

Disturbances, Their Interactions, and Cumulative Effects on Carbon and Charcoal Stocks in a Forested Ecosystem

Brian Buma,^{1*} Rebecca E. Poore,² and Carol A. Wessman²

¹*Department of Natural Sciences, University of Alaska Southeast, 11120 Glacier Highway, Juneau, Alaska 99801, USA;* ²*Department of Ecology and Evolutionary Biology & The Cooperative Institute for Research in Environmental Sciences, University of Colorado, Boulder, Colorado 80309, USA*

ABSTRACT

Disturbances have a strong role in the carbon balance of many ecosystems, and the cycle of vegetation growth, disturbance, and recovery is very important in determining the net carbon balance of terrestrial biomes. Compound disturbances are phenomena of growing concern which can impact ecosystems in novel ways, altering disturbance intensity, severity, and recovery trajectories. This research focuses on carbon stocks in a compound disturbance environment, with special attention on black carbon (charcoal), a potential source of long-term carbon sequestration. We report on a well-studied compound disturbance event (wind, logging, and severe fire) in a Colorado, USA subalpine forest that was extensively surveyed for impacts on carbon, black carbon, and regeneration. All major pools were considered, including organic and mineral soil (10 cm depth), and contrasted with

neighboring undisturbed forests as a reference. The disturbances had an additive effect on carbon loss, with increasing numbers of disturbances resulting in progressively decreasing carbon/black carbon stocks. This resulted from lower substrate availability and higher fire intensity. Surprisingly, there was no significant difference between reference and burned plots in terms of total black carbon. It appears that high-intensity fires do not significantly increase net black carbon in these forests (over the entire fire-return interval), with additional disturbances potentially resulting in a net loss. Disturbances, and their interactions, will have long-lasting legacies for carbon and black carbon.

Key words: multiple perturbations; compound disturbance interactions; carbon sequestration; charcoal; resilience; black carbon stocks.

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*Corresponding author; e-mail: brian.buma@uas.alaska.edu

INTRODUCTION

Disturbances have a strong role in the carbon (C) balance of many ecosystems, and it is vital to consider disturbances when calculating the C uptake and loss from terrestrial vegetation (Running 2008). C balance is a fundamental characteristic of ecosystems, and important to global climate and circulation patterns; the disturbance and recovery of forests, which cover approximately 4.17 Mha

globally and contain 1,240 Pg C in the biomass and soil (Lal 2005), are particularly important to regional and global C budgets. However, disturbances are increasing (Dale and others 2001). For example, North America is expected to see increases in fire likelihood (Moritz and others 2012) and longer fire seasons (Westerling and others 2006) with increasing climatic shifts. Background tree mortality is increasing as well, with changing climate being the likely cause (van Mantgem and others 2009). These increases in disturbance frequency and/or size distribution will result in increased amounts of overlapping disturbances, compound disturbance interactions, and an increased potential for “ecological surprises” (Paine and others 1998), meaning shifts in regime, lack of recovery, or other results not expected from either disturbance alone (for example, Kulakowski and Veblen 2007; Buma and Wessman 2011).

Compound disturbances are useful phenomena for study. First, they present a means to identify specific mechanisms by which species-level resilience is reduced or enhanced (Buma and Wessman 2012; Buma and others 2013), which aids in determining under what future conditions forests are likely to be resilient (or not) to disturbance. They also provide a window into a future where disturbances are potentially more prevalent (Dale and others 2001; Westerling and others 2006) and larger (for example, fire: Holden and others 2007).

Fires are one of the most common and destructive of natural disturbances, and strongly impact C cycling. On average, fires affect approximately 383 million ha year⁻¹ globally and release 2,078 T_g C year⁻¹ (Schultz and others 2008). Yet recovery from fire to a similar ecosystem state with a similar pre-disturbance biomass makes a burned landscape essentially C neutral, although it may be a protracted process to achieve that balance (Kashian and others 2006; Chapin and others 2006) and rates may vary spatially across the landscape (Kashian and others 2013). More frequent, short-interval fires are often associated with regime shifts (Donato and others 2009; D’Amato and others 2011; Brown and Johnstone 2012; Buma and others 2013) and C stock changes (Kashian and others 2006; Brown and Johnstone 2011; Bradford and others 2012).

There are several important C pools in post-disturbance ecosystems. *Detrital pools* (for example, woody debris) are, for the most part, degraded over time and released as CO₂. Regenerating C in *living biomass* will be maintained longer and increase as plants grow. *Soil pools*, both organic and mineral, are relatively slow to change and can hold large

amounts of C, although spatially heterogeneous (Lal 2005). All of these pools are subject to modification by future (compound) disturbances; for example, post-disturbance detritus (insect mortality, windthrow) may be partially lost to the atmosphere via combustion (fire), removed from the system (logging), or redistributed on the landscape (landslides).

There is a fourth C pool associated with fires that is extremely recalcitrant to degradation and potentially represents a long-term C sink: *charcoal*. As a thermochemically reduced C material, charcoal is less vulnerable to abiotic and biotic decomposition, and some have hypothesized that charcoal may be potentially useful in efforts to counteract rising atmospheric CO₂ emissions by functioning as a long-term C sink (DeLuca and Aplet 2008; Lehmann and others 2006; Czimczik and Masiello 2007). The global formation of charcoal is significant, estimated at 50–270 T_g year⁻¹ (Forbes and others 2006), but the extent to which charcoal may accrue on the landscape post-fire is relatively unknown. Fire intensity and duration can affect the quantity and chemical composition of charcoal formed in a fire (Forbes and others 2006), as can fuel load/type/condition, weather conditions, and substrate heterogeneity (Schmidt and Noack 2000). The chemical composition, in turn, can affect how resistant charcoal is to decay (Forbes and others 2006). We term the portion of charcoal that is resistant to decay, and therefore potentially a long-term C sink, “black carbon” (BC) and refer to the mass or volume of charred material as “charcoal.”

