
Aspen		— ^A	—	—	—	—
Pine	Burned	0.040	0.178	0.106	0.179	0.189
	Unburned	0.029	0.030	0.061	0.056	0.092

^ANo comparison owing to erosion loss of aspen stakes on the GNF.

likely affected by a different suite of microorganisms and soil properties than those active in the initial turnover of ‘fresh’ OM, such as wood stakes used in our study (Larionova *et al.* 2007).

Although we were not able to measure soil water in our study plots, higher water content in stakes from burned mineral soil indicates that increased water availability could also be a factor in decomposition after a fire. However, slower aspen stake decomposition from 0–10-cm soil depth than at 10–20 cm in the burned GNF mineral soil indicated higher soil temperatures may have lowered surface soil moisture contents and reduced the wood decay rate. Prescott *et al.* (2017) reported that litter bags containing residual forest floor materials decomposed 5–15% more slowly on the soil surface after harvesting and site preparation than litter bags buried 5–10 cm in the mineral soil because of drier surface soil. Rovira and Vallejo (2002) also found that litter bags containing fresh leaves, brown litter or pine needles had slower decomposition rates near the soil surface

(5 cm) than at the 20- and 40-cm soil depths, which they attributed to drier surface soil conditions.

Water was also a likely factor in the lower than expected decomposition of stakes on the surface of the burned soils. We assumed higher amounts of precipitation reaching the soil surface after a wildfire, combined with decreased water uptake by roots, would result in higher water contents in the burned soils, and a greater diffusion of water into the wood from the underlying mineral soil. However, the water content of stakes from the surface of the burned soils was lower or similar to the water content of stakes on the litter surface or at the litter–soil interface in the unburned stand. This indicated the water evaporation rate from the wood on the soil surface was faster than could be supplied by diffusion or the surface mineral soil was drier after the fires than the unburned soil. Unfortunately, we were unable to obtain adequate soil water data to answer this question.

In addition to soil temperature and water, changes in soil microbiology could also affect OM decomposition after fire. High-severity fires can significantly reduce soil microbial biomass near the soil surface, especially the abundance or heat tolerance of fungi (Robinson and Bougher 2003; Smith *et al.* 2005; Holden *et al.* 2013; Glassman *et al.* 2016) owing to the direct effect of heat transfer (Cairney and Bastias 2007) and indirect effects on soil physical and chemical properties (Neary *et al.* 1999). When microbial population diversity and function are altered, the return to the pre-burn microbial community may be slow (Reazin *et al.* 2016), often requiring more than a decade (Dooley and Treseder 2012; Holden *et al.* 2013; Oliver *et al.* 2015). However, if there were any long-term changes in the soil microbial communities in our fire-affected soils, they were not detrimental to the activity of wood decay fungi.

Higher mineral soil N content after both wildfires could have increased wood stake decomposition. However, litter decomposition in Minnesota was not altered by prescribed fire or decreased N availability; rather, it was the indirect effect of fire frequency that altered decomposition rates (Hernández and Hobbie 2008). Reduced soil acidity (higher pH) after fire would also affect microbial community structure and activity (e.g. El-Abyad and Webster 1968; Certini 2005; Hart *et al.* 2005; Hamman *et al.* 2007), and decrease soil OM decomposition (Bååth *et al.* 1995; van der Wal *et al.* 2015; Fravolini *et al.* 2016). Surface and mineral soil pine stakes on both wildfire sites consistently decayed more slowly than aspen, which is similar to the results from other wood stake studies (Risch *et al.* 2013; Finér *et al.* 2016) and from surface woody residue decomposition studies (Weedon *et al.* 2009; Russell *et al.* 2014). Pine wood has higher lignin concentrations and C:N ratios than aspen, which have been correlated with lower wood decomposition rates (Laiho and Prescott 1999; Weedon *et al.* 2009; Wang *et al.* 2018).