We explore two fairly novel aspects of post-disturbance C budgets: The influence of compound disturbances on C pools in the landscape, and the contribution of black C (charcoal) to those budgets. We consider the overlap of wind, logging, and fire disturbances, but are concerned with the more general question of the fate of C following severe fire in landscapes disturbed by recent, large-scale events. We ask the following questions:

Q₁: How do compound disturbances affect C pools in the forest system?

Q₂: How are post-fire charcoal/BC stocks altered by pre-fire disturbance history, and how much (relative to reference plots) are BC stocks increased post-fire?

METHODS

The study area is in north central Colorado, USA, in the subalpine forests of the Park Range north of Steamboat Springs (Figure 1), ranging from 2,500 to 3,300 m ASL and dominated by a mix of

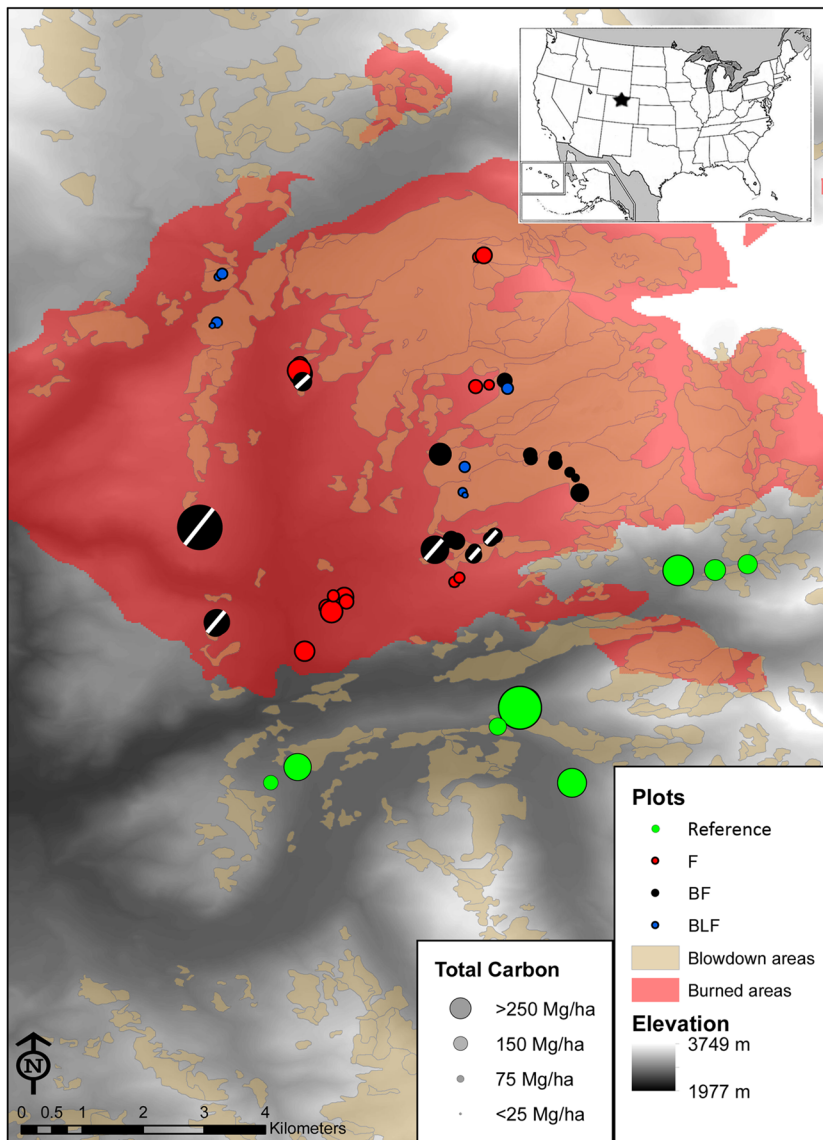


Figure 1. Map of the study area and location in the contiguous United States. *Points* represent plots. *Colors* refer to disturbance history. All plots except reference plots were located in areas of high fire severity (see “[Methods](#)”). Plots are shown as *circles*, with the size corresponding to total C (including black C). Blowdown + fire sites marked with a *white slash* had less than 43 downed trees ha^{-1} prior to the fire and were only included in the gradient analysis (Color figure online).

Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), lodgepole pine (*Pinus contorta*), and quaking aspen (*Populus tremuloides*). *Engelmann spruce* and subalpine fir compose the dominant overstory in undisturbed areas, with lodgepole pine dominating at slightly lower elevations, xeric sites, and in many post-burn areas (Buma and Wessman 2012). Quaking aspen is typically an early successional species, although it can form stable, self-replacing stands if Engelmann spruce or subalpine fir do not establish in the understory. Soils are classified as Cryochrepts and Dystrocryepts (USDA Forest Service 1999) from glacial deposits, pre-cambrian granites, and gneiss (Snyder and others 1987).

A series of large, severe disturbances hit the area from 1997 to 2002. In October 1997, an early

season blizzard and windstorm impacted approximately 10,000 ha of forest on the western slopes of the Park Range, the largest blowdown in recorded southern Rocky Mountain history with wind speeds estimated over 200 kph (Baker and others 2002). After the blowdown, salvage logging was conducted on approximately 935 ha of the high severity blowdown areas (Rumbaitis-del Rio 2006). Finally, in 2002, a large wildfire (the Mt. Zirkel complex, ~12,500 ha) burned through portions of the undisturbed forest, the blown down area, and the logged blowdown landscape. The fire was more likely to be high severity in areas of blowdown (Kulakowski and Veblen 2007), and the interactions had an impact on modeled fire intensity and post-fire conifer resilience (Buma and Wessman 2011).

Disturbance Histories

To investigate the various responses of C and charcoal pools to different disturbance histories, a total of 56 plots (each 15×15 m, referred to as “treatments”) were established: undisturbed (“R,” $n = 10$), fire-only (“F,” $n = 14$), blowdown + fire (“BF,” $n = 10$), and blowdown + logging + fire (“BLF,” $n = 8$), and additional blowdown–fire gradient plots ($n = 14$, see below). Fire-only plots had no recorded history of prior blowdown or logging. The blowdown + fire treatment was limited to areas that saw more than 50% of the trees blown down in the 1997 event to provide distinction between it and the fire-only treatment. Because percentages do not lend themselves to mechanistic interpretations (due to variance in stand density), this was converted to 43 blown down trees ha^{-1} , which is the 50th percentile of blowdown observed over all plots (see Baker and others 2002 for the blowdown severity map). All salvage-logged plots were located in areas of high blowdown severity (> 60 downed trees ha^{-1}), and all had the majority of their downed woody debris removed prior to the fire. A blowdown gradient of 38 plots, from 0 downed to 74 downed trees ha^{-1} (includes all F and BF plots), was used for the blowdown–fire gradient analysis of BC. See Appendix 3 in Electronic Supplementary Material for a graphical representation.

Undisturbed reference plots were investigated to determine the baseline and net change in C/BC as a result of the disturbances relative to pre-fire conditions. These reference plots were all identified as similar composition and density to the burned area (prior to the fire, USDA Forest Service mapping), and were mature spruce–fir dominated, closed canopy forest within 5 km of the fire boundary.

To control for variation in fire severity, all plots (except reference plots) were located in areas of severe fire, which met three conditions: complete aboveground mortality, no surviving individuals within 100 m, and complete organic soil consumption. The first condition ensured all plots started from a similar successional state. The second controlled for the influence of residual stands on seedling density and species (see Buma and Wessman 2011 for further discussion on this point). The third condition meant that soil pools were comparable between burned plots, and that the organic soil layers were not driving differences between disturbed plots.

Total Carbon Methodology

We considered the following C pools: Living tree species, living coarse roots, dead standing trees,

dead coarse roots, coarse woody debris (CWD), ground cover, organic soil C, and mineral soil C (10 cm depth). BC methodology is explained separately.

Living Trees

All living trees were counted on each plot. Seedlings shorter than 1.5 m were measured for height and represent the entirety of the living trees on all the disturbed plots. Trees above 1.5 m on the reference plots were measured for height (Halöf digital clinometer) and diameter at breast height (DBH). Biomass was calculated via allometrics from Jenkins and others (2003) using the USFS growth model, the Forest Vegetation Simulator (FVS) with the Fires and Fuels Extension (FVS-FFE; Rebaun 2010), and assuming 50% C by mass (alternative allometrics considered in Appendix 4 in Electronic Supplementary Material). Living root biomass was obtained from the tree via allometric equations from Jenkins and others (2003).

Dead Standing Trees

In the disturbed plots, all standing dead trees (“snags”) were measured for DBH and height. Biomass was calculated using allometrics from Kozak and others (1969), which uses species-specific tapering equations to calculate volume, after adjusting DBH for the absence of bark by adding in species and size-specific bark thicknesses from FVS allometrics. The use of species-specific tapering equations, instead of Jenkins and others (2003) as in the living trees, was necessitated by the charcoal quantification (see below). Volume of broken and leaning snags was calculated by projecting an unbroken height via Robinson and Wycoff (2004), and then integrating up to the broken height via the tapering equations. To obtain biomass from the volume, we assumed 50% C by mass and 405 kg m^{-3} wood (Harmon and Sexton 1996). It was not practical to gain a direct estimate of dead roots based on the field survey, because many of the snags had fallen, been broken, or removed via the salvage logging, causing difficulties in determining what should contribute to the dead coarse root pool. We used the mean FVS-calculated coarse root biomass for the reference plots, and assumed all of those roots would be passed to the dead coarse root detrital pool as a result of the fire. Because the plots were measured 9 years after the fire, the estimated root biomass was decayed according to the FVS Central Rockies root decay rate of $4.25\% \text{ year}^{-1}$ for 9 years; this value was assigned to the disturbed plots as the initial dead

coarse root biomass. This is statistically conservative, reducing the variance between the treatments.

CWD

Two 15 m Brown's transects (Brown 1974) were used to calculate CWD at each plot, sound and rotten wood were calculated separately. Because the blowdown resulted in non-random alignment of downed trees (parallel to the wind direction), transects were oriented at right angles.

Ground Cover

Ten 1 m² quadrats were randomly located in each plot. For each quadrat, percent cover of forbs/*Vaccinium* spp. and graminoids were estimated. *Vaccinium* individuals were low lying (<10 cm height) and very sparse, and so were included with the forb species. There were no shrub species other than shrub-form aspen on any site. To determine biomass, 1 m² samples of continuous forb/*Vaccinium* ($n = 21$) and graminoid ($n = 22$) cover were destructively sampled down to ground level; sampling was conducted in July and August when biomass is at its peak. All biomass in the square meter was clipped, and subsamples of each were run on a Carlo Erba 1108 CHN analyzer ("CE1108") to determine percent C. This percent C and the average g m⁻² (dry mass) were used to calculate C mass in the forb/*Vaccinium* and graminoid cover (independently) for each plot, based on the means of the percent cover survey. These were summed to get the composite total for C in the non-tree species understory.

Organic Soil Carbon

Because the burned sites had no organic soil, sampling for this pool was limited to reference plots. Five soil cores were taken to determine bulk density of the organic horizon (fine and coarse fraction density were calculated separately); the cores were chilled until they could be dried at 105°C for 24 h and weighed (see Appendix 1 in Electronic Supplementary Material). Five additional cores were taken for C analysis. Each core was homogenized in the field and a subsample taken. Samples were chilled until they could be dried (60°C/24 h) and sieved (2 mm mesh) in the lab. The organic fine fraction (<2 mm; O_{FF}) was ground and analyzed for percent C on the CE1108. The organic coarse fraction (>2 mm; O_{CF}) was sorted into charcoal, woody material, and rocks; woody material was assumed to be 50% C, and charcoal was run on the CE1108 to determine percent C (see "Charcoal/BC methodology" section).