Microsite variability

Differences in wood stake decomposition reflect the abiotic (e.g. temperature, water content, pH, N content) and biotic (e.g. microbial community, microbial biomass) properties of soil microsites around each individual stake. Therefore, we used the standard deviation of stake mass loss to estimate if fire-induced changes in soil microsites affected wood decomposition. Differences in mass loss among stakes increased as wood

Table 6. Moisture content of aspen and pine surface and mineral soil stakes in burned and unburned plots on the Bitterroot (BNF) and Gallatin National Forests (GNF) (averaged over 5 years)Asterisks indicate a significant difference at $\alpha = 0.05$ between forests for the same treatment and location

(a) Surface soil						
Species	Forest	Treatment	Location	Wood moisture content		P-value
				Average (%)	Range (%)	
Aspen	BNF	Wildfire	Soil surface	41.1a*	1–140	0.0002
		Unburned	Litter surface	31.3b*	1–60	
			Soil surface	48.4a	2–94	
	GNF	Wildfire	Soil surface	28.3a*	4–92	<0.0001
		Unburned	Litter surface	42.1b*	11–125	
			Soil surface	52.4b	1–205	
Pine	BNF	Wildfire	Soil surface	55.3a*	4–103	<0.0001
		Unburned	Litter surface	52.4a	4–123	
			Soil surface	65.0b	5–149	
	GNF	Wildfire	Soil surface	45.7a*	21–90	<0.0001
		Unburned	Litter surface	52.1a	12–123	
			Soil surface	62.7b	20–110	

(b) Mineral soil						
Species	Forest	Treatment	Location	Wood moisture content		P-value
				Average (%)	Range (%)	
Aspen	BNF	Wildfire	Mineral soil	94.9	43–157	0.0003
		Unburned	Mineral soil	55.2	27–100	
	GNF	Wildfire	Mineral soil	50.8	22–53	0.006
		Unburned	Mineral soil	32.8	16–65	
Pine	BNF	Wildfire	Mineral soil	89.8	41–162	0.04
		Unburned	Mineral soil	73.3	29–128	
	GNF	Wildfire	Mineral soil	73.9	54–86	0.003
		Unburned	Mineral soil	51.2	36–64	

decomposition progressed, especially in the mineral soil, but microsite variability was much larger in burned soil than in unburned soil. Many interrelated factors regulate OM decomposition within a given site, and large-scale climate variables may not be the main driver after high-severity fires (Prescott 2010; Fravolini *et al.* 2016; Bradford *et al.* 2017).

Small, localised differences in fire severity could cause pronounced microsite variability in soil OM, C and N content, pH, and microbial community structure (Baird *et al.* 1999; Hatten *et al.* 2005; Woods *et al.* 2007). High-severity wildfires increase mineral soil hydrophobicity, which would produce small-scale differences in water infiltration rates (Woods *et al.* 2007). Robichaud *et al.* (2016) found fire-induced hydrophobicity in burned soils on the BNF, which could have affected wood stake decomposition, particularly in the first year after the fire. In a European litter bag study, Bradford *et al.* (2017) found that the moisture–decomposition relationship was strongly scale-dependent. Differences in rock content can also cause variation in the spatial distribution of nutrients and OM released from burned-surface organic horizons into fine soil fractions (McNabb *et al.* 1986).

Conclusions

We show that wood decomposition in mineral soil can be quite rapid after a high-severity wildfire in two Montana forests.

As we hypothesised, higher mineral soil temperatures in the burned area were a major factor in faster wood decomposition in both forests. However, higher soil temperatures in the GNF soils likely lowered surface soil water levels, which reduced wood decomposition. Understanding wood decomposition changes associated with wildfire in these and other forest ecosystems is critical for adequately modelling climate change and C sequestration. Furthermore, we show that wildfire creates both fine and broad spatial scale variability in soil processes and these changes are important for determining ecosystem responses. The use of wood stakes as an index of soil microsite variability allowed us to assess wildfire impacts on OM decomposition both within and between site, and the factors affecting the decomposition process. Fire impacts on wood decomposition are also critical to understanding site-specific changes in soil C, the factors that control decomposition and how they are affected by forest management.

Conflicts of interest

The authors declare that there are no conflicts of interest.

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