The relative proportion of each was then multiplied by the coarse fraction bulk density and mean depth of the organic layer to determine areal C.

Mineral Soil Carbon

Ten cores, 10 cm deep from the organic–mineral soil interface were randomly located and extracted from each plot. This depth was chosen to match previous research in the area (for example, Morlingo-Bredlau 2009; Rumbaitis-del Rio 2006). Storing, drying, and sieving were the same as the organic soil methods. Mineral soil fine fraction (M_{FF}) areal C was calculated using fine bulk density measurements from Rumbaitis-del Rio (2004), which were measured on a subset of the sites used in this study. The mineral soil coarse fraction (M_{CF}) was sorted into charcoal, woody material, and rocks and processed in the same fashion as the organic soil. The relative proportion of each (coarse charcoal and woody material) was then multiplied by the coarse fraction bulk density (Rumbaitis-del Rio 2004) to determine the contribution of C in the coarse fraction. All bulk densities are available in Appendix 1 in Electronic Supplementary Material.

Charcoal/BC Methodology

Soil charcoal consists of fine fraction char (<2 mm) and coarse fraction char (>2 mm) in the mineral soil (all plots) and the organic soil (reference plots only); non-soil charcoal consists of charred material remaining on dead CWD and on dead snags. As noted above, not all charcoal can be considered BC, and so the calculations differed between those two categories. Charcoal percent C was calculated by analyzing coarse charcoal fragments on the CE1108; this percent was used in total C calculations. The percent of BC in the charcoal was determined via digestions.

Soil BC Percent, Fine Fraction (<2 mm)

Many methodologies exist for estimating BC in soils. Because of the diversity of charcoal compounds and their continuum nature, each method quantifies different portions of the continuum (Hammes and others 2007). Standardization between studies and methods is accomplished by use of a common reference char (described in Hammes and others 2008, available at www.geo.uzh.ch/phys/bc).

We used the KMD methodology for BC quantification (Kurth and others 2006) which uses a combination of hydrogen peroxide and weak nitric acid to chemically digest the charcoal. The KMD

method has been shown to be effective at the expected concentrations of C and BC in similar soils (Kurth and others 2006) and in other post-fire environments (Pingree and others 2012). Each sample of fine soil underwent digestion. The percent C of the post-digestion material was considered the recalcitrant, BC portion of the fine soil. This value was adjusted based on the mass lost in the digestion to avoid an upward bias due to loss of non-C material in the digestion. Methodological parameters, including incubation times, temperatures, mass loss correction, and the results of the reference char tests, can be found in Appendix 2 in Electronic Supplementary Material.

Soil Charcoal and BC, Coarse Fraction (> 2 mm)

After sorting, a subset of the charcoal was run on the CE1108 to determine total percent C of the coarse charcoal. Because charcoal fragments are not entirely BC, 14 subsamples of the coarse fragments were digested using the KMD methods as before. This percent BC was used to calculate BC totals, whereas the total percent C (undigested) was used when calculating total C. The coarse fraction (charcoal or charcoal-converted-to-BC) of each soil sample (10 per plot) was massed and converted to grams C, which was then converted to areal C or areal BC based on the coarse bulk density as described above. The methods were the same for the mineral and organic soils.

Non-soil Charcoal and BC

Charcoal on CWD was quantified using methods from Donato and others (2009). In essence, this is calculating a “rind” of charcoal around the uncharred inner part of the debris. The volume of char is converted to Mg ha^{-1} C by assuming 405 kg m^{-2} initial wood density (Harmon and Sexton 1996), 70% mass loss upon burning, and 75% C in the remaining mass (Donato and others 2009). We also noted the proportion of the circumference charred, as many pieces were not charred all the way around, and adjusted accordingly. For snag BC, we are aware of no standard methodology. The methods used in this study are as follows: For all snags on the plot, the presence of char at breast height was tallied. If char existed, its depth, proportion of the circumference, and height were noted. Height was calculated in the same way as for living trees. Total volume was calculated according to the methods presented above. Adjusting for the depth, height, and proportion of char gave the volume of the inner, uncharred core of the snag. The difference was the char volume, which was then converted into Mg ha^{-1} C using the same

coefficients as the CWD char and converted to BC totals using the same percent C as CWD.

Statistical Methods

Comparisons between all treatments were conducted via the Kruskal–Wallis rank sum test due to lack of normality in the data. If a treatment effect was found, pairwise comparisons between burned treatments (to determine any effect of compounding disturbances) were conducted with Wilcoxon rank sum tests, unless otherwise noted. Significance was set at $P < 0.05$, and the Holm (1979) method for adjusting P values was used to guard against Type I errors when appropriate. To investigate the relationship between compounding disturbances and charcoal, and the potential for increasing fire intensity to alter long-term BC stocks, we compared the pre-fire blowdown severity (downed trees ha^{-1}) to total plot-scale BC using quadratic linear regression. A quadratic regression was used to accommodate the potentially confounding effects of driving BC formation/consumption at different points on the interaction continuum. All analyses were conducted in R (R Development Core Team 2011).

RESULTS

Total Carbon (Table 1; Figure 2)

Overall, compounding disturbances reduced mean total C on the plots, with the highest number of disturbances corresponding to the lowest total C.

Living Trees

Differences in disturbance history caused significant differences in total stem density, including trees ($> 1.5 \text{ m}$) and seedlings ($< 1.5 \text{ m}$). Reference plots had significantly higher seedling densities, dominated by an abundant alpine fir understory. Density of Engelmann spruce seedlings was also significantly higher than the burned plots ($P < 0.05$). Among the burned plots, F and BLF were not significantly different in terms of overall seedling densities, although there was great variability. BF plots had significantly lower total seedlings compared to the BLF plots ($P < 0.05$) and moderately less than F plots ($P = 0.09$), driven by significantly lower aspen densities than BLF plots and significantly less lodgepole pine densities compared to F and BLF plots.

Living Tree Carbon

Reference plots had significantly higher above-ground live C in trees than in disturbed plots; little

Table 1. Pool Totals for Overall C (Mean C Mg ha⁻¹, Standard Deviation in Parentheses)

Disturbance history	Aboveground living trees	Living coarse roots	Snags	Dead coarse roots**	CWD	Forb/graminoid	Organic soil*	Mineral soil*	Mean total C
Fire-only (F) (n = 14)	0.09 (0.10) ^{1,2}	0.32 (0.37) ^{1,2}	18.62 (13.96) ¹	14.9 (0) ¹	19.36 (15.57) ¹	0.37 (0.18) ¹	0	36.28 (12.30) ¹	89.94 (25.31) ¹
Blowdown + fire (BF) (n = 10)	0.03 (0.02) ¹	0.14 (0.08) ¹	6.41 (9.36) ²	14.9 (0) ¹	20.75 (11.38) ¹	0.26 (0.07) ¹	0	38.45 (12.25) ¹	80.94 (27.35) ¹
Blowdown + logging + fire (BLF) (n = 8)	0.13 (0.10) ²	0.56 (0.46) ²	0.14 (0.35) ³	14.9 (0) ¹	7.62 (8.56) ²	0.29 (0.08) ¹	0	30.85 (9.82) ¹	54.49 (12.56) ²
Reference (n = 10)	80.74 (58.43) ³	17.81 (12.22) ³	17.34 (17.91) ¹	4.21 (3.31) ²	34.70 (18.35) ¹	0.35 (0.14) ¹	22.44 (8.95)	37.53 (9.64) ¹	215.12 (71.28) ³

Number of plots in each treatment shown; each plot contained ten individual samples. Superscript refers to significance groupings. C totals associated with the same superscript are not significantly different.

* Fine and coarse fractions; see text for individual totals.

** See "Methods."

total C is currently found in living trees in the disturbed areas. Reference plots had significantly more C than all the disturbed plots, and BLF plots were significantly higher than BF plots.

Snags and Dead Root Carbon

There was no significant difference between reference and F plots. BF plots were significantly lower than reference and F, and BLF the lowest of all the treatments. Reference plots had 4.21 Mg ha⁻¹ C in dead coarse roots. For the other plots, a value of 14.9 Mg ha⁻¹ was assigned (sum of living and dead coarse roots in reference plots, and after decaying from 2002 to 2012). This was significantly more than the reference plots dead roots total.

CWD

BLF plots had the lowest CWD levels, as a result of the salvage logging removal. F and BF plots were not significantly different. Mean CWD C in reference plots was higher, on average, than the disturbed plots, but not significantly higher than F and BF.

Groundcover Carbon

Forbs/*Vaccinium* contained 42.5% C, with a density of 179.1 g m⁻² dry weight. Graminoids contained 43.0% C, with a density of 164 g m⁻² dry weight. Combined with the cover measurements, there was no significant difference between any of the treatments.

Soil Carbon

Coarse fraction charcoal contained 56.7% C. The organic soil contained 22.44 Mg ha⁻¹ C in the reference plots, split between the fine (19.51 Mg ha⁻¹, SD = 8.69) and the coarse (2.93 Mg ha⁻¹, SD = 1.56) fractions. There were no significant differences between total mineral soil C for any of the treatments ($P = 0.06$), or between fine or coarse subsets. On average, F plots contained 30.84 Mg ha⁻¹ fine (SD = 10.80) and 5.43 Mg ha⁻¹ coarse C (SD = 3.05), BF plots 33.15 Mg ha⁻¹ fine (SD = 9.29) and 5.30 Mg ha⁻¹ coarse C (SD = 3.69), BLF plots 24.24 Mg ha⁻¹ fine (SD = 5.85) and 6.61 Mg ha⁻¹ coarse C (SD = 5.80), and R plots 31.95 fine (SD = 9.81) and 5.58 Mg ha⁻¹ coarse C (SD = 2.59).

BC Results (Table 2; Figure 3)

Overall, increasing numbers of disturbances resulted in decreasing net BC increase over reference plots; however, the differences between disturbance histories were slight. Charcoal was 38.6% BC

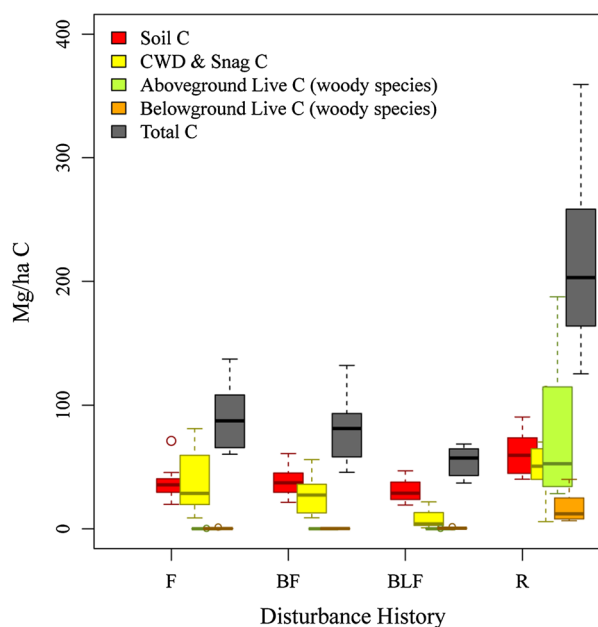


Figure 2. Total C and pool sizes for each disturbance history. Soil and dead material (snag and CWD) dominate the disturbed stands, although increasing layers of disturbance result in decreasing totals. Reference stands are a mix of living and dead, with significantly more total C. Groundcover not shown, as they were a small pool and not significantly different between the plots. *F* fire, *BF* blowdown + fire, *BLF* blowdown + logging + fire, *R* reference (undisturbed).

by mass, determined via digestions; detailed results and the reference char digestions are in Appendix 2 in Electronic Supplementary Material.

CWD and Snag BC

No BC was found on CWD in reference sites. Burned plots were not significantly different from each other, although BF plots had marginally more BC than the other burned treatments (vs. *F*, $P = 0.12$; vs. *BLF*, $P = 0.055$). Although many snags were charred, the total BC was small, and there was no significant difference between the treatments.

Mineral Soil BC

There was significantly less BC in the M_{FF} in reference plots when compared to *F* and *BF* plots, although not when compared to *BLF* ($P < 0.05$). *BF* and *BLF* plots were not significantly less than *F* plots when compared directly. There were no significant differences between M_{CF} averages regardless of treatment.

Organic Soil BC

Reference plots contained on average 1.29 Mg ha^{-1} BC in the fine portion of the organic horizons, and

0.27 Mg ha^{-1} BC in the coarse fraction. Because we only examined areas of severe fire, the burned plots had no organic soil.

Relationship Between Compound Disturbances and Charcoal

The entire gradient of pre-fire blowdown severities (downed trees ha^{-1}) was regressed against total BC. There was no significant relationship ($P > 0.05$, *F* and *BF* plots only). High plot-level variability was found all along the gradient (see Appendix 3 in Electronic Supplementary Material for plot-level BC results and blowdown severity contrast).

DISCUSSION

Q₁: How Do Compound Disturbances Affect Carbon Pools in the Forest System?

Increasing layers of disturbances resulted in progressively lower total C stocks in these highly disturbed locations. Fire plots saw $\approx 58\%$ decrease in C stocks relative to the reference plots, in large part due to the complete loss of the soil organic layer. A similar study of compound disturbances and C in the southern boreal forests saw less of a reduction (approx. 30%, Bradford and others 2012). However, their results only considered the top 10 cm of soil, whereas the results presented here consider the entirety of the organic soil layer, whatever depth, and the top 10 cm of the mineral soil. This could account for the discrepancy. Other studies in the boreal (for example, Lynch and others 2004; Clark and others 1998; and Czimczik and Masiello 2007, summarized in Forbes and others 2006) showed losses approaching 50%. *BF* plots contained lower C than *F* plots, indicating that the blowdown-fire combination produced a more intense disturbance (in terms of C stocks), as suggested by modeling results showing higher temperatures and longer fire residence times (Buma and Wessman 2011).

The *BLF* plots had the lowest C (a 75% reduction compared to reference plots) as a result of salvage logging operations that directly removed woody material. There was also lower M_{FF} C in the *BLF* plots, which was partially balanced by increased coarse fraction C and higher live C, although it was highly variable (Figure 2). This could be a result of woody material incorporated into the organic and mineral soil during salvage logging operations (Morliengo-Bredlau 2009). Although there was significantly more living tree biomass in *BLF* plots compared to the other burned plots, resulting from

Table 2. Black C Pools (Mean Mg ha⁻¹, Standard Deviation in Parentheses)

Disturbance history	CWD*	Snag*	Mineral soil (fine)	Mineral soil (coarse)	Organic soil (fine)	Organic soil (coarse)	Total BC
Fire-only (F) (<i>n</i> = 14)	0.22 (0.22) ¹	0.01 (0.05) ¹	6.13 (1.75) ¹	0.87 (0.93) ¹	0	0	7.24 (1.97) ¹
Blowdown + fire (BF) (<i>n</i> = 10)	0.39 (0.22) ¹	0.01 (0.03) ¹	5.66 (1.77) ¹	0.92 (0.56) ¹	0	0	6.98 (2.00) ¹
Blowdown + logging + fire (BLF) (<i>n</i> = 8)	0.20 (0.12) ¹	0 (0)	4.59 (1.14) ^{1, 2}	1.46 (1.37) ¹	0	0	6.26 (2.22) ¹
Reference (<i>n</i> = 10)	0 (0)	0 (0)	3.49 (0.84) ²	0.90 (0.85) ¹	1.29 (0.66)	0.27 (0.32)	5.96 (1.95) ¹

Significance groupings shown via superscript numbers.

* Wilcoxon test performed between pools with some BC only. Organic soil was not present on any disturbed site. No char was present on CWD or snags in reference sites.

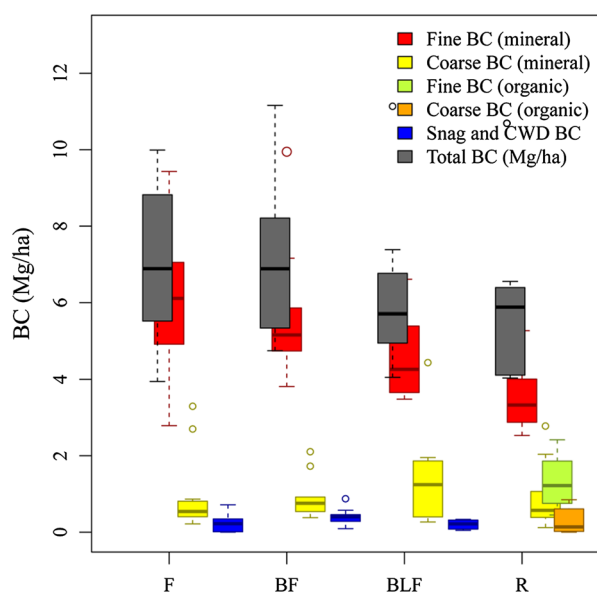


Figure 3. Total black C and BC distribution between the disturbance histories by components. Total BC increases with disturbances, although decreasing soil BC with increasing layers of disturbance is apparent. Reference plot BC in the organic layer is an important component, but does not balance out lower BC in the other pools. F fire, BF blowdown + fire, BLF blowdown + logging + fire, R reference (undisturbed).

heavy aspen establishment, it contributed relatively little to the overall C totals.

Overall, the differences in current total C stocks were driven first by the disturbances—all disturbed plots had less C than reference plots—and increasing number of disturbances resulted in less total C on the plots. This was mainly apparent in the CWD and snag pools. Lower C in these pools as a result of increased fire intensity (in BF plots) and as a result of human extraction (BLF plots) resulted in net lower C stocks compared to just fire.

At this in point in time, the contribution of tree regeneration to C is minor, but significant differences already exist (Table 1). Going forward, these

differences may grow via three mechanisms: different growth rates amongst those species, susceptibility to future disturbances, and climate change. Aspen is very fast growing, and thus the C recovery period may be shorter in plots with extensive aspen establishment due to their rapid C fixation (Buma and Wessman 2013). However, aspen litter is more rapidly degraded and may be more mobile, increasing losses due to leaching relative to conifer or graminoid cover types (Van Miegroet and others 2005), although the significance of that difference at large scales is still unknown. Aspen stands are less likely to be disturbed by wind (Baker and others 2002) and fire (for example, Fechner and Barrows 1976), so future disturbances may play less of a role, at least in the near term. In addition, climate change may alter species C fixation rates (Hu and others 2010). Therefore, the small, yet significant, differences in total C as a result of differential species composition may be exacerbated by different responses to climatic warming and the occurrence or severity of future disturbances.

Q₂: How are Post-fire Charcoal/BC Stocks Altered by Pre-fire Disturbance History?

Increasing disturbances lowered total BC, similar to total C. The hypotheses of decreasing BC were supported, although not significantly so—the only significant differences in BC were found between F and BF versus the reference plots in the mineral soil pool, and total BC was not significantly different between disturbance histories. Interestingly, this study found substantially more mineral soil BC than a recent study in the region (Licata and Sanford 2012) which used similar lab methodology; however, the lack of standards in that study precludes direct comparison.

Surprisingly, the total post-fire black C was not significantly higher than reference plots (Table 2; Figure 3), although a trend of decreasing BC with increasing layers of disturbances is apparent. This

suggests a potential balance between formation of BC, combustion of old BC, and decomposition. BC is formed during incomplete oxidation of woody biomass, and so should vary according to substrate availability and fire intensity. In terms of substrate, although the relationship between BC and total C was significant in the burned plots, it was weak ($P < 0.05$, $r^2 = 0.07$). Lower levels of BC in the BLF plots, however, suggest that lack of substrate could be preventing BC formation. In terms of fire intensity, Kane and others (2010) found higher levels of mineral soil BC on south facing slopes with less organic soil, which they interpreted to result from higher bulk densities on southern slopes promoting more smoldering combustion and lower fire intensity on northern slopes due to increased moisture. We could not investigate this directly in our burned sites, as the organic layer was completely combusted. There was no relationship between soil organic horizon thickness and total BC in our reference sites ($P > 0.05$, linear regression, \log_{10} transformed for normality), nor total BC and aspect ($P > 0.05$, linear regression) as in Kane and others (2010), however, this could result from the more intense fires typical of subalpine forests completely consuming the organic layer. High-intensity fires were also associated with less BC in Oregon (Pingree and others 2012) in the upper layers of the mineral soil, although they found increases in the organic layers post-fire. The trend toward lower levels in BF sites compared to F sites (Figure 3), where BF sites were more intense (higher temperatures, longer duration; Buma and Wessman 2011), support this consumption idea. The logging plots support a combined substrate/consumption hypothesis—they experienced high severity fire without large amounts of pre-fire C (the substrate for post-fire BC) and consequently retained the lowest BC of the disturbed plots (Figure 3).

If we only consider pre-fire C stocks (via the reference plots) and post-fire BC (fire-only plots, to eliminate compound disturbance effects), the percentage of combusted C-to-BC is approximately 6% (125.18 Mg ha⁻¹ C lost due to the fire, 7.24 Mg ha⁻¹ charcoal in burned plots). Considering only net increase in BC by subtracting out the BC already present on the unburned plots, the number drops to 1% (1.28 Mg ha⁻¹ difference in BC). This is slightly lower than the studies presented by the Forbes and others (2006) synthesis, which reports a range of 1.5–3.1% of consumed C being converted to BC in comparable settings. This could be due to the focus on high severity fire in this study. Further work on less severe fire scenarios

is needed to determine the relative balance between BC formation and consumption. Although rare in these ecosystems, less intense fires may produce more BC, especially fires which do not eliminate the organic soil.

The relative lack of differences between burned and unburned plots (in terms of BC) has interesting connotations for long-term BC dynamics. Because BC levels were only slightly elevated above reference plots, decay could be extremely slow and yet not produce an appreciable on-site C sink, and a long fire-return interval might result in a net loss of charcoal due to decay (relative to the unburned reference plots). A variety of decay rates for charcoal have been proposed in the literature (for example, Singh and others 2012a, b; Zimmerman 2010; Harden and others 2000; Kuzyakov and others 2009; Lehmann and others 2006), although a formal meta-analysis still needs to be conducted. Figure 4 presents these decay functions applied to our mean findings per disturbance history, compared to reference plot BC levels. Given that the typical fire regime is low frequency/high severity events (a compilation of fire rotation periods in N. Colorado reports estimate from 175 to 521 years, Baker 2009), this suggests that intense fires do not increase plot-level BC levels over the entire fire rotation period, but maintain it through the process of initial increase and subsequent decay. Multiple disturbances may reduce BC overall: BF plots will decay to unburned reference levels in about 175–325 years and BLF plots about 50–100 years. Thus, a loss of plot-level BC (over the entire disturbance return interval) may result from these multiple, interacting disturbances.

LIMITATIONS

As with all post-disturbance studies, several caveats exist. First, disturbance ecology is often an opportunistic field, and consideration of single event analysis, potential spatial autocorrelation, and other spatial effects must be acknowledged. The design here was intended to avoid these problems where possible, by using a gradient approach when appropriate (Parker and Wiens 2005), using a nested design with plot pairs isolated from each other (Buma and Wessman 2011), and only using published information on pre-fire conditions. We make the assumption that initial differences between sites were minimal and that burned sites were similar to the reference sites prior to the disturbances; this assumption is supported by prior USFS mapping which identified all locations as closed canopy coniferous forest (*unpublished data*).

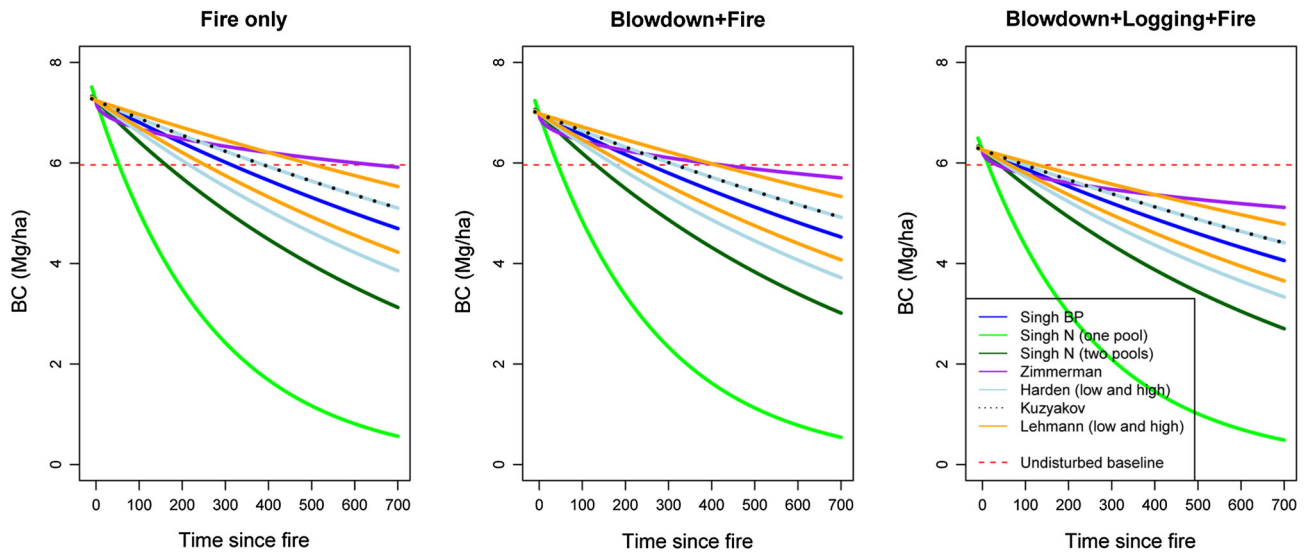


Figure 4. Literature-derived decay rates applied to the plot means for each disturbance history, and compared to the neighboring, undisturbed forest plot mean. The time at which each decay curve crosses the reference line (*horizontal, red dashed line*, representing the mean of the undisturbed plots) would be the time required to maintain a steady level of BC in the ecosystem, assuming similar fire characteristics in terms of production, consumption/emission, and subsequent erosion.

We cannot quantify surficial losses of BC, although experimental burning suggests it is minimal, at least initially (Lynch and others 2004). The sites were located in areas of minimal slope, limiting erosion (there was no relationship between BC totals and slope). Convective loss to the atmosphere during the fire event cannot be quantified, although the synthesis of Forbes and others (2006) indicates that it is likely less than 20% of the total produced. As the purpose of this study was to determine plot-level BC stocks, as opposed to net production, these two methods of BC loss are not a direct concern.

Predicting biomass via allometrics is always difficult. Here, we use the Jenkins and others (2003) metrics for live tree biomass, as they are the relationships utilized in FVS and therefore the most accessible to land managers. In general, using equations local to the southern Rocky Mountains gave similar results; calculations of aboveground live C using Brown (1978) estimated only slightly higher ($\sim 16 \text{ Mg ha}^{-1}$) in the reference plots, which corresponds to a change in total BC percentage from 2.79% (using Jenkins and others 2003) to 2.60%. In addition, the rank order of the treatments was the same as Jenkins et al. Therefore, this does not change the conclusions of the study. Several further combinations of potential allometrics are explored in Appendix 4 in Electronic Supplementary Material.

Finally, it is important to remember that these conclusions apply only to high-intensity fires. Although they comprise the dominant fire regime in the region (low frequency/high severity, Baker 2009), application to low severity fire regimes, or low severity areas within fires, should be done with caution.

CONCLUSIONS

Compound disturbances have impacts on C stocks via two primary mechanisms: By altering the magnitude of the cumulative event (in terms of intensity and severity) and by affecting the resilience of the constituent species. Mechanistically, the combination of fire and a downed overstory (resulting from the blowdown) led to higher fire intensity (temperature and duration, Buma and Wessman 2011), thereby reducing total C. Logging activities reduced C stocks through mechanical removal and, although it is likely the relative impact of the combined blowdown and fire was decreased, fire intensity was still likely higher than fire-only plots (Buma and Wessman 2011). Black C appears to have been similarly affected, with the contrasting effects of formation and consumption combining to reduce BC levels in the compound disturbances to the extent that areas experiencing more disturbances (that is, blowdown + logging + fire) had very little increase in BC over

unburned forest, despite the fire. Given decay rates from the literature, high-intensity fire appears to maintain black C in this ecosystem over the entire fire-return interval, but multiple high-intensity disturbances could result in a net loss over that time period. Further refinement of BC decay estimates, and investigations into BC totals in less severely burned areas (for example, areas without complete organic soil loss), are needed. Another impact of compound disturbance events could be differential recovery of the tree species, which will influence C stocks via growth rate, litter quality, susceptibility to future disturbances, and vulnerability to climate change-induced mortality. Going forward, the interaction of these disturbances will continue to have an influence on ecosystem structure, function, and C characteristics.

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